COMPOSITION AND DYNAMICS OF DEVONIAN TERRESTRIAL

ECOSYSTEMS FROM NEW YORK STATE, USA

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ABSTRACT

The application of acid maceration techniques to extract plant and animal cuticles from mid-Palaeozoic rocks has revealed some of the earliest known terrestrial animals. These arthropod fossils are preserved as carbonaceous cuticles in organic-rich mudstones, and represent moulted exoskeletons, carcasses, and rejectamenta of predators. Several potentially fossiliferous localities from south-central New York State were investigated for arthropod fossils, and the two largest assemblages were recovered from sediments at South Mountain and High Knob in Schoharie County.

The arthropod fossils are associated with plant material and represent allochthonous terrestrial detritus that was washed into an aquatic environment. Associated sediments were deposited in tropical latitudes by low-gradient, high-sinuosity rivers in close proximity to the palaeoshoreline. Red, root-churned sediments represent well-drained floodplain deposits that supported an autochthonous community of trees (*Eoaspermatopteris* and *Archaeopteris*) and herbaceous plants (zosterophylls and trimerophytes), growing as dense gallery forests. The presence of clams and ostracods suggests a brackish water environment.

Macerates from South Mountain are dominated by the arthropleurid *Eoarthropleura*, although estimates of population numbers indicate that *Eoarthropleura* is potentially represented by fewer individuals than some other taxa *e.g.* scorpions. At least two morphotypes of *Eoarthropleura* are recognised and these are interpreted as sexual dimorphs of the previously described *Eoarthropleura hueberi*. Scorpion cuticles are present at both sites and exhibit a combination of plesiomorphic and derived characters that are unknown from any other Palaeozoic scorpion. Characteristics such as long, slender pedipalps and a strong, powerful cauda ally the fossils with modern day Buthidae. Cuticles bearing distinct reticulations are assigned to the spider *Attercopus fimbriunguis,* and palaeocharinid trigonotarbids of the genus *Gelasinotarbus*. There is also evidence for a second species of spider, amblypygids, hexapods, and insects. Aggregates of spores recovered from South Mountain are interpreted as coprolites from a detritivorous arthropod and represent the only direct evidence for the cycling of primary productivity. Vertebrate remains preserved at the base of a sandstone channel at South Mountain include placoderm dermal plates, acanthodian fish scales, and a labyrinthodont tooth. The tooth is identified as a primitive polyplocodont tooth, representing either the first example of an osteolepiform fish from the study area, or the earliest example of a tetrapod body fossil in the world.

Quantitative analysis to obtain population estimates of the dispersed cuticle assemblages from South Mountain and High Knob, suggests that the majority of taxa are represented by less than five individuals. A comparison of three isotaphonomic assemblages indicates that local variations in the palaeoenvironment did impact community composition, and that the greatest diversity occurs amongst predators. In present day communities inhabiting newly exposed terrains with low primary productivity, predators dominate the food web and the main energy input is derived from allochthonous material. It is hypothesised that energy from marine or fluvial detritus also provided an input during the Silurian and Devonian, which helps to explain the apparent absence of herbivores from these early terrestrial ecosystems.

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Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Vicky MacEwan

Acknowledgements

Abbreviations

Abbreviations used in text figures are as follows:

a–anterior

ar–articulation

Bt – basitarsus

C–chelicera

Cx–coxa

di–distal

dk–dorsal keel

Fe–femur

il–inferior lateral keel

ly–lyriform organ

med lam–medial lamella

mgl lam–marginal lamella

mlk–median lateral keel

MS–mesosoma

ms–macroseta

mss–macrosetal socket

Mt–metatarsus

mto–metatarsal organ

p–posterior

Pa–patella

PCx–pedipalp coxa

PFe–prefeumr

po–peg organ

PoFe–postfemur

pr–proximal

pt–pectinal teeth

pys–pygidial socket

S–sternum

sl–slit sensilla

slk–superior lateral keel

sm–submarginal ridge

Sp–spore

Ta–tarsus

Ti–tibia

Tr–trochanter

trc–trichobothria

CHAPTER 1   INTRODUCTION

Huge advances in the understanding of terrestrialisation in the Siluro-Devonian have come from the application of acid maceration techniques to extract plant and animal cuticles from mid-Palaeozoic rocks. These have included some of the earliest land animals in Silurian rocks of Shropshire and the earliest land animals from North America (New York State). Later work on these biotas has revealed a unique ecosystem structure and generated novel hypotheses in evolutionary biology. However, current knowledge of these fauna, much less the ecological relationships in early terrestrial ecosystems, is still fragmentary and many animals are known only from isolated pieces.

1.1 Project outline

This project was conceived in the light of promising new localities and material in Devonian strata of New York State (NY) and Pennsylvania. The discovery of a unique fossil fauna at Blenheim-Gilboa in the Catskill Mountains of New York State, which includes the earliest fossil spider (Shear *et al.*, 1989b; Selden *et al.*, 1991) and pseudoscorpion (Shear *et al.*, 1989a; Schawaller *et al.*, 1991), naturally led to the search for coeval, or even earlier sites. Promising finds made at the nearby South Mountain quarry (Kjellesvig-Waering, 1986; Wilson and Shear, 2000) resulted in the collection of new material, which forms the basis of this research. Collecting was later expanded to include other quarries within the Catskill region with a similar lithology (see chapter 2 for details).

1.1.1 Aims

The principal aims of this research are as follows:

1) To further the knowledge of the palaeoenvironment and fossil fauna at South Mountain.
2) To identify potential new fossiliferous material of a similar age but different depositional setting for comparison.
3) To determine the palaeoenviroments and identify the fauna of new sites.
4) To compare and contrast previously known sites with new sites, with respect to depositional settings and cuticular types.
5) To reconstruct aspects of the palaeoecology based upon the faunal assemblage.
6) To compare and contrast these observations with other Siluro–Devonian sites and those of present day.

The aims of this research will be met with the following objectives:

1) Collection of sedimentary samples from the field area for petrographic analyses and construction of stratigraphic logs.

2) Exploration of shale pits and exposures within the Catskill region for potential new material, and collection of preliminary samples from these sites for maceration.

3) Maceration of new samples and identification of cuticle specimens. Data to be entered into a database of cuticle types for comparison with other known cuticle assemblages.

4) Quantitative analysis of cuticle types to gain insight to community structure and dynamics.

1.1   Geology of the Catskills

Most of southern New York State, from the Hudson River to Lake Erie, is composed of Devonian strata. In the Catskill region these sediments form a gentle anticline resting unconformably upon Cambrian and Ordovician siliciclastics, which overlie an undifferentiated Proterozoic basement. Upper Devonian sediments were eroded from much of New York State and occur further west, predominantly in Pennsylvania. This sequence of sediments was deposited during the Taconian and Arcadian orogenies (corresponding to the Caledonian orogeny of Britain and Scandinavia) as the Iapetus Ocean closed, culminating in the collision of North America with northwest Europe.

Early Devonian limestones (Helderberg Group) were deposited as a transgressive sequence deposited in a shallow sea that stretched west from the Taconian mountains of western New England to the edge of the continent. Continent–continent collision compressed and rotated the Traveler block (central New England and New Brunswick) in between Armorica and Laurentia, and resulted in the formation of the Acadian mountains (Kent, 1985). At their zenith, the Acadian mountains stretched from northern Greenland to just South of New York State. Erosion and drainage of this vast mountain range deposited sediments as part of a westward prograding delta system draining into the Appalachian basin. The full extent of the Appalachian basin is shown in figure 1.1.

Two major masses of sediments were deposited onto the early Devonian limestones in a foreland basin adjacent to the Acadian fold-thrust belt. These were the offshore marine shales and limestones of the Appalachian basin and the terrestrial deposits of the Catskill Delta Complex. Central New York State sits on the northeastern margin of the Appalachian basin and is covered largely by the Catskill delta clastic wedge. This thick sequence of fluvial and deltaic sediments was deposited during the middle and late Devonian and comprises the Plattekill, Manorkill, Oneonta and Walton Formations of the Catskill magnafacies.

To the west and south lie carbonates and shales generally progressing into deeper water environments. A stratigraphic section through New York State is illustrated in figure 1.2.

The Catskill Delta was deposited in tropical palaeolatitudes, and palaeomagnetic data taken directly from the Catskill rocks in New York State indicate a palaeolatitude of only one degree (Kent and Opdyke, 1978). The delta formed part of a much larger continental mass that extended twenty degrees either side of the equator. The central Appalachians preserve coastal plain deposits that are characterised by low relief and numerous small permanent streams. Meandering streams and relatively fine-grained sediments are seen in the lowland areas, with coarser grained sediments occurring on the more upland parts of the coastal plain (Woodrow *et al.*, 1973). The palaeolatitude, lithology and palaeontology all suggest that the climate was hot, with seasonal rainfall to the south of the continent and more consistent year-round rainfall to the north. Winds in the central Appalachians appear to have blown towards the west and northwest (Woodrow *et al.*, 1973).

The Catskill Delta is well known for its fossil flora (Arnold 1939; Banks *et al.*, 1985), and in particular the tree stumps of the Gilboa forest discovered during the rebuilding of a bridge washed away by a storm in 1869 (Goldring, 1927). Examples include *Eospermatopteris, Archaeopteris, Lepidosigillaria* and *Leclerqia* (Banks *et al.*, 1972). Fossil fauna from the Catskill Delta includes clams, eurypterids, jawless fish (*Cephalaspis*), sarcopterygians (*Holoptychus*), lungfish and a tetrapod (Daeschler, 2000a, 2000b; Ahlberg, 2001). Also known from these terrestrial Devonian sediments are well-preserved fossil arthropods caught up amongst compressed plant material. These may represent some of the earliest animal pioneers into the terrestrial environment and are the main focus of this thesis. The evidence for terrestrial life during the Palaeozoic is outlined below.
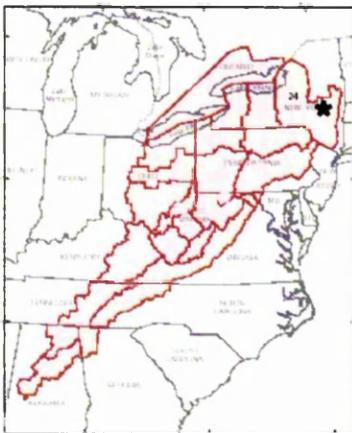
Figure 1.1 Extent of the Appalachian Basin across North America, shown in red. Field area in New York State marked with a star. Figure modified from Swezey (2003).
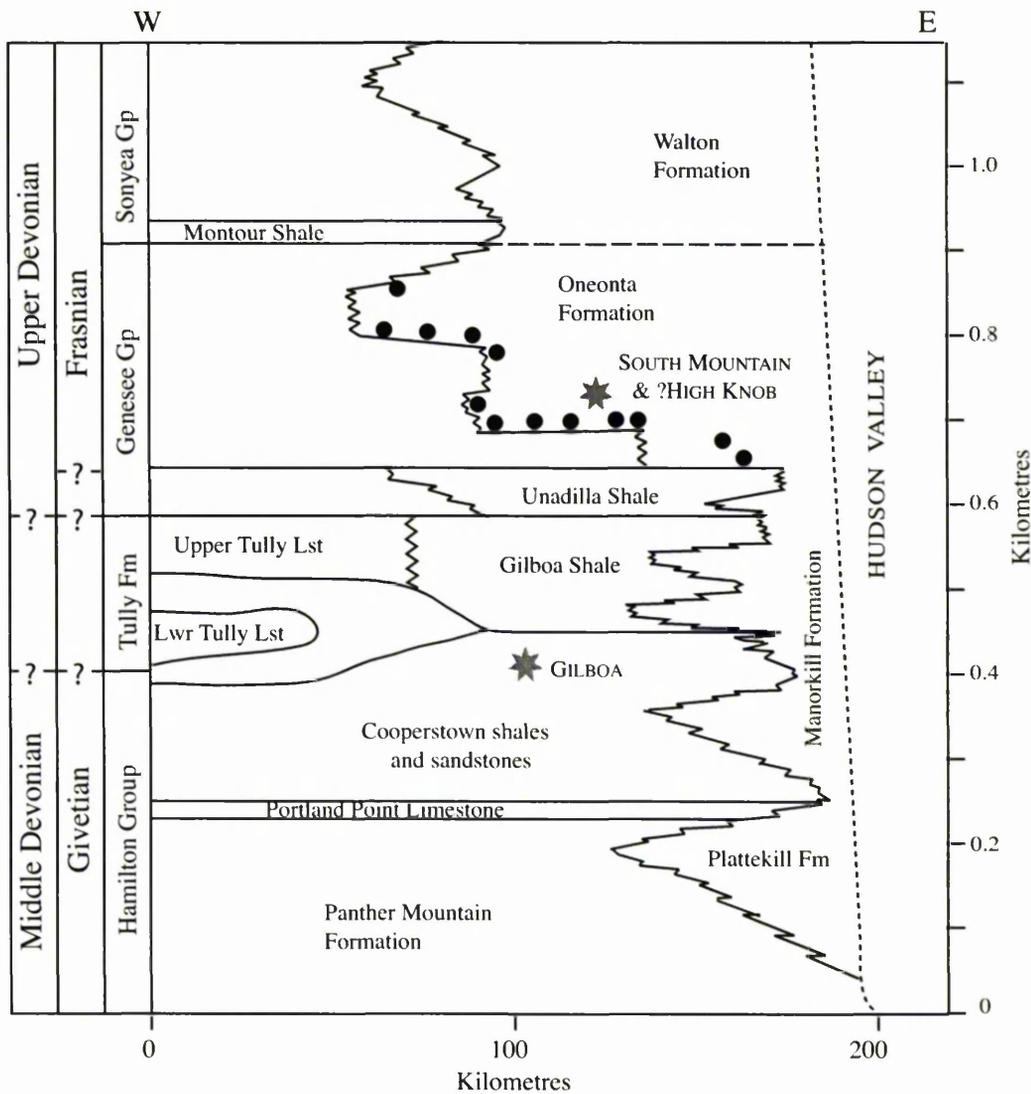
Figure 1.2 East-West stratigraphic section of New York State showing relative positions of Blenheim-Gilboa, South Mountain and High Knob. Circles mark approximate postions of brackish facies deposits and correspond to approximate palaeoshoreline. Redrawn from Sevon and Woodrow (1985) with additional information from Knox and Gordon (1999).

1.2   Palaeozoic terrestrial ecosystems

Significant events in terms of evolution and ecology took place during the Palaeozoic era. The land was colonised by non-vascular plants; vascular plants appeared and diversified and arthropods radiated into the terrestrial environment. Air-breathing vertebrates appeared for the first time, the amniotes rose to importance and tetrapod herbivory was developed (DiMichele and Hook, 1992). The origin and diversification of terrestrial ecosystems is arguably one of the most important evolutionary events in Earth's history, yet in comparison to others, *e.g.* the apparent metazoan radiation in the Cambrian, it has received little press.

This is partly a reflection of the limited number of known terrestrial faunas from this time, but is also due to the generally small and fragmented nature of the fossils, which have historically been dismissed in favour of larger, more palpable specimens.

Palaeozoic terrestrial ecosystems were reviewed by Beerbower (1985), Shear and Kukalová-Peck (1990), Shear (1991), Behrensmeyer *et al.* (1992), Edwards and Selden (1993) and Edwards (1996). Rolfe (1990, 1985, 1980) reviewed the biology of early to mid Palaeozoic terrestrial arthropods, highlighting the poor representation of terrestrial fossils in the geological record and emphasising the dramatic effect new finds can have upon current hypotheses on terrestrialisation. The most recent review (Shear and Selden, 2001) examined the fossil evidence in terms of faunistics and trophic relationships, and provided a comprehensive overview of the terrestrial records of animal life from the Devonian and earlier. The following provides a review of the current knowledge on terrestrial ecosystems from the Devonian and earlier.

1.2.1   *Terrestrial invertebrate trace fossil assemblages*

Trace fossils, though sometimes contentious in their interpretation, provide the earliest indirect evidence for terrestrial animal life. Documented records from the Devonian and earlier are summarised in table 1.

Ancient trackways reported from subaerial sediments of the Upper Cambrian to Lower Ordovician Potsdam Group near Kingston, Ontario in Canada, might be the earliest known example of animal life on land. They have been attributed to euthycarcinoids and probably represent short excursions into the terrestrial environment to mate and lay eggs, much as modern horseshoe crabs do today (MacNaughton *et al.*, 2002).

Ichnofossils from the Ordovician include mid to late Ordovician (Llandeilo-Caradoc) trackways from the Borrowdale Volcanic Group in northwest England (Johnson *et al.*, 1994) and burrows from the Upper Ordovician (Ashgill) Juniata Formation near Potters Mills in central Pennsylvania. The straight and meandering trackways occur in subaerial volcanic sediments that are otherwise barren of fossils, and are thought to have been produced by millipedes (Johnson *et al.*, 1996). Subvertical burrows from Potters Mills are also attributed to millipedes. Their polymodal size distribution suggests that the producer grew in distinct increments or moults, and fine striations on the burrow walls are attributed to an animal bearing bilaterally symmetrical limbs with fine points or bristles. The burrows occasionally contain ferrugenised faecal pellets (Retallack and Feakes, 1987; Retallack, 2001).

Table 1 Summary of known terrestrial arthropod trace fossil assemblages from the Devonian and earlier.

	TRACE FOSSIL			TRACE MAKER		AGE / REFERENCES	
Ichnogenera	Substrate	Palaeoenvironment	Inferred taxa	Behaviour	Age	References
?	Finely laminated sandstone	Coastal aeolian dunes	Euthycarcinoidea	Walking	Late Cambrian to Early Ordovician	MacNaughton et al., 2002
Diplodichnus *Diplichnites*	Volcanogenic sediments	Fluvial / lacutsrine	Diplopoda	Walking	Ordovician Llandeilo-Caradoc	Johnson et al., 1994 Johnson et al., 1996
Scoyenia	Red calcareous palaeosol	Well drained flood-plain	Myriopoda	Burrowing	Upper Ordovician	Retallack & Feakes, 1987 Retallack, 2001
Diplichnites	Red sandstone	Fluvial / aeolian	Myriapoda Eurypterida Scorpiones Euthycarcinoidea	Walking	Late Silurian ?Late Ordovician	Trewin & McNamara, 1995
Diplichnites	Red sandstone	Fluvial mud-sand flats	Myriapoda *Eoarthropleura*	Walking	Late Silurian Pridoli?	Wright et al., 1995
Diplichnites *Palmichnium* *Taenidium*	Cross-bedded quartzarenites	Coastal barrier island system	Myriapoda Eurypterida Myriapoda?	Walking Walking Burrowing	Lower Devonian	Draganits et al., 1998, 2001
Palmichnium	Rippled sandston	Shallow water, marginal fluvial	Eurypterida? Scorpiones?	Walking – swimming	Middle Devonian	Braddy & Milner, 1998

Trace fossils from the Ordovician and earlier predate the body fossil record by twenty to thirty million years and have been widely questioned as evidence for a truly terrestrial fauna (Shear and Kukalová-Peck, 1990; Shear, 1991). Non-marine myriapod like animals are known from the early Silurian (Mikulic *et al.*, 1985) and may have been responsible for some of the traces reported. However, new discoveries are constantly pushing back the age for the earliest known terrestrial animal, and it may not be so unlikely that fully terrestrialised fauna were established during the Ordovician or even earlier.

The Silurian apparently witnessed a considerable increase in terrestrial diversity. The Upper Silurian Tumblagooda Sandstone of western Australia preserves trackways representing up to eleven species of arthropods (not all of them terrestrial), with some trackways extending for several meters across exposures (Trewin and McNamara, 1995). The traces are attributed to myriapods, eurypterids, scorpions and euthycarcinoids – the only group to be represented with a complementary body fossil (McNamara and Trewin, 1993). The exact age of the Tumblagooda Sandstone is uncertain and may in fact be Late Ordovician (Iasky *et al.*, 1998).

Millipede trackways from the Upper Silurian Clam Bank Formation of Newfoundland, Canada were attributed to the arthropleurid *Eoarthropleura* (Wright *et al.*, 1995). However, the identification was made assuming that *Eoarthropleura* had a similar leg structure to the Carboniferous arthropleurid *Arthropleura*. More recent work has found this not to be the case (Shear and Selden, 2001).

Trace fossil diversity is maintained into the Devonian with eighty trackways and rarer burrows reported from the Lower Devonian Muth Quartzite of Spiti in northern India (Draganits *et al.*, 1998, 2001). The traces are assigned to styloneurid eurypterids migrating across the shoreline and myriapods. A trackway also attributed to a large stylonurid eurypterid or scorpion from the middle Devonian of Gaspé shows the transition from walking to swimming.

The ichofossil assemblages from the Tumblagooda Sandstone and the Muth Quartzite bear some similarities with each other and also with early Devonian ichnofauna from the Taylor Group in the Darwin Glacier area of Antarctica (Gevers *et al.*, 1971; Woolfe, 1990). The three ichnofaunas were analysed by Draganits *et al.* (2001) who concluded that their faunal similarities and contemporaneous occurrence on the margin of Gondwana identify a recurrent assemblage (ichnocoenosis) around the margins of eastern Gondwana during the early Devonian.

As with all trace fossils it is often difficult to identify the tracemaker with a high degree of certainty and arguing for the subaerial nature of the sediments does not necessarily imply a strictly terrestrial fauna. The earliest body fossils of terrestrial arthropods do not occur until the middle Silurian, and it is likely that some of the tracks represent periodic

excursions onto the land from marginal aquatic zones rather than a truly terrestrial mode of life. The ichnological record of early continental invertebrate life was reviewed by Buatois (1998).

1.2.2   Terrestrial body fossil assemblages

Body fossils of terrestrial arthropods appear from the Silurian onwards. Terrestrial organisms typically have a poor fossil record and occur much more sporadically in the geological record than their aquatic counterparts. The low preservation potential for terrestrial organisms without a bio-mineralised exoskeleton, means that terrestrial arthropod assemblages are limited to sites where conditions have permitted exceptional preservation. These Konservat-Lagerstätten are often the result of unusual depositional conditions, resulting in deposits that are rich in palaeontological information (Seilacher, 1970, Seilacher et al., 1985). Such assemblages tend to be stratigraphically isolated and provide only a brief snapshot of past ecosystem biotas. However, they do provide a more complete representation of the original than can be provided by some other fossil remains. Key sites preserving terrestrial body fossils are summarised in figure 1.3 and are outlined in more detail below.

MIDLAND VALLEY, SCOTLAND (Middle Silurian)

The oldest known terrestrial animal is a chilognath millipede from the Middle Silurian (late Wenlock–early Ludlow) Cowie Formation of the Stonehaven Group at Cowie Harbour in Scotland (Wilson and Anderson, 2004). Preserved spiracles represent the earliest known example of air-breathing amongst the arthropods. Millipedes are also known from a number of other Siluro-Devonian locations across the Midland Valley of Scotland (Almond, 1985; Wilson and Anderson, 2004), and are found in fluvial and lacustrine (probably allochthonous) deposits.

LUDFORD LANE, ENGLAND (Upper Silurian, Prídolí)

Prior to the description of the Scottish millipedes the earliest accepted terrestrial body fossil was a trigonotarbid found in Upper Silurian (Prídolí) sediments at Ludford Lane in Shropshire, England (Dunlop, 1996). Other terrestrial animals from Ludford Lane include fragments of scorpions (Jeram et al., 1990), eoarthropleurids (Shear and Selden, 1995) and scutigeromorph centipedes (Shear et al., 1998). These animals probably inhabited a Rhyniophytoid / cryptospore plant saltmarsh environment and were mixed with shallow marine fauna after storms washed components of the ecosystem into the estuarine environment (Edwards and Selden, 1993).

355 Ma

Devonian

Famennian

Red Hill, USA. Arachnids, myriapods. Lowland fresh water.

Frasnian

375 Ma

South Mountain, USA. Arachnids, myriapods, eurypterid, ?archaeoagnath. Progymnosperms. Deltaic.

Givetian

380 Ma

Gilboa, USA. Arachnids, myriapods, eurypterid. Lycopsids, progymnosperms. Deltaic mudstone.

Eifelian

Trout Valley, USA. Reported arthropod cuticle associated with *Pertica quadrifaria*.

390 Ma

Gaspé, Québec. Myriapods, ?archaeoagnatha. Trimerophytes, zosterophylls, lycopsids. Fluvial swamp.
New Brunswick, Canada. Scorpion, myriapod.

Emsian

Alken-an-der-Mosel, Germany. Arachnids, eurypterids, xiphosaurans, crustaceans. Lycopsids, algae. Brackish lagoon.

400 Ma

Rhynie, Scotland. Arachnids, myriapods, crustaceans, ?collembolan. Algae, zosterophylls, rhyniopsids. Terrestrial hot spring.

Pragian

Lochkovian

410 Ma

Silurian

Pridoli

415 Ma

Ludford Lane, England. Arachnids, myriapods, eurypterids. Rhyniophytoids. Sub- and intertidal lag deposit, salt marsh.

Ludlow

425 Ma

Midland Valley, Scotland. Myriapods. Fluvial and lacustrine.

Wenlock

Figure 1.3 Summary of known Siluro-Devonian terrestrial invertebrate fossil assemblages. See text for details.

RHYNIE, SCOTLAND (Lower Devonian, Pragian)

The Rhynie Chert fauna in Aberdeenshire, Scotland represents an ancient thermal spring that flooded hot, silica-saturated water onto the surrounding vegetation, silicifying plants and animals *in situ* (Trewin, 1994; Trewin, 2001). The Rhynie fauna includes trigonotarbids (Hirst, 1923; Shear *et al.*, 1987), centipedes (Shear *et al.*, 1998), mites (Hirst, 1923; Dubinin, 1962), collembolans (Greenslade and Whalley, 1986) and the earliest known insect (Engel and Grimaldi, 2004). The palaeoecology of the Rhynie Chert was discussed by Powell *et al.* (2000).

New terrestrial and freshwater arthropods including a euthycarcinoid, scutigeromorph centipede, crustaceans, trigonotarbids and a new arthropod of myriapodous affinity have been recovered from the nearby Windyfield Chert, which forms part of the same hot-spring complex (Anderson *et al.*, 1998a; Anderson and Trewin, 2003).

ALKEN-AN-DER-MOSEL, GERMANY (Lower Devonian, Emsian)

The Lower Devonian (Emsian) fauna of Alken-an-der-Mosel, Germany was originally described in a series of papers by Størmer (1970–76). New material has since been described by Braun (1997), Anderson *et al.*, (1998b) and Dunlop *et al.*, (2001). The sediments at Alken were deposited in temporary lagoons on tidal sand-flats, and were bordered by a mangrove type vegetation. They contain a mixture of both terrestrial and aquatic organisms that includes arachnids, arthropleurids, eurypterids, xiphosaurans, crustaceans, a scorpion (probably aquatic) and trigonotarbids.

QUÉBEC AND NEW BRUNSWICK, CANADA, (Lower Devonian, Emsian)

The Battery Point Formation on the Gaspé peninsula in Québec is unusual in that both compression and impression fossils occur together. Shear *et al.* (1996) described four species of millipedes from Québec, and arthropleurids and a scorpion from New Brunswick. The scorpion is of particular significance, because it was found preserved with book-lung tissue and is the earliest example of air-breathing in this group. Large arthropod trackways attributed to a large stylonurid eurypterid or a scorpion compliment the body fossils, suggesting that, unlike other cotemporaneous fossil assemblages, macroarthropods were a significant component of the ecosystem (Braddy and Milner, 1998).

NEW SOUTH WALES, AUSTRALIA (Lower-Middle Devonian)

Two species of the genus *Maldybulakia,* of possible myriapodous affinity, have been described from two Devonian sites in New South Wales, Australia. The earliest is from the fluvial Sugarloaf Creek Formation, in the Taemas-Wee Jasper area, and is dated as latest Lochkovian to earliest Pragian. The second is from lacustrine mudstones of the Boyd

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Volcanic Complex near Eden and is dated as late Givetian to early Frasnian (Edgecombe, 1998). The specimens are alleged to be terrestrial on the basis of preserved spiracles and, in the fossil from Eden, their association with a terrestrial fauna. These specimens have since been re-examined and are probably xiphosuran tails (Selden *pers. comm.*) Similar animals from Lower Devonian sediments from central Kazakhstan were also attributed to a myriapod-like animal but are very poorly preserved (Tesakov and Alekseev, 1992).

TROUT VALLEY FORMATION, MAINE, USA (Middle Devonian, Eifelian)

Minor amounts of unidentified arthropod cuticle were reported from the Trout Valley Formation in north-central Maine. The cuticles are associated with vascular plant material, including *Pertica quadrifaria*, and are flattened and carbonised. Apart from the brief report given by Nelson *et al.* (2001) nothing has been published on this since.

BLENHEIM-GILBOA, NEW YORK STATE, USA (Middle Devonian, Eifelian-Givetian)

Middle Givetian shales from the Panther Mountain Formation near Gilboa have been found to contain a number of well-preserved arthropods (Shear *et al.*, 1984) including trigonotarbids (Shear *et al.*, 1987), centipedes (Shear and Bonamo, 1988; Shear *et al.*, 1998), mites (Norton *et al.*, 1988; Kethley *et al.*, 1989), spiders (Shear *et al.*, 1989b; Selden *et al.*, 1991), pseudoscorpions (Shear *et al.*, 1989a; Schawaller *et al.*, 1991) and arthropleurids (Shear and Selden, 1995; Wilson and Shear, 2000). The cuticles at Blenheim-Gilboa are found amongst dense mats of the lycopsid *Leclercqia* which are thought to have grown around stream banks and ponds where they acted as a filter to the transported cuticles.

SOUTH MOUNTAIN, NEW YORK STATE, USA (Middle Devonian, Givetian-Frasnian)

South Mountain is a slightly younger site than Blenheim-Gilboa, lying several miles to the east in the Catskill Mountains. The flora differs from the lycopsids of Gilboa and consists of psilophytes, liverworts and archaeopterid trees, which would have afforded dense shade and deep litter by their spiral arrangement of leaves and deciduous habit. Scorpion material with 'white, spongy gill-like structures' was described from South Mountain by Kjellesvig-Waering (1986) but later reinterpreted as an arthropleurid (Shear and Selden, 1995). Subsequent maceration of shales from South Mountain has revealed a fauna of scorpions, arthropleurids, trigonotarbids, spiders and possible archaeognath hexapods.

Key to sites:

1 - Red Hill
2 - South Mountain
3 - Blenheim-Gilboa
4 - Trout Valley
5 - Gaspé
6 - New Brunswick
7 - Alken-an-der-Mosel
8 - Spiti
9 - Rhynie
10 - Ludford Lane
11 - Newfoundland
12 - Midland Valley
13 - Tumblagooda
14 - Potters Mill
15 - Borrowdale
16 - Potsdam

○ Body fossil assemblage

● Trace fossil assemblage
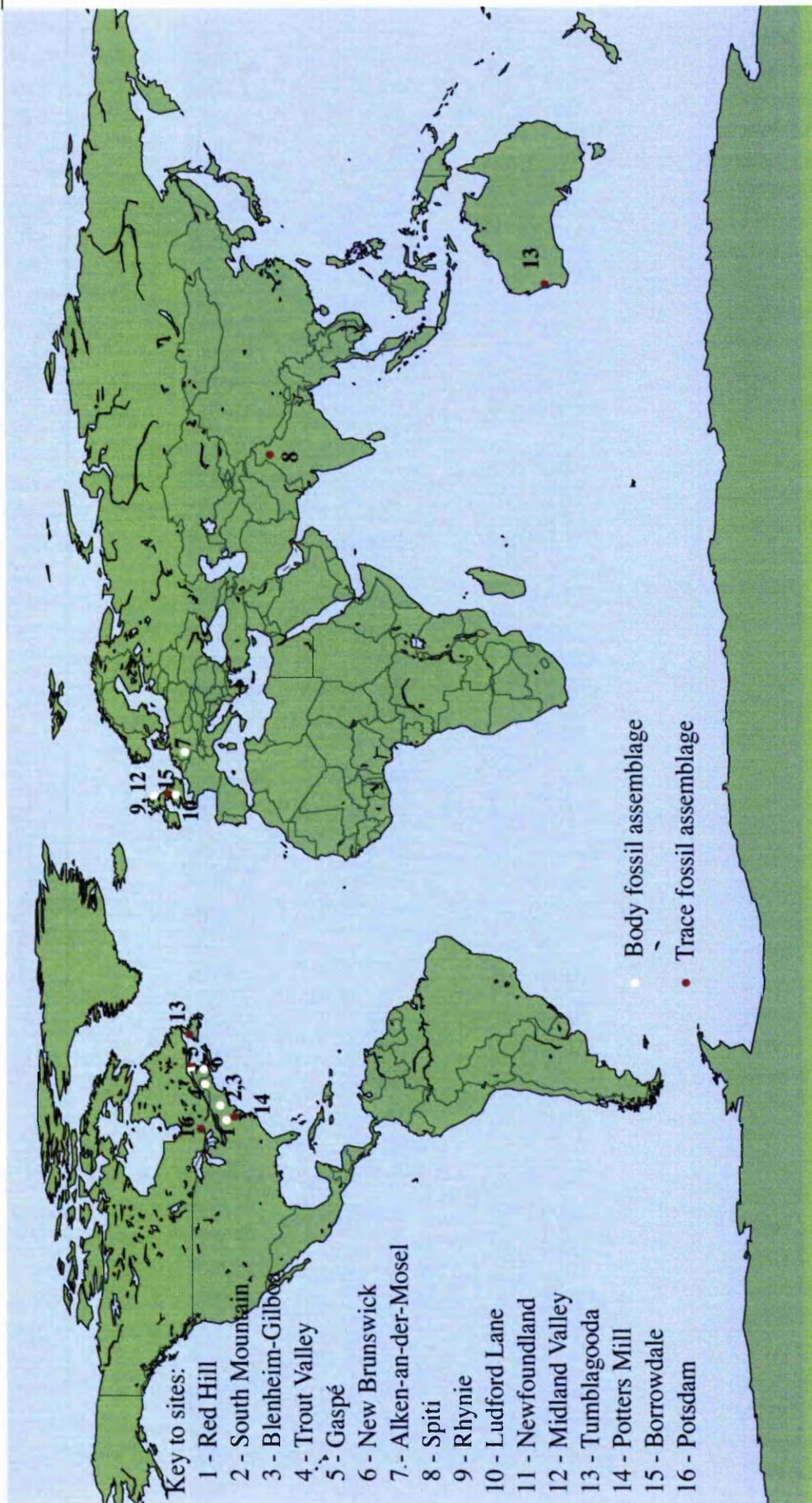
Figure 1.4 Global map of currently known Silurian and Devonian terrestrial invertebrate fossil assemblages.

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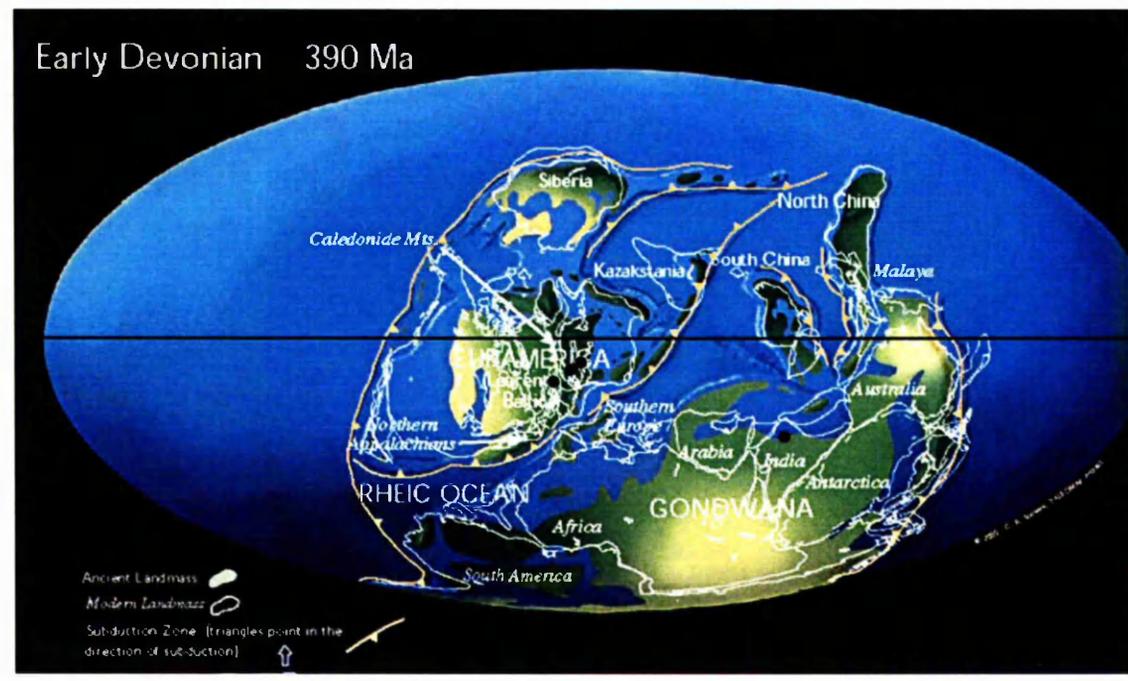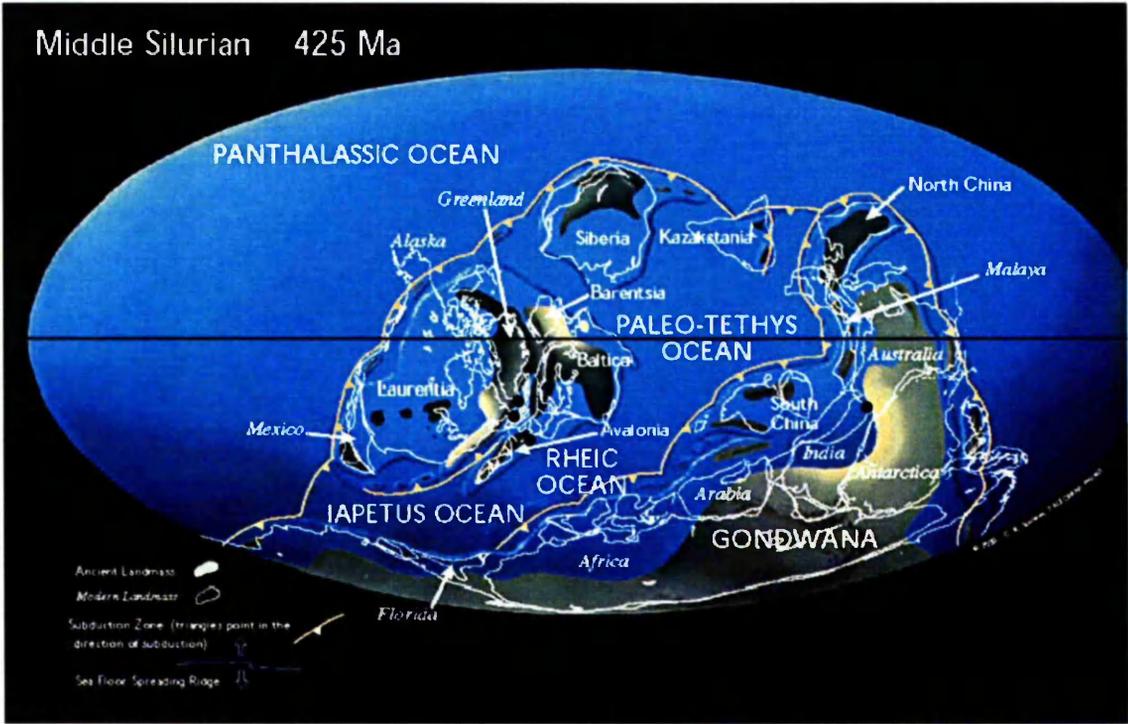
Figure 1.5 Palaeogeographic maps for the early Devonian and middle Silurian. Principal terrestrial fossil assemblage sites marked with black cirlces. Scotese (2001).

The youngest site (late Famennian) with terrestrial arthropods from the Siluro-Devonian is Red Hill in Pennsylvania. The sediments were deposited in an abandoned channel and are associated with well-preserved plant macrofossils including *Archaeopteris, Rhacophyton,* lycopsids and gymnosperms. Arthropods associated with fossilised litter were recovered by Shear (2000) and include an unidentified trigonotarbid, two scorpions, and arthropod material of probable myriapodous affinity. The site has also yielded fossil charcoal (mainly burnt *Rhacophyton*) indicative of a tropical climate with annual wet and dry seasons (Cressler, 2001). This site is probably better known for its vertebrate fossils and is home to the oldest amphibian known from North America (Daeschler, 2000). Other sites from around the New York State, Pennsylvania area that have yielded small amounts of arthropod material are reported in Shear and Selden (2001).

The distribution of Palaeozoic terrestrial invertebrate fossils is strongly skewed towards sites in Britain, Canada and North America (figure 1.4), with the majority of evidence for early terrestrial arthropods in Gondwana limited to trace fossils assemblages. This concentration of sites around the tropical latitudes of Pangaea (figure 1.5) may reflect more favourable preservational conditions at a continental margin. It may also reflect the differences in floral changes between the two landmasses so that conditions in Gondwana were less favourable to the emergence of animal life on land (Solem and Yochelson, 1979).

1.3 Ecosystem structure

The structure of terrestrial ecosystems during the Palaeozoic was markedly different to that of modern day systems. Virtually all terrestrial animal fossils from the Silurian and Early Devonian are arthropods, and communities were diverse. Predators (trigonotarbids, spiders, scorpions, centipedes) dominate the assemblages and decomposers (mites, millipedes) would have formed the primary nutrient pathway between plants and animals. Although there is evidence for detritivores (millipedes), fungivores (mites and springtails) and, more equivocally, saprophytes, true herbivory on growing plant tissue appears to have been absent.

This apparent dominance of carnivorous arthropods and absence of herbivores in early terrestrial communities raises the question as to how energy enters the animal food web. Beerbower (1985) argued that detritivores dominated over herbivores because the detritus was of a higher nutritional value than the biomass was at that stage. Shear (1993), however, suggested that herbivory was effectively deterred by the plants themselves. The storage of toxic by-products, formed during the synthesis of lignin, in cell walls and dead plant tissue, would have rendered it useless to arthropods which had not yet developed the necessary gut microfloras to aid in the breakdown of the toxins or the lignin (Shear, 1991;

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Edwards and Selden, 1993). Alternatively it may be that food-limited predators suppressed herbivore populations so that the effects of herbivory on plants were negligible. Although the greatest proportion (over ninety percent) of primary production passes through the decomposer chain in modern terrestrial ecosystems (Seastedt and Crossley, 1984), it is also possible that some components have failed to be preserved and are missing. As of yet, there are no known terrestrial fossil assemblages from the Siluro-Devonian in which any soft-bodied organisms are preserved. Terrestrial molluscs have a poor Palaeozoic fossil record, and the first land snails do not appear until the Lower Carboniferous (Solem and Yochelson, 1979). Terrestrial oligochaetes are also unknown with any degree of certainty from the fossil Palaeozoic (Conway Morris *et al.* 1982) and no terrestrial crustaceans have been recorded. However, the predominance of predators does appear to be a pervasive pattern in early terrestrial ecosystems and predator-dominated communities also characterise Carboniferous and early Permian terrestrial tetrapod assemblages (DiMichelle and Hook, 1992).

1.3.1   *Terrestrial arthropods*

Ten orders of terrestrial arthropods are represented in the Siluro-Devonian fossil record, eight of which have survived relatively unchanged through to the present day. The scorpions are the only taxon with a complete record from aquatic through to terrestrial forms. The following provides an outline of the Palaeozoic terrestrial arthropod fossil record, detailing their age range, occurrence and morphology. The highly adaptive nature of the animals in terrestrial Lagerstätten has lead to the notion that the emergence of life into the terrestrial environment predates the ages of the fossil assemblages by some considerable time. The palaeophysiology of terrestrialisation in the chelicerates was discussed by Selden and Jeram (1989), and adaptations to life on land for the whole of the Arthropoda were discussed in full by Little (1990).

Trigonotarbida (Upper Silurian–Lower Permian)

Trigonotarbid arachnids are primitive spider-like animals and have been established as the most pleisiomorphic members of the subclass Pulmonata (Shear *et al.*, 1987). A divided opisthosoma, absence of spinnerets, lack of a poison gland, setose cheliceral fangs and the possession of separate lateral and median eye tubercles distinguish them from true spiders. They were probably carnivorous animals, macerating food with their chelicerae and sucking up liquid remains (Dunlop, 1994b).

The earliest representative of the order is *Palaeotarbus jerami* Dunlop 1996 from the late Silurian of Shropshire. Although poorly preserved, the single specimen is almost complete and apparently lacked lateral eyes (Dunlop, 1996, 1999). Five species and two genera have been described from the early Devonian Rhynie chert. These are probably

the best known and most complete specimens, preserving book lungs (Claridge and Lyon, 1961), mouthparts (Dunlop, 1996) and even muscle tendons. Undescribed trigonotarbids are also known from the associated Windyfield Chert (Anderson and Trewin, 2003). Two genera and three species of trigonotarbids have been recorded form Alken-an-der-Mosel (Størmer, 1970; Brauckmann, 1987), three genera and six species from Blenheim-Gilboa (Shear *et al.*, 1987), and a 'large' (7mm long) palaeocharinid from Upper Devonian sediments of Red Hill (Shear, 2000).

Shear and Selden (2001) recognised two ecomorphotypes within the Trigonotarbida. Palaeocharanid trigonotarbids are generally small (1-6mm long) with remnant lateral eyes and appear to be confined to the Devonian and maybe the Silurian. These include the Rhynie trigonotarbids and those from Blenheim-Gilboa and were probably inhabitants of the leaf litter. The larger, more robust aphantomartid trigonotarbids range from the Silurian to the Permian and may have been surface dwellers or even arboreal. The paleoecology of Carboniferous trigonotorabids was discussed by Dunlop (1994a).

Araneae (Middle Devonian–Recent)

Spiders are considered the seventh largest arthropod group, surpassed only by the Acari and five orders of insects. They are predatory and virtually ubiquitous throughout the world excluding polar regions (Brescovit *et al.*, 2002).

The oldest recorded spider is *Attercopus fimbriunguis* Shear, Selden and Rolfe 1987, described from Middle Devonian compressed cuticles at Blenheim-Gilboa, New York State (Shear *et al.*, 1989b; Selden *et al.*, 1991). Similar cuticle occurs at South Mountain. This is the only known Devonian spider and is considered to belong to a taxon forming the sister group to all other spiders. The morphology does not differ significantly from living spiders, and the well-developed spinnerets were probably used to line a burrow and/or construct simple trip-lines (Selden and Shear, 1991).

Amblypygi (?Middle Devonian–Recent)

Recent amblypygids are nocturnal and inhabit the leaf litter, hollow trees, rock crevices and caves. They have a flat body, raptorial pedipalps and antenniform first legs that are used as feelers (Weygoldt, 2002).

Material from Gilboa was tentatively described as the amblypygid *Ecchosis pulchibothrium* Selden and Shear 1991 on the basis of leg podomeres, in particular distinctive spination on the patella (Selden *et al.*, 1991). The first unequivocal example of a fossil amblypygid, however, is *Britopygus weygoldti* from the Lower Cretaceous Crato Formation of Brazil (Dunlop and Martill, 2002), which bears two large spines on the patella of the pedipalp.

SCORPIONIDA (Silurian–Recent)

Modern scorpions have a wide geographic distribution and occupy most terrestrial habitats. They are found in deserts and rainforests, at altitudes up to 5560m and in caves as deep as 800m (Lourenço, 2002). They are nocturnal predators and feed mainly on other arthropods.

Scorpions are the only known taxon with a complete fossil record from aquatic through to terrestrial forms. Sixteen species of scorpions in fifteen genera have been described from the Silurian and Devonian, most from a single specimen (Jeram, 1998). Mesoscorpion cuticle has been recovered from Ludford Lane, Gilboa, South Mountain and Red Hill (Shear and Selden, 2001), and the earliest physical evidence for air-breathing in a scorpion is preserved book lung tissue from the Lower Devonian (Emsian) of New Brunswick, Canada (Shear *et al.*, 1996).

Kjellesvig-Waering (1986) divided the order Scorpionida into two suborders based on the structure of abdominal plates. Briefly, these comprised the aquatic Branchioscorpionina and the terrestrial Neoscorpionina. Stockwell (1989) largely rejected this scheme and reclassified the scorpions based upon a cladistic analysis which recognised three orders within the class Scorpionida; Protoscorpiones, Palaeoscorpiones and Scorpiones. Members of Protoscorpiones and Paleaoscorpiones lacked terrestrial adaptations and were probably aquatic (Jeram, 1994), whilst the mesoscorpions of the order Scorpiones possess features suggestive of a terrestrial mode of life (Shear *et al.*, 1996). This scheme was later revised by Jeram (1998) in his classification of Silurian and Devonian scorpions. Jeram introduced the Proscorpiidae plesion, roughly equivalent to Stockwell's Palaeoscorpiones and fully aquatic; the Palaeophonidae, roughly equivalent to Stockwell's Protoscorpiones, and retained the Mesoscorpiones with some modifications.

PSEUDOSCORPIONES (Middle Devonian–Recent)

Pseudoscorpions are small, predatory arthropods that live under stones, moss or bark, and sometimes in books or furniture. Their pedipalps contain poison glands, and silk glands in the chelicerae are used to weave nests for moulting and resting. The earliest known example of a pseudoscorpion is *Drachochela deprehendor* Schawaller and Shear 1991 from the Middle Devonian of Blenheim-Gilboa (Schawaller *et al.*, 1991). The two Devonian specimens show all the autapomorphies of modern pseudoscorpions and have apparently changed very little over some 380 million years. *D. deprehendor* is the only recorded fossil pseudoscorpion from the Palaeozoic, with all other known specimens occurring in amber from the Oligocene and later (Shear *et al.*, 1989a).

ACARI (Middle Devonian–Recent)

Mites are small to microscopic with a fused head, thorax and abdomen. They are extremely diverse and virtually ubiquitous on land today, yet are relatively poorly represented in the fossil record. This is probably a reflection of their small size and low preservation potential (Shear, 1990). The earliest mites are those from the Rhynie Chert (Hirst, 1923), which may represent as many as four distinct families (Dubinin, 1962). Both Oribatid mites (Norton *et al.*, 1988) and alicorhagiid mites (Kethley *et al.*, 1989) have been recovered from Gilboa. The fossil record for oribatid mites is incomplete, and although the earliest mites existed during the middle Devonian, they do not reappear in the fossil record until the Early Jurassic. The role of oribatid mites in Palaeozoic swamp forests is discussed by Labandeira *et al.* (1997).

CHILOPODA (Middle Devonian–Recent)

Centipedes are predatory animals possessing poison claws and inhabiting temperate and tropical regions. The oldest known centipedes are *Crussolum* sp., described from distinctive leg segments from the Upper Silurian Ludford Lane sediments and the Lower Devonian Rhynie chert, and *C. crusseratum* from Gilboa (Shear *et al.*, 1998). The leg segments have a pentagonal cross section, marginal setae and serrations, and are attributed to the long legged, terrestrial Scutigeromorph centipedes. The only other known centipede from the Siluro-Devonian is *Devonobius delta* Shear and Bonamo 1988, placed in the centipede order Devonobiomorpha. Both groups were adapted for fast running.

DIPLOPODA (Wenlock–Recent)

Millipedes, with few exceptions, are detritivores and live in humid habitats under stones, or rotting logs. The oldest known terrestrial millipede is *Pneumodesmus newmani* from Cowie Harbour near Stonehaven in Scotland (428Ma). The animal has preserved spiracles representing the oldest physical evidence for a tracheal respiratory system in both Diplopoda *and* Arthropoda and suggesting that terrestrialisation, at least in the Myriapoda, began during the Ordovician or maybe even earlier (Wilson and Anderson, 2004). Wilson and Anderson also described five species of millipede in five genera from four Lower Devonian localities in the Midland Valley of Scotland. Cylindrical millipedes are known from the Emsian of Canada (Shear *et al.*, 1996), and flat-backed millipedes from the Middle Devonian of the Delaware Valley (Shear and Selden, 2001). Silurian and Devonian millipede fossils were reviewed by Almond (1985, 1986) and the fossil record and evolution of the Myriapoda is reviewed by Shear (1997).

The arthropleurideans are an extinct group of myriapodous arthropods ranging from

the late Silurian to early Permian and comprising three monogeneric orders: Arthropleurida, Eoarthropleurida and Microdecemplicida. The Eoarthropleurida first appear in the fossil record in the Silurian mudstones of Ludford Lane (Shear and Selden, 1995) and are also known from the Lower Devonian of Alken-an-der-Mosel (Størmer, 1970) and New Brunswick (Shear et al., 1996). Both Eoarthropleurida and Microdecemplicida have been described from the Middle Devonian of Blenheim-Gilboa and South Mountain (Shear and Selden, 1995; Wilson and Shear, 2000). *Microdecemplex* preserves the only known cephalic features known for arthropleurideans, which suggest their inclusion within the Diplopoda (Wilson and Shear, 2000). A third order, the giant Arthropleurida, is confined to the Carboniferous and later. Some species reached over two metres in length (Wilson, 1999). Preserved gut contents from the arthropleurid *Arthropleura* contain lycopsid plant material suggesting a detritivorous mode of life (Rolfe and Ingham, 1967).

HEXAPODA (?Middle Devonian–Recent)

Collembola (springtails) are known from the Lower Devonian Rhynie Chert, resembling the living family Isotomidae (Greenslade and Whalley, 1986). They were probably semi-aquatic and may have lived on algal mats and low, emergent vegetation (Rolfe, 1985; Shear and Kukalová-Peck, 1990). Modern collembolans are an important component of soil and leaf litter faunas, and are a significant food source for small arachnids, insects and predatory mites.

Primitive wingless insects are known from the Devonian and possibly the Silurian. Possible representatives of the Archaeognatha (bristletails) are known from Gaspé (Labandeira et al., 1988), Blenheim-Gilboa and South Mountain. The authenticity of the Gaspé specimen has been question by Jeram et al., (1990), who argued that the diagenesis is not consistent with contemporaneous fossils, and that it may be a Recent contaminant. Scraps of cuticle resembling modern archaeognaths have been recovered from Ludford Lane, Gilboa and South Mountain, but as yet there is insufficient diagnostic material to confirm this identification. Living bristletails feed on decaying matter and inhabit damp places under leaves, bark, or stones. Some species inhabit the intertidal zone, feeding on algae and lichens, and this may have been the case in the Devonian as they made their way onto land (Shear and Kukalová-Peck, 1990).

A fragmentary fossil from the Rhynie Chert, was originally noted as insect-like by Tillyard (1928) but placement of the specimen was left open. A recent re-examination of *Rhyniognatha hirsti* has revealed short triangular mandibles with a dicondylic structure characteristic of the pterygote insects and clearly used for chewing (Engel and Grimaldi, 2004). Winged insects were thought to have originated in the early Carboniferous, and their more primitive wingless forebears during the Devonian. However, if the interpretation of

the insect mandibles from Rhynie is accepted then a Silurian origin for insects, with wings developing some time during the Devonian is more likely. Interestingly, this hypothesis is congruent with results obtained from molecular data which suggests that the earliest insects diverged from a common ancestor some time in the late Ordovician to early Silurian (Gaunt and Miles, 2002).

1.3.2 Terrestrial plants

The colonisation of barren land surfaces by plants was a crucial precursor to the migration of arthropods into the terrestrial environment. Not only did the plants bind and stabilise the sediment surface, they also moderated temperature and humidity fluctuations, providing damp, sheltered microhabitats. In the long term, the rise of vascular plants had a dramatic effect on atmospheric carbon dioxide as increased organic matter caused an accelerated rate of weathering in calcium and magnesium silicates. Transport of calcium and magnesium ions to the oceans, and the subsequent precipitation of carbonates, resulted in a carbon sink that ultimately led to the Permo-Carboniferous glaciation (Berner, 2001).

The fossil record for terrestrial plants is much more complete than it is for fossil arthropods, which probably reflects their larger size and the durability of cutin and lignin. Much of the information concerning land plants from the Silurian and earlier comes from phytodebris consisting of microscopic spores, cuticles, tracheids and fungal hyphae (Gensel et al., 1990). Moist land surfaces in the early Palaeozoic may have been coated with a green scum of cyanobacteria and eubacteria, which would have stabilised surfaces and eventually resulted in a limited build up of humus (Gray, 1993). Middle Ordovician to early Silurian spores and cuticles support the suggestion of an early land flora of liverwort-like plants, and are consistent with plylogenetic studies which point towards small and morphologically simple plants at this time (Kenrick and Crane, 1997).

During the Silurian, the monotonous obligate permanent tetrads of the Ordovician were replaced by increasingly diverse trilete spores, possibly representing a second major radiation as plants approached and attained the vascular grade of vegetative organisation (Gray, 1985). Plant megafossils begin to appear and increase in diversity from the middle Silurian onwards. Such early plant fossil assemblages are known from the the lowermost Upper Silurian of Bolivia (Morel et al., 1995) and China (Tims and Chambers, 1984), the Upper Silurian of arctic Canada (Kotyk et al., 2002) and the uppermost Silurian of China (Cai et al., 1996). An early rhyniophyte flora of Cooksonia and Salopella is typical of late Silurian Euramerican deposits, forming a low vegetation growing on channel banks and bar tops (Edwards and Fanning, 1985).

During the late Silurian to early Devonian zosterophylls and rhyniophytes were established throughout the tropics, forming monospecific patches of clonal growth in

continually moist habitats. Together they formed two distinct lineages that would later give rise to the lycopods and all other vascular plants (Gensel and Andrews, 1987). Examples of early Devonian plant assemblages include those from the Rhynie Chert (Remy *et al.*, 1993; Powell *et al.*, 2000), the Gaspé peninsula of Canada (Gensel and Andrews, 1987; Hotton *et al.*, 2001) and Australia (Tims and Chambers, 1984).

Lycopsids and trimerophytes, appearing in the mid–late early Devonian, added new architectural elements to the terrestrial landscape. The development of stronger roots and secondary vascular tissue enabled the plants to grow taller and the roots to penetrate shallow soils in floodplain environments (Scheckler, 2001). During the middle Frasnian, archaeopterid progymnosperms increased in abundance and aneurophytalean progymnosperms, herbaceous ferns and lycopsids became rare to absent (DiMichelle and Hook, 1992). By the end of the Frasnian stratified forest communities were prevalent and the flora demonstrated a wide range of ecological strategies with vegetational patterns strongly reflecting physical habitat (DiMichelle and Hook, 1992).

1.3.3   Plant–animal interactions

All known early terrestrial arthropod assemblages are associated with plant material. Although arthropods undoubtedly benefited from the moderating effects of vegetation cover, evidence for reciprocal interaction between plants and animals is uncommon, but nonetheless present, during the Silurian and Devonian. Plants were probably the main primary producers, and would have supported animal life through a detritus chain. Detritivores would have ameliorated soil development and nutrient cycling, which, in turn would have benefited the plant communities and ultimately provided more diversity in habitat (Rolfe, 1985). Plant-animal interactions in the form of feeding, shelter, transport, reproduction and coevolution during the Palaeozoic are summarised in papers by Kevan *et al.* (1975), Scott and Taylor (1983), Chaloner *et al.* (1991), Scott (1991) and Labandeira (1998). Documented examples of plant-arthropod interaction from the Devonian and earlier are summarised in table 2.

Circumstantial evidence for plant–animal interaction includes the increasing complexity of spore structure through the Silurian and Devonian. The function of this is discussed by Kevan *et al.* (1975) who speculated that the increasing ornamentation could be an adaptation serving to increase buoyancy and thus aid air dispersal, or that it increases the chances of dispersal by animals. The association of arthropods with sporangia is demonstrated by the exoskeletons of trigonotarbids preserved within the empty sporangia of *Rhynia major* (Kevan *et al.*, 1975). Although this may suggest that the trigonotarbids were feeding on the spores, the presence of another trigonotarbid within a hollow stem suggests that they had probably crawled into the protective space before moulting, or were incidentally transported there after death.

Table 2 Summary of known plant-arthropod interaction from fossil assemblages of the Devonian and earlier.

	PLANT			ARTHROPOD			AGE / REFERENCES	
Taxon	Organ	Tissue	Inferred taxa	Functional feeding group	Evidence type	Age	References
?		Fungal hyphae	?	Detritivore	Coprolite	Silurian (Ludlow)	Sherwood-Pike & Gray (1985)
RHYNIOPHYTES							
Apiculiretusispora / Synorisporites	Sporangia	Spores	Myriapoda	Detritivore	Coprolite	Late Silurian	Edwards et al., 1995
?	Sporangia Stem	Plant spores and tissue Fungal spores	Myriapoda?	Detritivore	Gut contents	Early Devonian	Anderson and Trewin, 2003
RHYNIOPHYTES							
Streelispora / Aneurospora	Sporangia	Spores	Myriapoda	Sporivore / detritivore	Coprolite	Early Devonian	Edwards, 1996; Edwards et al., 1995
Rhynia	Stem	Epidermis, cortical parenchyma, vascular tissue	Acari	Piercer and sucker	Plant damage	Early Devonian	Kidston & Lang, 1921; Kevan et al., 1975
TRIMEROPHYTES *Psilophyton*	Stem	Epidermis, cortical parenchyma	Acari	External (foliage) feeder	Plant damage	Early Devonian Emsian	Banks, 1981; Trant & Gensel, 1985; Banks & Colthart, 1993.
Psilophyton	Stem	Cortical parenchyma	Collembola	Piercer and sucker	Plant damage	Early Devonian Emsian	Banks & Colthart, 1993; Labandeira & Pillips, 1996

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Axes bearing sharp spines occur amongst many early terrestrial land plants and could be interpreted as a defensive mechanism against herbivory. Shear and Selden (2001), however, pointed out that the spines are too large to have significantly obstructed the arthropods known to have occurred with the plants at that time. Lesions attributed to attack from arthropods are known (see below) and some outgrowths may have been an adaptation to increase photosynthesis whilst minimising water loss.

The earliest evidence for a direct association between plants and animals occurs in sediments from the Silurian and earlier. Coprolites from Silurian and Devonian sediments of the Welsh Borderland consisting of undigested land-plant spores were reported by Edwards *et al.* (1995). They are thought to have originated from terrestrial animals since they consist largely of land-derived debris and lack identifiable aquatic remains. The concentration of undigested spores suggests incidental ingestion, and Edwards *et al.* deduced that the coprolites were produced by detritivores feeding on litter. Their size was considered too large for mites, collembolans and nematodes, and too small for earthworms. Millipedes were concluded to be the most likely producers of these coprolites, and their terrestrial forms are now known from coeval deposits. This hypothesis is supported by an enigmatic arthropod of myriapodous affinity preserved in the Lower Devonian Windyfield chert. The animal contains broken plant tissues, various plant spores, and fungal spores in a well-defined gut infill suggestive of a detritivorous mode of life. This is the earliest known record of gut contents in a terrestrial animal. The next example occurs as preserved lycopsid tissue within the gut of a Carboniferous arthropleurid (Rolfe and Ingham, 1967).

Ludlovian faecal pellets from Sweden containing fungal hyphae have been cited as evidence for the presence of fungivorous arthropods during the late Silurian (Sherwood-Pike and Gray, 1985). However, it has been suggested that the fungal material may have grown within the pellets at a later stage and was not an original component (Chaloner *et al.*, 1991). A critical assessment of coprolites from the Silurian and Devonian is given in Shear and Selden (2001). Faecal pellets from microarthropods constitute a major fraction of humus in modern leaf litter communities (Seastedt and Crossley, 1984) and their presence in Silurian sediments demonstrates the cycling of primary productivity early on. It is likely that coprolites have been underrepresented in the fossil record, appearing as unremarkable, poorly aggregated pellets, which are easily overlooked. By the Carboniferous, coprolites are significantly more abundant (Scott and Taylor, 1983).

Evidence for herbivory in the form of tissue damage to plants is well documented from the Carboniferous and later (see Scott and Taylor, 1983). Fern frond petioles with internal tissues consumed by piercers and suckers, and stems and roots damaged by borers have both been reported (Labandeira, 1998). Wood boring and leaf eating extends from the Late Carboniferous onwards (Chaloner *et al.*, 1991). Plant tissue damage from the Devonian,

however, has been documented from only two fossil assemblages. Surficial wounding attributed to biting and chewing, and internal damage from piercing and sucking are known from permineralised stems of *Psilophyton* from Gaspé in Canada (Banks and Colthart, 1993). Kidston and Lang (1921) have also reported lesions in the plant axes of *Rhynia* from the Rhynie chert in Scotland. These lesions are notch like, extending into the vascular tissue and filled with dark necrotised material indicating that the injury was sustained whilst the plant was alive. There are areas of enlarged cortical cells, and some empty spots where stem material has been removed with no apparent effect on the surrounding cells (Kevan *et al.*, 1975). The wounds have been attributed to the piercing and sucking behaviour of mites and springtails, both of which are found amongst the plants at Rhynie. At both Rhynie and Gaspé it is difficult to rule out fungi or abiotic trauma (volcanic gases, wind blown sand grains, or damage from spines of adjacent plants) as the possible cause of tissue damage. Fungal spores found in the inner cortex of small branches of *Psilophyton*, and in the lumen of collenchyma cells may have been introduced by sap sucking animals (Banks and Colthart, 1993). However, unlike at Rhynie, no animals have been found in association with the plant material from Gaspé. Only the aerial portions of the plants have been recovered so far and it has been argued that the culprits responsible may be preserved in the litter at the base of the plants, waiting to be uncovered. These plants do, however, come from the same Emsian Battery Point Formation from which a possible bristletail (Labandeira, 1988) and millipedes (Shear *et al.*, 1996) have been described. If the presence of tissue damage is consistent with damage caused by animals with piercing and sucking mouthparts, then this would suggest that there were already highly adaptive animals in existence. However, such animals are unknown until the Permian, and the evidence remains controversial until the Carboniferous.

CHAPTER 2   MATERIALS AND METHODS

This chapter outlines the location and collection of materials, and details the methods used to extract and observe fossils collected from the field. Location maps are included together with location reference numbers and rights of access.

2.1   *Materials*

All materials referred to in this research have come from localities across Schoharie, Greene and Delaware counties in New York State, USA (figures 2.1 and 2.3).

2.1.1   *Field work and sample sites*

Fossiliferous shales and previously prepared slides of arthropod cuticle from South Mountain quarry in New York State were examined during a visit to Dr William Shear at Hamden-Sydney College (HSC), Virginia in July 2000. During July 2001 samples were collected from South Mountain quarry in New York State for maceration and petrographic analysis and sediments were logged. A single vertebrate specimen was also collected. New quarries within the Schoharie county area were investigated for potential fossiliferous material, resulting in the collection of some preliminary samples from a quarry at High Knob. After some promising finds at both South Mountain and High Knob another trip was made to collect in the field during July 2002 in collaboration with Dr William Shear (HSC) and Linda Van Aller-Hernick, Ed Landing and Sharon Mannolini from the New York State Museum (NYSM) in Albany. The quarry at South Mountain was excavated more extensively to search for new fossiliferous material (Figure 2.2). Additional material and sedimentary details were collected from High Knob and preliminary samples were collected from Cairo quarry and Oak Hill. During July to October 2003 Sharon Mannolini and Linda Van Aller-Hernick collected additional material from Dutton Ridge, Hilltop Road and Kropp Road. For quarry locations refer to figure 2.3.

South Mountain quarry lies within the New York State Forest Reservation and permission from the New York State Department of Environmental Conservation (NYSDEC) in Stamford, Schoharie County, was required before removing any material from the site. A collecting license was granted for all field-work carried out during this research.
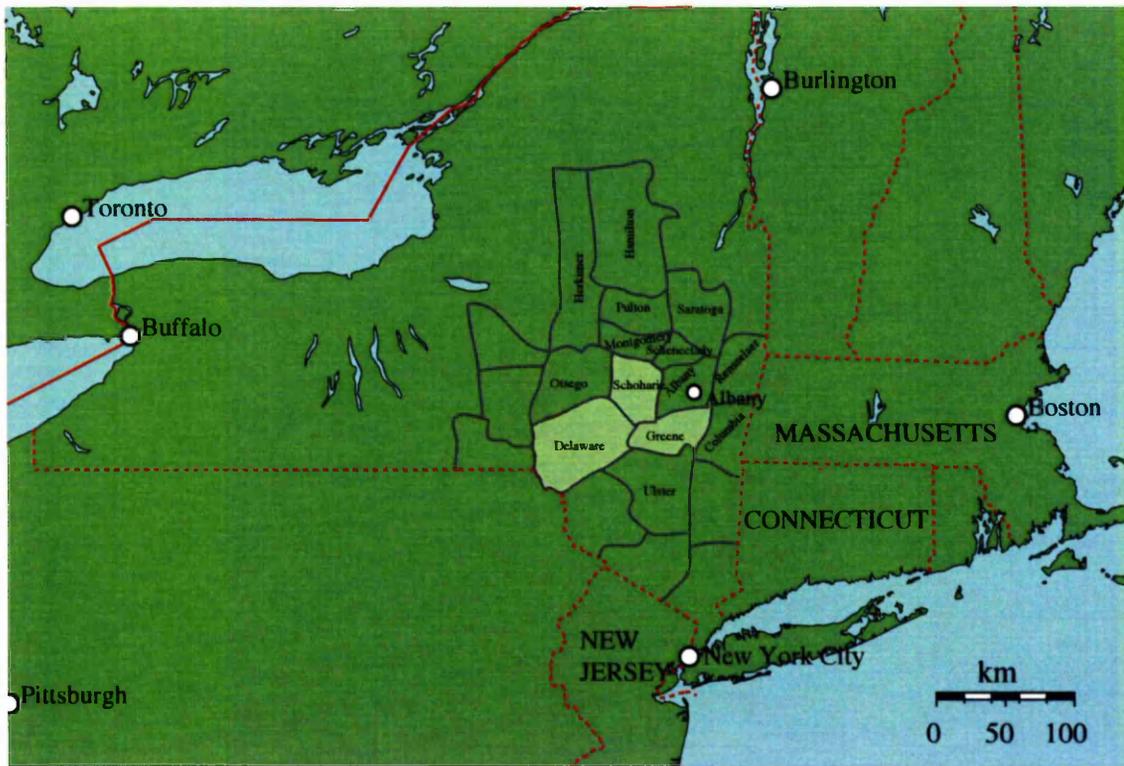
Figure 2.1 Location map for Schoharie, Green and Delaware counties, North America

Figure 2.2 Digging with the back-hoe at South Mountain quarry, New York State, USA. Loosened material in middleground.
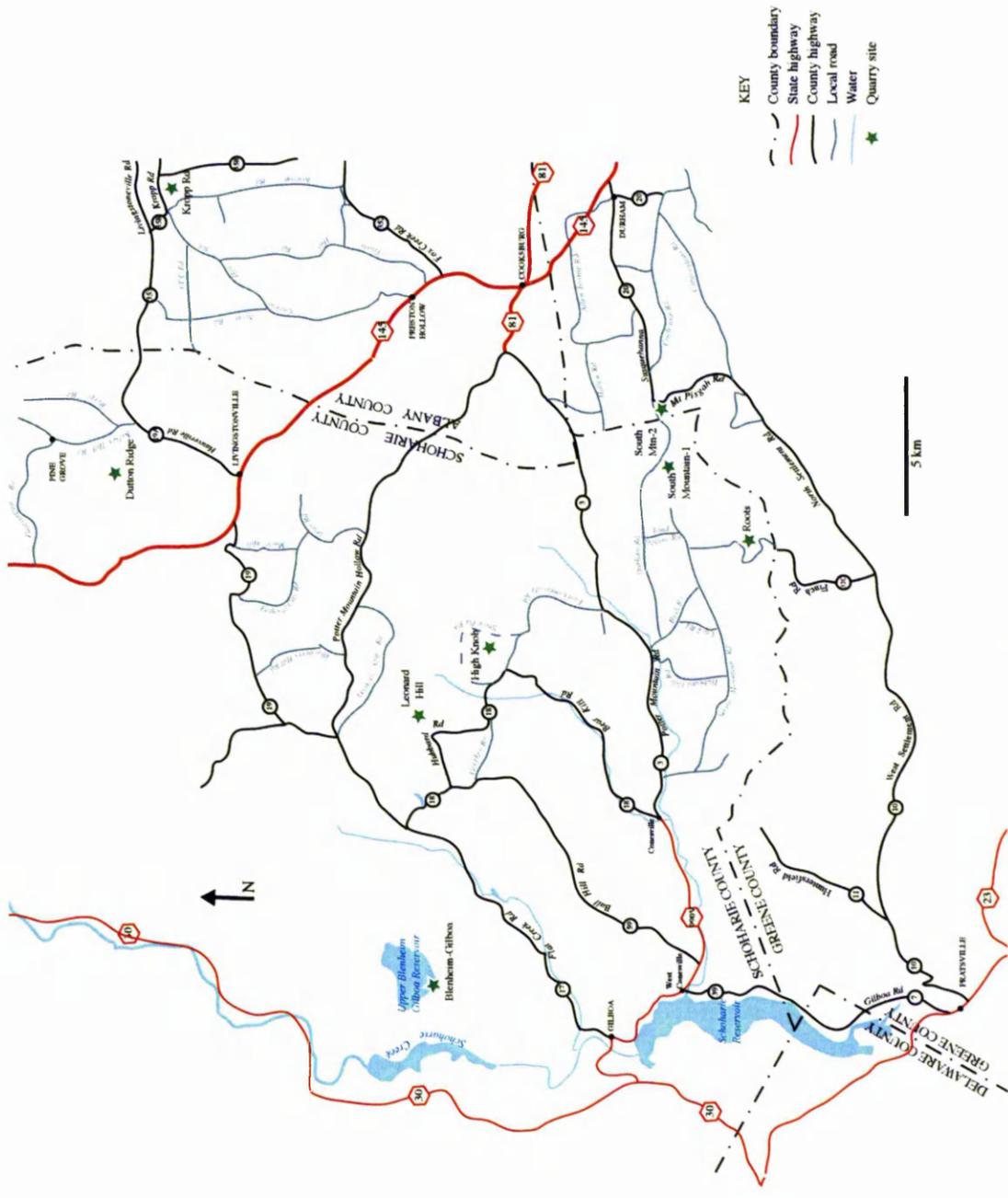
Figure 2.3 Location map of quarries in the Schoharie, Greene and Delaware counties of New York State, North America

2.1.2   Sample collection

Slabs of dark grey, organic rich, argillaceous shales were collected from the quarries in New York State. Material from the quarry floor was loosened using the back-hoe of a mechanical digger and hand picked for suitable samples (figure 2.2). Selected samples were bagged up, labelled and shipped back to Manchester, UK for maceration (section 2.2.1). Some larger plant fossils were removed and taken to the NYSM in Albany.

Since the arthropod fossils are not visible in hand specimens, sampling was based on lithology. Fine-grained samples with a high plant fossil content were preferentially selected as these contained the most abundant and complete arthropod cuticles. The best samples were found in discrete, laterally discontinuous lenses of fine-grained mudstones lying within coarser grained mudstones and sandstones on the quarry floor.

2.1.3   Sedimentary logging and sampling

Sedimentary details were logged in the field, noting colour lithology, texture, sedimentary structures and fossil content at each site. Samples were collected at intervals from within the major lithological units for petrographic analysis.

2.2   Material preparation

To extract the organic cuticles from the host rock, samples were macerated using 40–60% concentrate hydrofluoric acid (HF). The resulting residue of translucent plant and animal cuticles were then picked through, sorted, and examined using a microscope with transmitted light (section 2.3.1). Potassium hydroxide (KOH) and Schultz's solution (a mixture of nitric and hydrochloric acid) were both investigated as alternatives to hydrofluoric acid but the results were found to be unsatisfactory as the samples did not break down sufficiently and it was impossible to extract the cuticles.

Hydrofluoric acid is an extremely toxic chemical and appropriate safety precautions were taken (see appendix A for safety data sheets). Maceration was carried out in a fume cupboard equipped with a scrubber, and protective clothing, including neoprene gauntlets, apron and visor were worn. All equipment (beakers, Petri dishes, stirrers etc) was plastic, since any glass would dissolve and any metal would corrode. This method is only intended for use with organic rich sediments. Samples containing carbonate minerals should first be treated with hydrochloric acid to dissolve the carbonate before using hydrofluoric acid to dissolve silicates.

2.2.1   Hydrofluoric acid maceration and disposal of waste acid

1)   Samples were broken into pieces approximately three centimetres square. These were then rinsed well with distilled water to reduce the risk of contamination with modern

fauna.

2)   Cleaned samples were placed in separate plastic beakers inside the fume cupboard with the scrubber running. Hydrofluoric acid was carefully poured over the sample until it was just covered. The beaker was covered and pushed to the back of the fume cupboard.

3)   After two to three days the sample was digested and resembled a muddy sludge in the bottom of the beaker. Agitating the sample periodically expedited this process. The macerate was filtered through a twenty-micron grade polyester mesh to retrieve the organic cuticle and the waste acid was collected for disposal. Some cuticle rich samples clogged the mesh, in which case a vacuum pump assisted drainage of the waste acid.

4)   The macerate was rinsed well with distilled water and transferred into a clean beaker with distilled water or a weak solution of hydrochloric acid to inhibit fungal growth.

5)   The macerate was decanted into sealed tubes or bottles, labelled appropriately and transferred to a shallow Petri dish for picking.

6)   The waste acid from the maceration was collected and stored in a safe container in the fume cupboard until a sufficient amount (approximately one litre) had been collected for neutralisation and disposal.

7)   To neutralise the waste acid it was placed in a large bucket and powdered calcium carbonate was gradually added. After some time a thick paste of calcium fluorite (CaF_2) formed, which eventually dried out into a solid. The process usually required approximately 1.5kg of calcium carbonate for a litre of waste acid, and took about one and a half hours to neutralise. The resulting solid was then double bagged and disposed of appropriately with other hazardous solid waste. Care was taken when handling the calcium fluorite and it remained within the fume cupboard until it was bagged up, at which point it was immediately transferred to a secure storage for disposal.

2.3   Examination of extracted cuticles

Several techniques were employed in the analysis of the fossil cuticles. Fine cuticular details were examined using transmitted light microscopy (section 2.3.1), surface topography was imaged using the scanning electron microscope (SEM) (section 2.3.2), and the composition of the animal cuticle was investigated using the electron microprobe (section 2.3.3). Vertebrate remains were analysed using high-resolution computed tomography (section 2.3.4) and both sediment samples and vertebrate remains were thin sectioned for petrographic analysis (section 2.3.5).

2.3.1   Transmitted light microscopy

The rinsed macerate was examined initially with an Olympus SZH stereo zoom microscope using transmitted light. The cuticles were picked through and all arthropod

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cuticles removed with a fine paintbrush or needle and mounted in epoxy resin on biological slides. At this stage the arthropod cuticle could usually be distinguished from the plant cuticle by its golden brown colour and translucent nature (see chapter 3). Some larger and thicker arthropod pieces, which would have yielded little information under a light microscope, were retained for examination with the SEM.

Prepared slides were examined for fine cuticular details using a Nikon Optiphot stereo compound microscope under transmitted light. Specimens were photographed with a Nikon D1X digital camera, and drawings were made with a camera lucida drawing tube attached to the Nikon microscope.

2.3.2   *Scanning electron microscopy (SEM)*

Suitable pieces of cuticle were picked from the macerate and placed onto a small square of double-sided tape fixed to the top of a numbered SEM stub and left to dry. The stubs were vacuum coated with a thin film of gold to avoid charge accumulation on the specimen surface during analysis. Stubs were placed in a stage ready to go into the specimen chamber in the SEM for imaging. The SEM essentially works by firing a finely focused, high-energy beam of electrons from an electron gun at the sample, which is held in a specimen chamber pumped to a high vacuum. Scan coils scan the beam from side to side over the specimen and electron detectors form a topographic image of the specimen using secondary electrons. Since surface topography influences the back scattering of electrons, accurate qualitative analysis of the cuticle was not possible.

Pieces of arthropleurid cuticle and some unidentified organic debris were successfully imaged using the SEM. Illustrations and discussions of these images are given in the relevant chapters.

2.3.3   *Electron microprobe analysis*

The chemical composition of Devonian arthropod cuticle was investigated using the Manchester Electron Microprobe Facility (MEMF) Cameca SX100. The microprobe was selected over other methods of quantitative analysis because it can analyse elements with a low atomic number and has a high analytical resolution. It works by bombarding the sample with a beam of highly charged electrons. The resulting effects are used to extract various types of microscale information such as atomic density and elemental abundance.

A polished thin section of a shale sample preserving organic cuticles from New York State was analysed together with a sample from the Rhynie chert in Aberdeenshire. Since the organic cuticles in shales lie parallel to the grain, and thin sections were made perpendicular to the grain, they are hard to distinguish from the matrix and have a much smaller surface area. In the Rhynie chert, however, plant and arthropod cuticles are clearly distinguishable thus facilitating focusing of the beam directly onto the specimen. Results from the Rhynie

chert cuticle were therefore extrapolated to the cuticles preserved in shale.

Both samples were polished using a diamond paste and initial analyses were conducted using only silver paint to earth the beam of ions. This proved insufficient to stabilise the beam, so a thin film of carbon (kept to a minimum, so as not to skew the analysis) was eventually applied. Carbon, silica, sulphur and oxygen elemental maps were produced for the Rhynie sample of known arthropod cuticle, with the electron beam focussed to about two microns. An organic layer of cuticle in the South Mountain shale was probed and a chemical trace produced. Results are discussed in chapter 4.

2.3.4 High-resolution computed tomography

High-resolution computed tomography was used to image plant and animal cuticles *in situ* (chapter 4), and to image the internal structure of a vertebrate tooth from South Mountain, New York State (chapter 11). Samples for analysis were taken to the high-resolution computed tomography unit at the University of Texas, USA (UT-CT).

The facility at UT-CT utilises a 150-kV microfocal x-ray source to map density contrasts in the subject material. A tungsten filament produces 'hard' x-rays, which are ideally suited for imaging the interior of solid geological objects. The x-rays travel from the filament, through the object to a detector placed on the opposite side that records the amount of attenuation in the x-rays. Differences in x-ray absorption can be equated with differences in electron density and are used to map density contrasts within the specimen. Readings are taken at incremental positions over the specimen, resulting in a series of graphic 'slices', which can be stacked and rendered into a three-dimensional form replicating the internal features of the original. For a fully comprehensive overview of high-resolution computed tomography see Ketcham and Carlson (2001).

Two labyrinthodont teeth were taken to UT-CT for imaging. The unidentified tooth from South Mountain was trimmed with a rock saw to remove as much of the surrounding matrix as possible and the known labyrinthodont tooth was left as it was. Both teeth were placed in the x-ray chamber for scanning supported by a piece of bluetack at their base (for technical details of operation see appendix B). A continuous series of 108 horizontal slices, each 30μm thick, was obtained for the tooth from South Mountain. Thirty horizontal slices were obtained over 10 regular intervals down the long axis of the known labyrinthodont tooth. The digital images were stacked and exported as QuickTime movies, and the data resliced vertically using ImageJ—a freeware public domain image analysis program.

2.3.5 Petrographic analysis

Polished thin sections, ground to a thickness of 50μm were made from siliciclastic sediment samples collected from South Mountain, Brink and High Knob quarries. These were examined for mineral content and diagenetic information using a Nikon petrographic

microscope. They were photographed under plane-polarised light with a Nikon D1X digital camera. Details from the thin sections were used to refine the sedimentary logs and interpret the depositional setting more fully. Results from petrographic analyses are discussed in chapter 5.

2.4   Comparison of assemblages and reconstruction of palaeoecology

Sedimentary, taphonomic and biological data were all compiled for individual sites as far as was possible in order to most accurately reconstruct the original communities. A flow chart outlining this process is illustrated in figure 2.4. After establishing as much information as possible for each site it was then possible to compare and contrast assemblages in terms of community composition, palaeoenvironment and taphonomy. Analysing each site in this way permits a much more reliable and robust comparison between sites since taphonomic and palaeoenvironmental biases affecting the fossil samples area all taken into account.
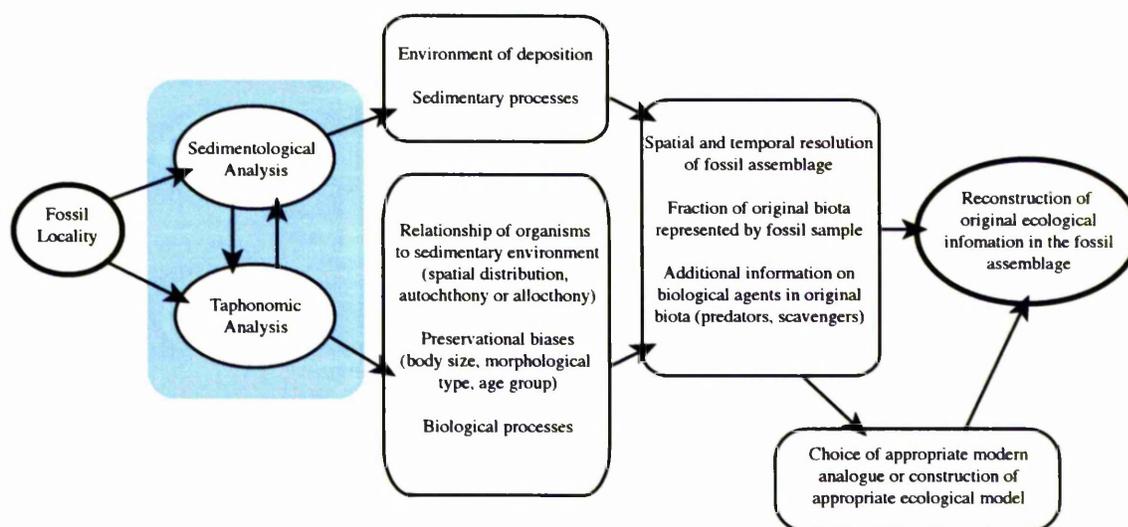
Figure 2.4 An idealised structure for the palaeoecological analysis of palaeontological sites in which sedimentologic and taphonomic analysis provides the foundation for successive levels of inference. Modified from Behrensmeyer and Hook (1992).

The bulk of the fossil material collected from New York State and described herein consists of dispersed arthropod cuticles recovered from organic-rich shales by HF acid maceration. Disseminated arthropod cuticles are frequently recognised in palaeobotanical preparations (Bertram *et al.,* 1987), but their small size and fragility means that they are frequently overlooked as sources of palaeontological data. Although they are often fragmented and disarticulated they exhibit a level of preservation unsurpassed by most other arthropod fossils, and as such represent an extremely valuable source of morphological data.

3.1   *Identification of dispersed cuticles*

Discriminating arthropod from plant cuticle, particularly small and broken fragments, can be difficult. Whilst some cuticles can be identified by neontological comparison or comparison with known fossils, others are less straightforward and there are examples of plant cuticle subsequently redescribed as arthropod cuticle (Rolfe, 1969). This problem was addressed by Gray *et al.* (1990) in their paper on early land plant phytodebris. They cited jagged or cuspate margins, margins with angular corners, warty tubercles, polygonal scales and the presence of setae as criteria for distinguishing arthropod from plant cuticle. For the most part, however, it is usually possible to sort on the basis of colour and shape, at least in the first instance. In a filtered macerate residue viewed under transmitted light, arthropod cuticles appear as golden brown to orange and are often more buoyant than the plant material which tends to be coalified and sink to the bottom of the sample.

The identification of dispersed arthropod cuticle to a higher taxonomic level can also prove problematical. Whilst Recent fauna are grouped and classified using whole organism morphology, it is impractical to apply the same system to the identification of disassociated sclerites. As a result, the taxonomy and identification of dispersed and fragmented arthropod cuticle must rely on more universal features. Features common to nearly all sclerites include cuticle microsculpture and the presence of sensory organs such as setae and slit sensilla. Cuticle microsculpture and ultrastructure have successfully been used in the identification of Carboniferous scorpions (Jeram, 1989) and the phylogeny of spiders (Lehtinen, 1996) and several arthropods have been described solely from preserved cuticle (see chapter 1). Some complete sclerites can be identified on their morphology alone, proving the presence of a particular taxon. Such autapomorphic characters include the pectines of scorpions and the opisthosomal spinnerets of spiders. The cuticular microsculpture and patterning of such

sclerites can then be matched to other, less diagnostic, cuticle fragments. In this way a comprehensive database of cuticle types can be created, with new finds constantly adding to or revising the data.

Figure 3.1 is a key intended as an aid to identification of dissacociated sclerites recovered from macerations based upon gross morphology and microsculpture of material recovered from New York State. It is intended only as a rough guide and it is likely that with increasing finds and further research the identifications will change or amalgamate. However, at this stage it is important to form some kind of cohesive framework within which to place the cuticle types so that both past and future identification may be facilitated and consolidated.

3.1.1   Sclerite morphology

In their simplest form arthropods consist of a body (cephalon, thorax and abdomen – tagma variously fused) and a number of jointed appendages of various functions. All of these can potentially disarticulate into individual podomeres and sclerites, so that any one arthropod has the potential to disassociate into numerous pieces, the greater portion consisting of podomeres.

Podomeres are often recognisable as elongate structures with parallel to subparallel margins and varying degrees of emargination at either end. Sensory organs in the form of setae and setal sockets, and slit sensilla may be present. Since podomeres are essentially tubular structures that have been compressed in the sediment, they are usually preserved as a double thickness of cuticle and may therefore be more robust than some other sclerites. In comparison, body segments are fewer and considerably larger. Generally they will be flattened sheets of single thickness cuticle, and may break more easily than other sclerites. Other sclerites of known morphology can usually be identified by comparison with extant or fossil fauna. Some of the more commonly occurring sclerites are illustrated in figure 3.1.

3.1.2   Sclerite microsculpture

Cuticle pieces are frequently fragmented into broken scraps with no true margins and no recognisable morphology. In these cases cuticle can often be identified, or at least sorted into associations, by the surface microsculpture. Microsculpture may include surface ornament of the cuticle (e.g. reticulate thickening), the shape, structure and arrangement of setae or setal sockets and the presence or absence of sensory organs. More detailed descriptions of cuticle structure and topography are given in the relevant chapters and figures indicated on the key of figure 3.1.

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Cuticle microsculpture	Typical sclerites	Current Identification	Published figures	Figures in this thesis
Cuticle characterised by triangular thickenings often forming a double spine surrounding a small setal socket. Distinctive pattern of terrace lines.		Diplopoda: Arthropleuridea: Eoarthropleurida: *Eoarthropleura* Tergites, K-plates, B-plates, sterna and podomeres	Størmer, 1976. Kjellesvig-Waering, 1986. Shear and Selden, 1995. Wilson, 1999.	Tergites: 6.2, 6.3, 6.4, 6.5 K-plates: 6.6, 6.7, 6.9, 6.10, 6.11 B-plates: 6.6, 6.7, 6.9, 6.10, 6.12 Sterna:6.6, 6.7, 6.8 Podomeres: 6.13, 6.14, 6.15, 6.16, 6.17, 6.18
Granular cuticle surface with conspicuous setal sockets and rare setae. Frequent spines and cuticular thickenings.		Scorpiones Metasomal segments, pectines and chelae	Jeram, 1989 (unpublished)	Tergites: 7.1, 7.2, 7.3 Pectines: 7.3, 7.4, 7.5. 7.6 Pedipalps: 7.7, 7.8, 7.9 Podomeres: 7.10, 7.11, 7.12, 7.13 Metasoma: 7.14, 7.15
Reticulate cuticle entire. Individual polygons thicken distally. Long fine setae. Frequent silt sensilla and lyriform organs.		Araneae *Attercopus fimbriunguis* Mainly podomeres	Selden et al., 1991 Shear et al., 1987	8.3, 8.4, 8.6, 8.7, 8.9, 8.10
Reticulate cuticle entire elongated and arranged in rows.		Palaeocharinidae: *Gelasinotarbus?*	Shear et al., 1987	8.12, 8.13
Reticulations restricted to margins of carapace and podomeres.		Trigonotarbida: Palaeocharinidae: *Palaeocharinus; Gelasinotarbus*	Shear et al., 1987	8.14, 8.15
Cuticle with little ornamentation. Characterised by thickened ribs and cross-hatched sculpture.		Trigonotarbida? Round sterna with curved coxae and short, stubby podomeres	N/A	8.16, 8.17, 8.18, 8.19. 8.20, 8.21
Cone-shaped sockets arranged in short, staggered rows over the surface of the cuticle.		Hexapoda: Archaeognatha? Occurs as single sheets occasionally with attached, ribbon-like scales.	Labandeira et al., 1988 Shear et al., 1998	9.2, 9.3
Cuticle with irregular surface and fringed with ornament of minute spines.		Hexapoda? Rounded podomere shaped structures, resembling spores but articulated.	Jeram et al., 1990	9.5
Characteristic lunules ornament cuticle surface		Eurypterida Occurs as small, indiscrimnate scraps		5.16
Aggregates of spores and arthropod cuticle		Occur as regular (spore dominated) and irregular masses	Edwards et al., 1995	9.8, 9.9
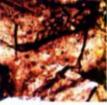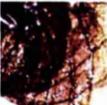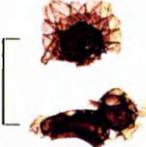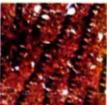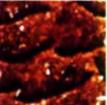
Reticulate Cuticle

Figure 3.1 Cuticle key for dispersed arthropod cuticles from the Silurian and Devonian. Based upon material recovered from New York State, USA.

CHAPTER 4   TAPHONOMY OF ARTHROPOD CUTICLES

The cuticle of an organism provides a vital barrier between the soft tissues and the outside environment. A rigid exoskeleton provides support and protection whilst modifications ensure that sensory functions are still enabled. Arthropod cuticle is a highly resistant material found preserved in marine and non-marine environments in sediments from the Cambrian through to the Recent (Briggs and Clarkson, 1989; Shear and Kukalova-Peck, 1990; Butterfield, 1990, 1994). Recent arthropod cuticles are composed largely of protein and chitin, sometimes impregnated with a biomineral (often calcium carbonate). In some taxa (*e.g.* Scorpiones) the cuticle is further strengthened by cross linkages between protein elements. This tanned protein is called sclerotin.

All of the known terrestrial arthropod faunas from the early to mid-Palaeozoic are found preserved in deposits that are unusually rich in palaeontological information (see section 1.3.2). These conservation Lagerstätten are notable for their quality of preservation, particularly of organisms with soft tissues. Examples from the Catskill region of New York State occur at a number of sites where arthropod cuticles are found preserved amongst plant material. Although they are frequently disassociated and fragmented the cuticle itself is almost perfectly preserved, having altered very little over some three hundred and eighty million years.

4.1   Biostratinomy

There are a number of variables affecting a moulted exoskeleton, or the carcass of a terrestrial arthropod, between its demise and the point of deposition and burial. These are summarised in figure 4.1, which also illustrates the likely condition of the cuticles following deposition. In the short term the principal agents acting upon a cuticle are biological decomposition, scavenging and physical breakdown. In turn, these are affected by factors such as oxygen content, environmental energy and sedimentation rates.
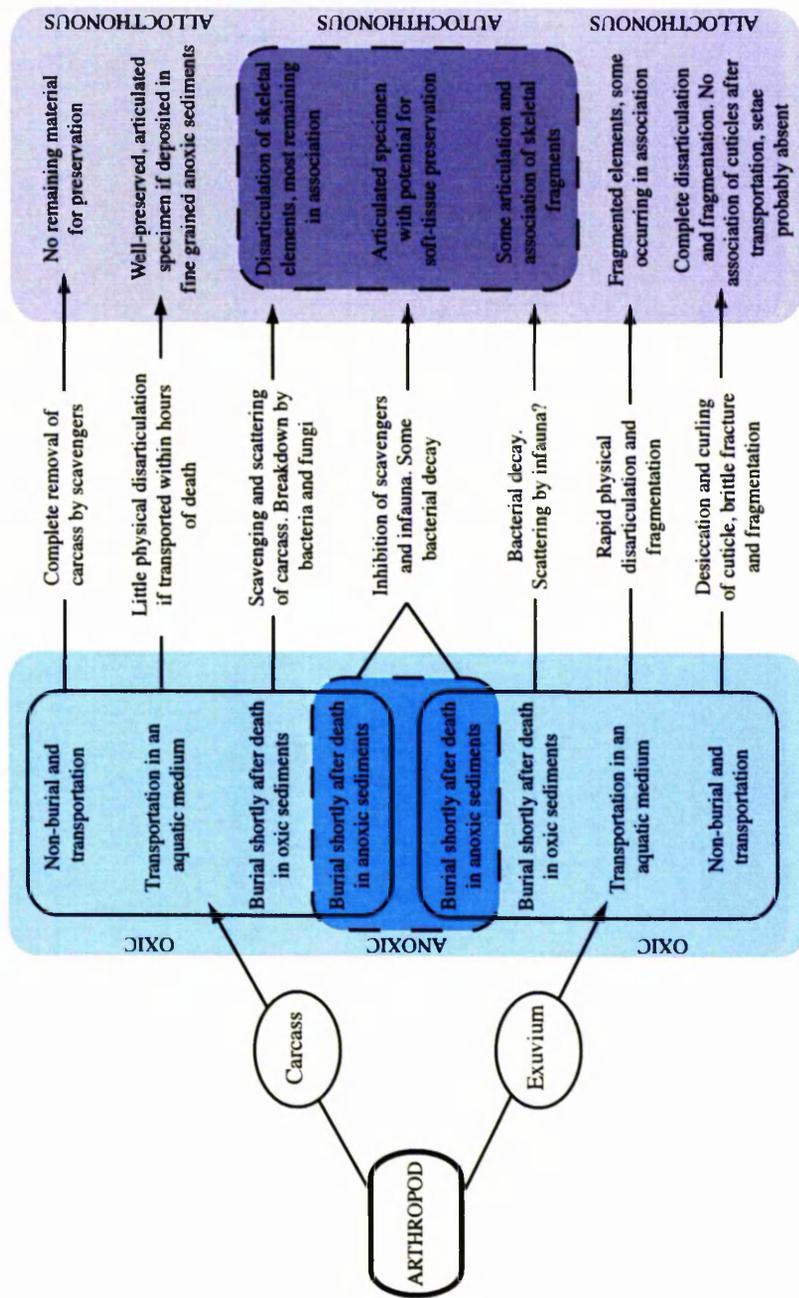
Figure 4.1 Hypothetical model for taphonomic processes affecting arthropod exoskeltons. The column on the left shows possible pathways to deposition and the column on the right indicates the resulting compoments that would potentially be available for fossilisation.

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4.1.1   Biological decomposition

Seastedt and Tate (1981) examined the breakdown of arthropod carcasses buried in forest litter in North Carolina and Georgia. Using millipede and crickets as examples they estimated that it would take about five years for the carcasses to completely disappear. They concluded that arthropod remains resulting from the unconsumed portions of prey, and exoskeleton remains produced during moults probably decompose at a similar rate to whole carcasses. This was based upon the similarity in estimates of standing crops calculated from decomposition rates and those obtained by hand sorting of litter and humus. In experiments on the preservation of chitin, thick sclerotized cuticles of beetles were found to decay significantly slower than the thinner cuticles of flies, although Okafor (1996a) reported recognisable fragments of a desert locust wing after it had been buried for three hundred days. This contrasts with the decomposition of arthropod cuticle in marine sediments, which occurs with much more rapidity (Plotnick, 1986).

The key organisms responsible for the decomposition of the chitinous fraction of arthropod cuticle are fungi, bacteria, nematodes and protozoa (Okafor, 1996b). Bacteria and fungi are also responsible for the decomposition of chitin in marine environments. Most chitinoclastic bacteria are aerobic, though some are facultatively anaerobic, and occur in seawater, sediments, animal guts and on arthropods. High concentrations of chitinoclastic bacteria occur in inter-tidal and freshwater sediments (Plotnick, 1986).

Evidence for the microbial attack of Carboniferous arthropods was reported by Jeram (1989). Bleached patches, in which the surface pattern was absent, were noted on several specimens of scorpion cuticle. SEM images showed these to correspond with small (20μ) pits on the cuticle surface, which were attributed to degradation by clumps of bacteria. Dendritic patterns were similarly attributed to actinomycetes, suggesting that the cuticles had resided within the leaf litter for some time prior to burial. Bleached spots were not observed in any of the Devonian cuticles from New York State, which could indicate that the cuticles were transported to their site of burial fairly rapidly and had a short residence time in the leaf litter. Alternatively, this could reflect an absence of chitinoclastic bacteria and/or fungi at that time, although some unusual patterning on cuticles could have resulted from bacterial or fungal attack.

4.1.2   Scavenging

Scavenging, probably by crabs, was observed to be a primary cause of disarticulation and scattering of buried shrimp carcasses in intertidal localities on San Juan Island, Washington (Plotnick, 1986). In terrestrial environments, the initially rapid mass loss of millipede and cricket carcasses reported by Seastedt and Tate (1981) was attributed to consumption by maggots, ants, beetles and other macroinvertebrates. A slower rate of decomposition after

the first two weeks was attributed to microfloral respiration and microarthropod consumption (Seastedt *et al.*, 1981). Carcasses left on the leaf litter surface completely disappeared within twenty-four hours, largely due to the action of vespid wasps and ants. Those buried in the leaf litter persisted for longer and were attacked initially by maggots, ants and beetles and later on by collembolans and mites. Seastedt *et al.* (1981) concluded that microbial breakdown of exoskeletal fragments may be the primary agent of decomposition, while microarthropods perform an auxiliary function by fragmenting exoskeleton materials and grazing upon both arthropod remains and microflora.

Scavenging during the early and mid-Palaeozoic may not have contributed to the breakdown of arthropod carcasses to such an extent as it does now. In particular, the principal groups attracted to carrion in the studies performed by Seastedt and Tate (1981) and Seastedt *et al.* (1981) had not yet evolved. However, mites and collembola were present and there are tentative reports of fungal hyphae, which may have assisted in the biological breakdown of cuticles.

4.1.3   Physical disturbance

Experimental studies have demonstrated that arthropods, echinoderms, and even soft-bodied organisms can potentially be transported tens of kilometres without disarticulating, provided that this happens within the first few hours following their demise (Brett and Allison, 1998). Conversely, arthropod moults are considerably more fragile, and articulated specimens or fragments found in association can be a sensitive indicator of in place burial.

Disturbance by burrowing infauna (detritivores) churns the sediment and redistributes arthropod remains. Plotnick (1986) discussed an interesting hypothesis on the preservation of soft-bodied faunas and articulated arthropods. He argued that if arthropod preservation necessitates an inhibition or absence of bioturbation, and if rates of bioturbation have increased through the Phanerozoic, then the preservation potential for articulated arthropod fossils may have decreased over time. Bioturbation is certainly a dominant feature of sediments over- and underlying fossiliferous strata in New York where it completely overprints original sediment fabrics. It is conspicuously absent from the fossil-bearing strata themselves.

Investigation of decay processes in shallow freshwater pools by Anderson and Trewin (2003) revealed that gas buoying of moulted cuticle fragments (possibly from photosynthetic algae and/or decomposition of the animal itself) might play a role in disarticulating and scattering components, independent of the action of scavengers, detritivores or agitation of the water body. Articulated moults were sometimes observed in the standing bodies of water, but lacked soft tissues or gut contents. Upon desiccation these exuviae became brittle, curled up and were easily fractured and fragmented.

4.1.4   Oxygen

Levels of available oxygen immediately surrounding a buried cuticle can have a dramatic effect on its preservation potential. Lack of oxygen precludes scavengers from the carcass, reduces microbial activity and inhibits bioturbation. In marine sediments, the decomposition of chitin occurs much more rapidly in the upper, aerobic sediment layers and slows or stops under anoxic conditions (Plotnick, 1986). However, controlled laboratory experiments conducted by Plotnick (1986) also showed that although the initial rate of decomposition was faster under oxic conditions whilst soft tissue disintegrated, no appreciable difference in decomposition rates of shrimp carcasses were observed after the first two weeks under both oxic and anoxic conditions. This experiment was executed under controlled conditions (in sealed jars) and therefore excluded the potential for scavenging by external fauna. Analyses of Pleistocene insect cuticles in lake sediments at Willershausen, Germany give a more realistic picture. Briggs *et al.*, (1998) demonstrated that the preservation of chitin is enhanced in the deeper water anoxic facies, and conclude that environmental setting is a more important control on preservation than geological age.

4.1.5   Sedimentation rates

High sedimentation rates rapidly bury organic remains, protecting them from physical disturbance and removing them from the upper oxic layers. Conversely, slow sedimentation rates cause organic material to be exposed at the surface for longer, promoting corrosion and physical disturbance.

The presence of pyrite within the cuticle bearing sediments from the Catskill region of New York indicates that conditions were reducing and that anaerobic bacteria were present. Its presence also suggests a moderate rate of sedimentation since rapid rates can dilute organic matter and denies sufficient time in the upper zone of sulphate reduction to permit development of pyrite (Curtis, 1980). Many of the sediment samples collected for maceration from New York contained varying amounts of pyrite. At South Mountain it was sparse and disseminated, whereas at High Knob there was abundant pyritised plant material. This probably reflects the marked differences in organic matter observed at the two sites and may also be due to differences in sedimentation rates (see chapter 5 for further details).

Samples from Dutton Ridge containing differing amounts of pyrite were compared to see what effect, if any, pyrite had on the preservation of arthropod cuticle. The samples were known to produce relatively consistent levels of eurypterid cuticle, and were therefore the most suitable for comparison. Macerates with pyrite appeared to contain larger plant fragments but broke down less easily than samples containing less pyrite. Overall there was no appreciable difference in the levels of arthropod cuticle recovered from each sample. More generally, samples containing abundant pyrite were avoided because the pyrite was

observed to break down into small cubes thus destroying any structures it may have been preserving.

4.2 Diagenesis of arthropod cuticle

The majority of the fossil arthropods examined have closely related modern ancestors and it is likely that the chemical composition of their cuticles were similar. Investigations of the ultrastructure of Carboniferous scorpions using a scanning electron microscope (SEM) by Jeram (1989) failed to detect any original laminations, and he concluded that the fossil scorpion cuticles were homologous with the hyaline exocuticle of Recent scorpions. However, investigation of fossil and Recent scorpion cuticles by Stankiewicz et al., (1998), using both scanning and transmission electron microscopy (TEM) did not support this interpretation. TEM images through fossil scorpion illustrate a single thick amorphous layer, which may correspond with the central exocuticular layer of Recent scorpions. Only one specimen exhibits a thin surface layer corresponding to the hyaline exocuticle, and it appears that most of the laminated structure in fossil arthropod cuticles has been lost during diagensis.

Analyses of fossil arthropod cuticles using pyrolysis-gas chromatography / mass spectrometry (py-GC/MS) have demonstrated that the organic components of cuticles from the Mesozoic and earlier have a typically aliphatic signature and do not yield pyrolysis products which might indicate the presence of original chitin or protein (Stankiewicz et al., 1997a, 1997b, 1998; McCobb et al., 1998; Briggs et al., 1998; Briggs 1999). The oldest traces of original chitin are preserved in the thick sclerotised cuticles of Oligocene (25Ma) beetles from Enspel, Germany (Stankiewicz, 1997a). There are two alternative hypotheses for the preservation of cuticle with an aliphatic signature. The original chitin may have been replaced by more resistant aliphatic organic matter from an external source (Baas et al., 1995), or by cuticular waxes and/or lipids from internal tissues that were polymerised during diagnesis (Stankiewicz et al., 1997b). Stankiewicz et al. (1998) argue that cuticle chemistry and morphology are characteristic of a particular taxon relating to the original chemical constituents of the organism and therefore that aliphatic moieties in the cuticles must arise from polymerisation of the associated epicuticular, cuticular and/or tissue lipids during diagenesis. Polymerisation of lipids within the cuticle would also explain the lack of ultrastructure seen in the fossil arthropod cuticles due to the degradation of non-waxy constituents and the infilling of voids by polymerised cuticular and/or tissue lipids (i.e. aliphatic polymer) (Stankiewicz et al., 1998).

4.3　Preservation of cuticles in Devonian shales from New York

Devonian arthropod fossils from New York State are preserved in fine-grained, dark grey shales and exhibit a range of preservational states. The cuticles are flattened and frequently bear the imprints of sediment grains impacted onto their surface (figure 6.1C). The cuticles vary from articulated exoskeletal elements to disarticulated whole elements and fragmented and broken sclerites. It is not clear how the cuticles are arranged spatially within the rock (*i.e.* how closely associated or even connected they are), however it is evident that cuticle types exhibit a degree of 'clumping'. Throughout this research it has become apparent that some samples are more productive than others, and that 'good' finds *i.e.* recognisable sclerites and jumbles of articulated exoskeletal elements appear all at once. In between are periods when nothing will be recovered from the samples at all. Figure 4.2 graphically illustrates all productive bulk rock samples from South Mountain and the quantity of arthropod cuticle that was recovered from each. It is clear from these data that arthropod cuticles are not distributed evenly throughout the sediments. SM1.115, for example, was a particularly prolific sample producing lots of arthropod cuticles. Furthermore, some cuticle types were recovered from only one bulk rock sample, suggesting a degree of original association or even articulation within the rock matrix. Since cuticle-rich samples are macerated more than samples producing only small amounts of cuticle, the peaks in the graph are artificially amplified to some degree but nevertheless give a reasonable qualitative picture.

Several questions arise from these findings. Do all of the cuticle pieces originate from a single disarticulated individual, or does the apparent clumping represent a localised accumulation of cuticle pieces from different animals? Furthermore, does the number of cuticle pieces recovered directly relate to the original number of individuals in the community, or do they represent the moulted exoskeletons of just a few?
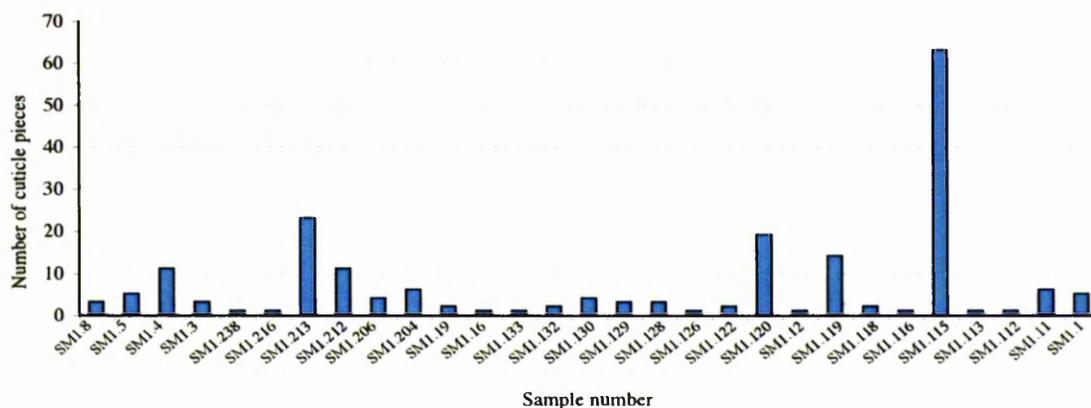
Figure 4.2 Absolute abundance of arthropod cuticles recovered by acid maceration of shale samples from South Mountain quarry, Schoharie County, New York State, USA. Non-producing samples not shown.

4.3.1 Moults, mortalities or rejectamenta?

All arthropods moult, thus each individual leaves several exoskeletons behind, including its last, all of which are potential fossils. Although moulted exoskeletons are more fragile, they are less likely to attract scavengers, which are capable of completely destroying carcasses. This, combined with their greater abundance would suggest that moults are generally better represented in the fossil record.

Distinguishing between preserved moults and preserved carcasses, particularly in dispersed exoskeletal elements, can be difficult. Shear *et al.* (1987) argue that the shrivelled nature of arthropod cuticles from Blenheim-Gilboa and Ludford Lane, and the occurrence of isolated body parts is an indication that they are primarily moults. Further evidence in support of this comes from the Rhynie chert. Here a trigonotarbid exoskeleton is reported from a stem, where it may have been sheltering for protection during ecdysis, and a podomere within the abdomen of a trigonotarbid clearly represents a moult (Shear and Selden, 2001). Further evidence for moulted exoskeletons is cited by Kjellesvig-Waering (1986) who describes the telescoping of posterior sclerites forwards, which would have occurred as the arthropod emerged from its cast moult.

In a very quiet, low-energy environmental setting such as the hot sinter deposits at Rhynie it might be expected that the majority of fossil material is composed of the moulted exoskeletons which collect at the bottom of the pool, as observed in experimental studies of rapidly moulting arthropods (Anderson and Trewin, 2003). However, in environments where a degree of transportation is envisaged, such as those seen at South Mountain, it is more likely that at least some articulated material represents mortalities since moulted exoskeletons disarticulate much more readily, particularly during transport (Brett and Alison, 1998). Nonetheless, there are undeniable examples of moulted exoskeletons from amongst the material recovered from South Mountain and elsewhere (*e.g.* telescoped scorpion mesosoma, figure 7.3E). Moults are almost certainly represented by the more disarticulated and fragmented material.

Many of the recovered fragments are flattened and folded, resulting from the compaction of the sediment onto pliable cuticles. However, some are twisted and folded to an extent that cannot be explained by compaction alone. Shear *et al.* (1987) suggested that these contorted fragments represent the rejectamenta of arachnid predators, discarded after crushing and digestion of soft tissues.

4.3.2 Distribution of cuticles within the host rock

To assess the distribution of arthropod cuticles within the host rock, an attempt was made to image digitally the organic remains *in situ*. Chemical analysis (see section 4.4) indicated that the organic cuticles had sufficient electron density contrast with the surrounding

sediment to be imaged using high-resolution computed tomography. However, in practice the cuticles proved to be too thin to be resolved vertically. Since they were less than one voxel (three-dimensional volume element) thick, data from the cuticle were averaged with data from the matrix causing the cuticles effectively to disappear in the image.

Even though the cuticle failed to be imaged *in situ*, certain inferences can be drawn from the relationship of cuticle type and abundance with bulk rock sample. Bulk rock samples were bagged together according to the horizon and location from which they were sampled. Therefore sample numbers from the same bag, and the corresponding extracted cuticles, were locally associated to within a few centimetres of each other and were deposited approximately contemporaneously. The range of preservational states and infrequency of articulated specimens seen in the recovered cuticles could indicate that the deposits, at least at South Mountain, have originated from the erosion of a stream bank which held a 'bank' or source of arthropod material in varying stages of decay. Periodic storm activity or flooding would have eroded material from here and deposited the cuticles at the foot of the delta foreset representing a combination of moulted exoskeletons and disarticulated carcasses in varying stages of decay. This may also account for the consistently small size of the recovered cuticles which have resulted from the hydraulic sorting of suspended particulates.

The articulation of delicate skeletal elements provides unambiguous evidence for episodic burial within the mudstones rather than long term condensations, which would be characterised by highly eroded material. The fossils occur in discrete, laterally discontinuous beds, examples of which were not observed to be repeated stratigraphically above or below within the available exposures suggesting that the episodic sedimentation that deposited the arthropod fossils occurred against a background of intermediate to rapid sedimentation.

The highly fragmented fraction of the cuticle residues could have resulted from the desiccation of moulted exoskeletons in the litter prior to burial, or may also have occured at some point during the maceration process. Maceration could cause fragmentation either by the physical agitation involved in the process, or in removing the support beneath cuticles that had already fragmented within the sediment through authigenic mineral growth. However, since there is a degree of association, and sometimes articulation, of components it can be hypothesised that at least some of the cuticles were transported as complete individuals and were disarticulated and locally scattered after deposition.

4.4   Composition of Devonian arthropod cuticle

The elemental composition of Devonian arthropod cuticle was investigated using an electron microprobe (see section 2.3.3 for sample preparation details). The electron microprobe provides quantitative data for a wide range of elements including those with

low atomic numbers such as carbon and nitrogen. It uses a well-collimated ion beam so that analysis of micrometer scale areas is possible (Shimizu, 1997) and was therefore ideally suited to the analysis of disseminated arthropod cuticle.

In thin section, cuticles preserved in shales from South Mountain were difficult to isolate because they were so thin and arranged parallel to the grain of the host rock. It was also impossible to tell whether they were plant or animal cuticles. However, arthropod cuticles preserved in the translucent Rhynie Chert are easily visible in thin section and therefore a sample of this was used as a proxy from which to extrapolate the results for the cuticles preserved in shales. Although the cuticle in the Rhynie Chert is taphonomically different to the South Mountain cuticle, it is of a similar age and was easier to handle.

4.4.1   Rhynie chert sample

The Rhynie chert sample contained a walking leg from a trigonotarbid (Dunlop *pers. comm.)* Initial analysis was attempted using only silver paint as a conductor. Notable differences in elemental composition were detected around the edge of the podomere but the beam was insufficiently stable. To stabilise the beam further a very thin coat of carbon was applied to the sample, which permitted a more detailed analysis. The electron beam could be focussed to about two microns, which was slightly larger than the cuticle at its thickest point, but a trace was produced for both the chert (silica blank) and the cuticle (leg), results of which are summarised in table 3.

Table 3 Quantitative elemental anlysis of a trigonotarbid walking leg (leg) in the Rhynie chert (silica blank), using an electron microprobe. Sample RORC.

		C	O	Si	S	Total
Leg	Measured	16.28	45.42	45.04	0.10	106.84
Silica blank	weight %	6.13	52.98	46.45	0.00	105.56
Leg	Normalised	15.24	42.51	42.16	0.10	100
Silica blank	weight %	5.81	50.19	44.00	0.00	100
Leg	Atomic %	23.37	48.93	27.65	0.06	100
Silica blank		9.32	60.47	30.20	0.00	100

Weight percentages in the Rhynie leg and matrix both total around 106%. Since the matrix is entirely silicate (see atomic percentages) the 6% carbon recorded from the matrix (silica blank) can be attributed to the carbon coating applied to the specimen. Therefore the microprobe analysis indicates the trigonotarbid leg is composed of about 10% carbon, the rest being made up of silica, oxygen and minor amounts of sulphur. Even after tightening the beam diameter to about two microns it was still larger than the thickness of exposed cuticle therefore there was significant contamination by surrounding chert and the results reflect this.

An elemental map of the trigonotarbid cuticle in chert is shown in figure 4.3. The most striking features of this map are the carbon enrichment on the perimeter of the podomere and the carbon shadow in the centre. To ensure that the carbon levels were not the result of remnant diamonds from the polishing procedure, beam fluorescence was checked. The bright fluorescence characteristic of diamonds was not detected, thus eliminating them as a potential source of carbon.
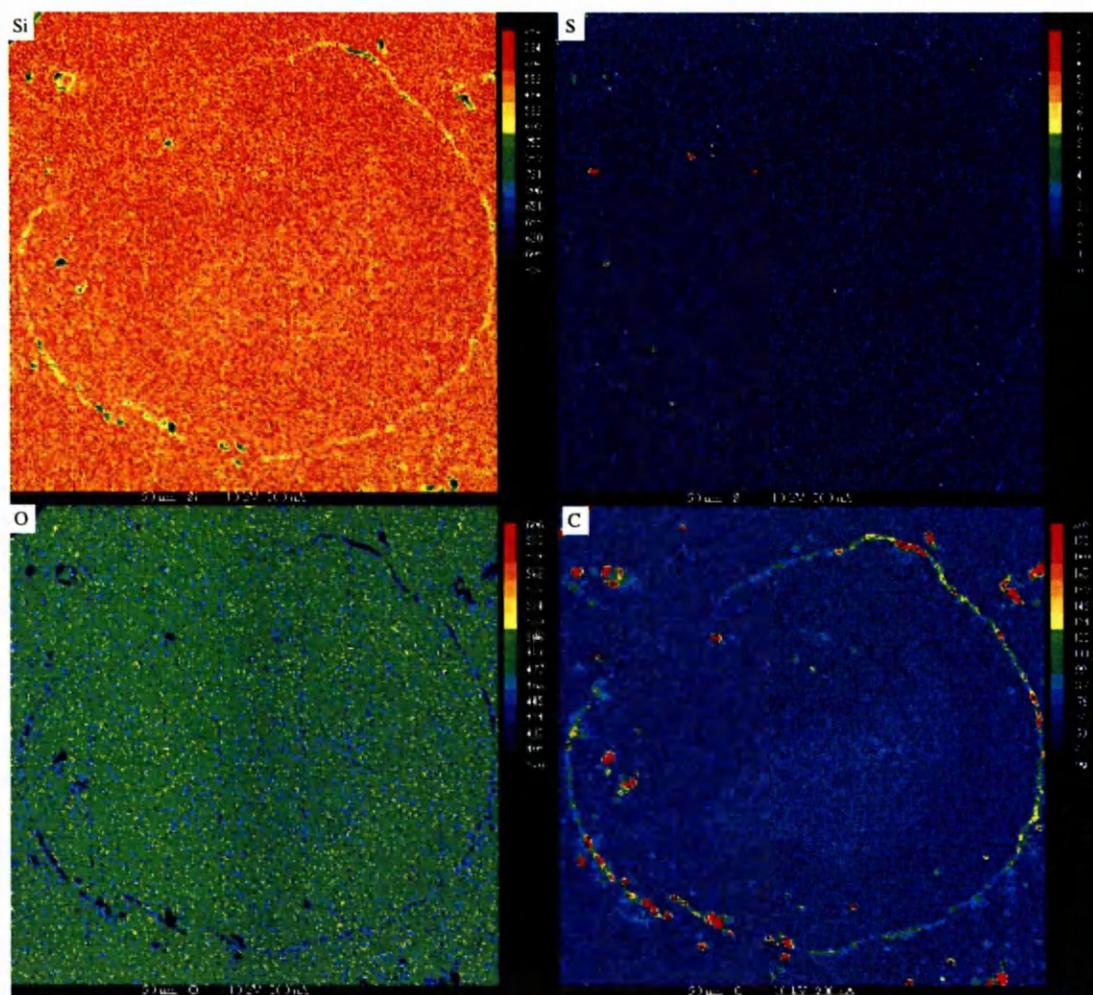
Figure 4.3 Elemental distribution maps of silica, sulphur, carbon and oxygen in the walking leg of a trigonotarbid in chert from Rhynie, Scotland. Scale bars indicate relative concentrations from high (red) to low (blue). Sample RORC.

When the elemental maps are compared to a transmitted light photograph of the same specimen the carbon shadow in the centre of the leg tallies with a brown pork-chop shaped area seen in thin section under transmitted light. Elemental and light photographs do not often match up exactly, which excludes the possibility that is in an artefact. The presence of carbon in the centre of the trigonotarbid leg probably represents the original soft-tissue.

4.4.2   South Mountain sample

Results from the electron microprobe analysis for organic cuticles in a shale sample from South Mountain are given in table 4. Since the cuticles were considerably harder to isolate in the shale than in the chert, an elemental distribution map was not produced.

Before normalisation, the weight percentages total between 94% and 97%. The remaining few percent probably constitutes elements from minerals within the sedimentary matrix. The principal difference between these cuticles and those from the Rhynie chert is that they constitute over 85% carbon and contain more sulpher, which can be attributed to the anoxic conditions in which the sediments were deposited. This would give a more than adequate density contrast with the matrix material to be imaged using high-resolution computed tomography. The differences in carbon content probably explain why maceration of the Rhynie chert fails to recover the same quality of cuticle as can be observed in thin section. Their structural integrity appears to be reliant on the surrounding chert matrix, which has flowed into and around the cuticle, whereas cuticles preserved in shale have only suffered from the compaction of grains onto their surfaces.

Table 4 Quantitative elemental anlysis of an organic cuticle bearing shale from South Mountain, New York State, using an electron microprobe. Sample SM1.206.

		C	O	Si	S	Total
Analysis # 1	**Measured weight %**	83.58	9.69	0.40	3.52	97.19
Analysis # 2		83.00	8.62	0.05	2.15	93.82
Analysis # 1	**Normalised weight %**	86.00	9.97	0.41	3.62	100
Analysis # 2		88.47	9.19	0.05	2.29	100
Analysis # 1	**Atomic %**	90.51	7.88	0.19	1.43	100
Analysis # 2		91.92	7.17	0.02	0.89	100

4.5 Summary

Arthropod cuticles must survive scavenging, bacterial breakdown and physical stresses if they are to become preserved in the fossil record. Decay and burial in anoxic rather than oxic, and terrestrial as opposed to marine conditions appear to enhance preservation, whilst the long-term preservation relies on diagenetic alteration to an aliphatic composition.

Arthropod fossils in shales from New York are preserved as carbonaceous cuticles representing moulted exoskeletons, carcasses and rejectamenta of predators. The range of preservational states observed at South Mountain suggests that the fossil deposit samples a cross section of arthropod detritus, which was eroded from the stream bank during periods of episodic sediment deposition.

CHAPTER 5   STRATIGRAPHY

This chapter describes sedimentary and palaeontological details for four exposures of Devonian mudstones and sandstones in New York State. Sediments were macerated from each site and examined for arthropod cuticle. For those sites that yielded very little fossil material a brief illustrated account is given here; the bulk of arthropod material, however, is discussed in chapters 6–9. The locations and names of exposures are shown in figures 2.2 and 2.3. For an overview of the geology of the Catskill region see section 1.1.

5.1   Regional stratigraphy

The sediments from south-central New York lie within the Catskill clastic wedge, on what was the north-east margin of the Appalachian basin (figure 1.1). The relatively small and scattered outcrop exposures in New York State make correlation within the non-marine strata of the Catskill clastic wedge difficult. Tracing of Formation boundaries is hampered by the regional structural dip, lateral changes of facies, a lack of marker horizons, and the absence of seismic profiles (Bridge, 2000). South Mountain lies approximately on the boundary between the Genesee and Hamilton Group sediments (figure 1.2). Further west these two groups are separated by the Tully Limestone, but in central New York this is absent and the Genesee and Hamilton Groups are conformable. Hueber and Banks (1979) dated sediments from South Mountain as Early Frasnian and from the Oneonta Formation (Genesee Group) equivalent to the Geneseo black shales of central New York. Regional stratigraphic charts show the Genesee Group as earliest Frasnian (Swezey, 2003), whilst palynological work by Beck (1998) on sediment samples from South Mountain, suggests a latest Givetian to early Frasnian age. Strata correlating with this age are probably lower Genesee Group as opposed to Hamilton Group (Sweezey, 2003).

5.2   South Mountain

South Mountain forest reserve is located just south of route 20 in Schoharie County, towards the border with Greene County (figure 2.3). To the south of the road lies a small, shallow shale quarry (SM-1), originally used for road surfacing but now under state preservation (figure 5.1). The site has long been known for its plant fossils (Hueber 1961, Banks *et al.*, 1985), and more recently its arthropod fossils (Kjellesvig-Waering, 1986; Selden and Shear, 1992; Shear and Selden, 1995; Wilson and Shear, 2000). A second quarry (SM-2) lies on the eastern side of South Mountain and is located just west of SM-1, at the

Figure 5.1 Photograph and sedimentary log of South Mountain Quarry, New York State, USA. Log corresponds to exposed sediments in photograph, for key see figure 5.3. Numbered sample locations are shown in bold on the left and correspond to samples indicated in figure 5.2. View north-east. Target in foreground is approximately one metre high.

junction of route 20 and Mount Pisgah road (figure 2.3). Permission for collecting was not granted for this site and so only a brief description is given here. Access to this site is currently being negotiated with the owner of the quarry (Landing, *pers. comm.*).

5.2.1   *Sedimentology*

Sedimentary logs for SM-1 and SM-2 are illustrated in figure 5.2. The sediments at SM-1 are characterised by thick sequences of red mudstones and sandstones with abundant root casts, green and red root-mottled sandstones and siltstones, grey shales and cross-bedded sandstones. Many of the sediments have been reworked by root penetration, which overprints the original fabric of the sediment when seen in thin section (figure 5.4). The sediments are quartz rich (70-80%), with varying amounts of organic matter. Quartz grains show undulose extinction (sourced from the Acadian mountains) and minor amounts of chlorite are present in some samples. Sedimentary grains are generally angular to subangular with low sphericity, suggesting that the sediments were deposited relatively close to their provenance. The sediments are moderately indurated, and sandstones exposed in the quarry dip gently towards the west. This pattern of alternating cross-bedded sandstones and

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South Mountain Quarry
SM-1

SOUTH MOUNTAIN FOREST
RESERVE

GR: 741610 422315

Sandy mudstone with
moldic plant debris

SMQ4

Mottled, purple sandy
mudstone with roots

SMQ3

6m

Trough cross
bedding in green-
grey sandstones

SMQ2

Brink Quarry
SM-2

Lens-shaped,
arthropod-rich
horizon with
abundant fine
plant material

SMQ1

4m

Red mudstone

Green medium-grained
sandstone with trough
cross bedding

Grey-green mudstone

Red sandy mudstone
with root traces below

SMQ5

Fine grained sand-
stone with planar
laminae

Fish bed conglomerate
with pebbles and wood
Debris flow with sand-
stone pebbles and wood
to 0.5m

Red-brown sandy
mudstone

2m

Gray-green, fine-grained
mudstone with rare
Archanadon, Eustheria
and fish plates

Red-brown medium-
grained sandstones.
Root churning overprints
original structures

mud

f. sand

m. sand

mud

f. sand

m. sand

Figure 5.2 Sedimentary logs for South Mountain quarry (SM-1) and Brink quarry (SM-2), on the Schoharie-Durham county border, New York State, USA. Oneonta Formation. Additional information provided by Ed Landing (NYSM). See figure 5.3 for key.
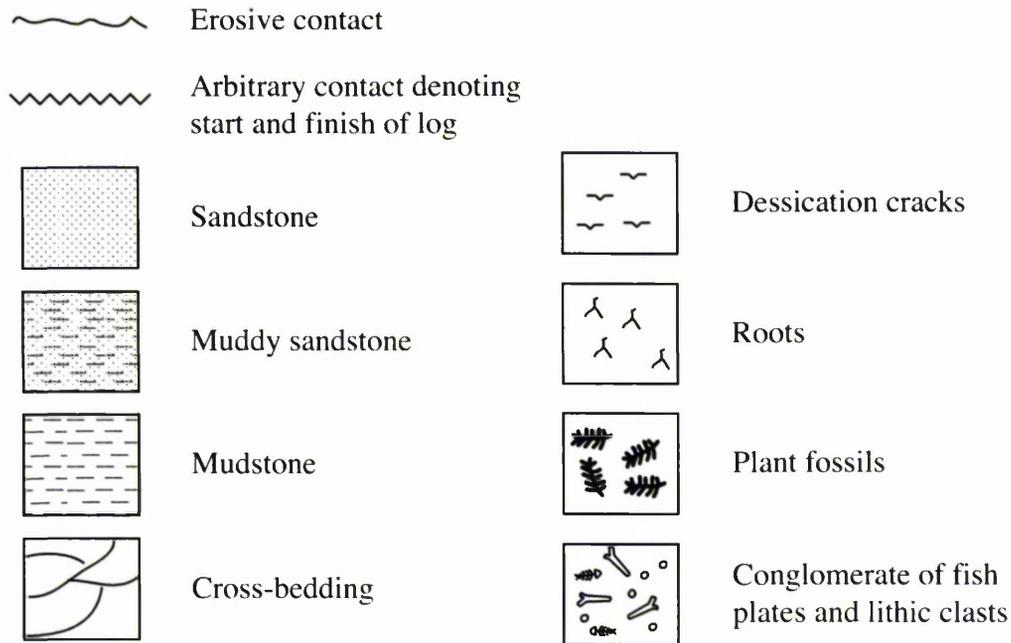
Figure 5.3 Key to sedimentary logs in figures 5.2, 5.12 and 5.15.

mudstones can be seen repeated in sediments exposed in a shallow stream channel all the way up South Mountain. On the eastern side of South Mountain is a thick (>10m) exposure of red sandstone containing abundant root traces and casts (figure 5.5). The roots appear as fibrous, bifurcating strands and range from several centimetres thick to only a few millimetres. They are predominantly horizontal, running across the surface of bedding planes and cutting relict ripples (figure 5.6). Vertical roots also occur, but with less frequency.

On the eastern side of South Mountain (SM-2) dispersed and disarticulated vertebrate remains occur in beds of well-indurated, fissile, grey shales. Stratigraphically above this, vertebrate remains are concentrated in a poorly sorted matrix of plant material and lithoclasts preserved at the base of a trough cross-bedded sandstone. In the field these coarse sediments are bordered by a large (0.5m) tree branch (figure 5.7). Samples from the bone bed seen in thin section contain abundant fish scales and dermal bone in a poorly sorted matrix of lithoclasts up to 2mm (figure 5.8). Towards the top of the quarry these sediments are capped by a red mudstone.
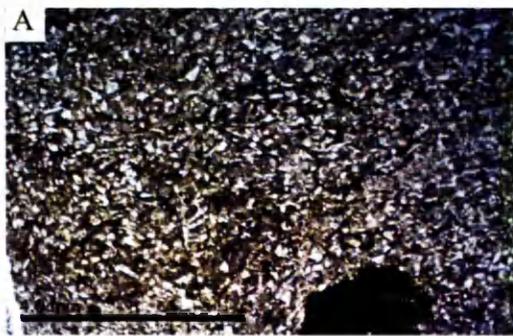
SMQ1

Grey to green, fine to medium grained, well sorted sandstone with disarticulated plant material. Sand sized grains up 0.3mm. Grains are angular to subangular with low sphericity and comprise of quartz (80%), clay sized material (some chlorite) and lithic fragments. Quartz grains show undulose extinction. Clay sized grains wrap around and are deformed by quartz grains. Very fine quartz veins with organic material adhering to margins. .
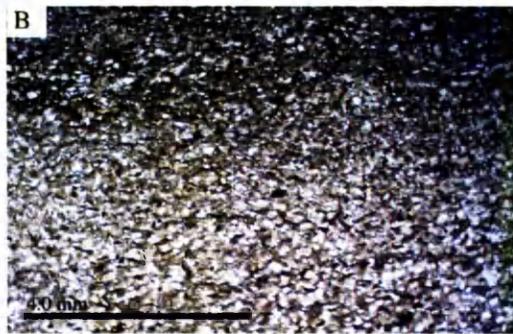
SMQ2

Grey to green, fine grained, massive sandstone. Grains angular to subangular with low spherecity. Larger quartz grains supported by matrix of silt and clay sized material. Section fines upwards into a sandy siltstone with increasing organic material
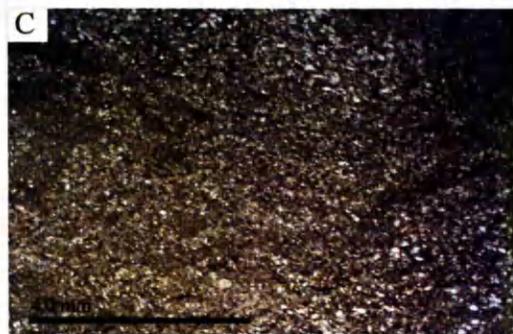
SMQ3

Green-grey to purple, mottled sandy siltstone. 40% quartz, subangular to subrounded grains with low sphericity. Fabric of sediment is disrupted by roots mixing silt and sand grade sediments.
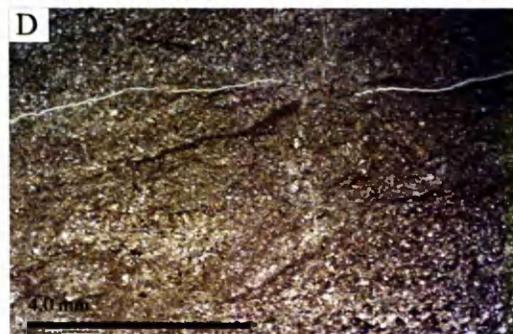
SMQ4

Green to grey blocky sandy siltstone, weathering to purple on exposed surfaces. Some associated fragmentary plant material. 30% quartz, subangular to subrounded grains with low sphericity. Root penetration has partially mixed silt and sand. Quartz veins run parallel to bedding, up to 30mm long
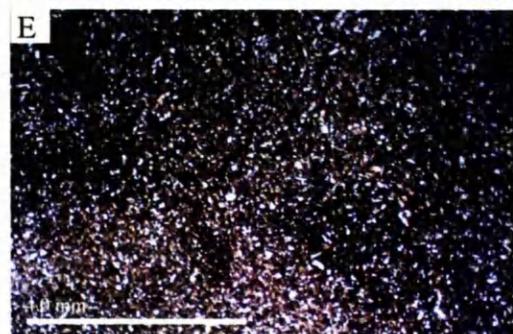
SMQ5

Purple, blocky sandstone with root casts. 80% quartz, grains subrounded to subangular. Distribution of organic material by roots varies through section producing mottled texture.

Figure 5.4. Thin sections and descriptions of sediments from South Mountain quarry (SM-1), Schoharie County, USA. See sedimentary log, figure 5.2, for exact horizons.

Figure 5.5 Abundant horizontal root traces of varying scales on a loose block of red sandstone from an exposure on the eastern flank of South Mountain, Schoharie County, New York State. Geological hammer measures approximately 0.3m long.

Figure 5.6 Horizontal root traces running across a loose block of red sandstone with asymmetrical ripples. From an exposure on the eastern flank of South Mountain, Schoharie County, New York State. Geological hammer is approximately 0.3m long.
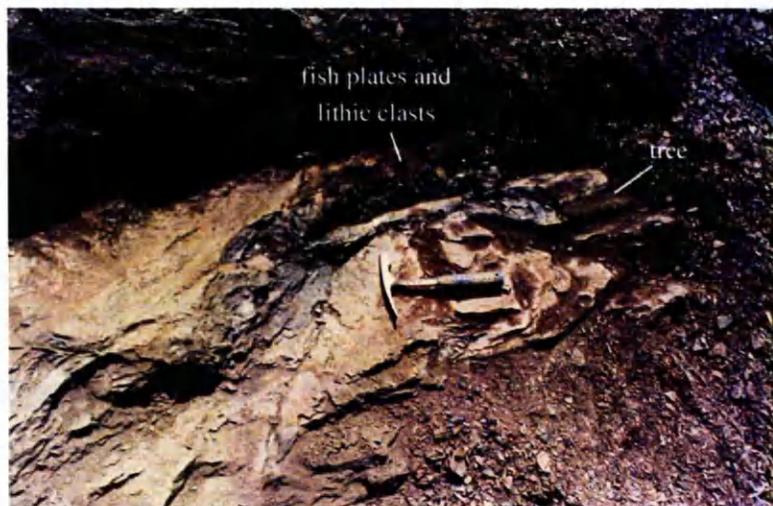
Figure 5.7 SM-2, Schoharie County, New York. Concentration of fish plates and lithic clasts behind a large branch or log. Gelogical hammer is approximately 0.3m long.

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Banks *et al.* (1985) described fossil plant remains from a 'country road metal quarry on N flank of South Mountain, 1.1 miles west of Schoharie–Greene county line on W. Durham to Conesville road'. They reported the presence of liverworts (*Pallaviciniites*), zosterophylls (*Sawdonia, Serrulacaulis*), lycopods (*Colpodexylon*), ferns (*Pseudosporochnus, Cladoxylon*), seed ferns (*Stenokoleos*) and progymnosperms ((*Archaeopteris, Callixylon* (form genus for wood from *Archaeopteris*), *Eospermatoperis*)).

Plant macrofossils are not abundant at South Mountain, although rare pieces of lycopod were noted in the field, and local collectors reported that they had removed specimens from the site. Fossil plant remains recovered from macerated sediments are illustrated in figure 5.8. The most common plant microfossils found in macerates from South Mountain are fibrous, fusiform sporangia, often with a longitudinal slit where dehiscence occurred (figure 5.8C). These are possibly from *Archaeopteris*, but also bear a strong resemblance to *Leclercqia* sporangia from Gilboa (Banks *et al.*, 1972). Cuticle fragments comparable to the liverwort *Pallaviciniites* (figure 5.8A, B) occur as fine sheets of parenchymous cells and bundles of tubular structures, which formed the rhizomatous portion of the plant (Hueber, 1961). Fragments of cuticle with of a number of circular holes, each containing a small central point of cuticle, are almost identical to an enigmatic cuticle figured in Gensel *et al.* (1990), from the Lower Devonian of New Brunswick. Edwards (1986) erected an artificial form genus for reticulate plant cuticle formed of polygonal units, which she named *Cosmochlaina*. Much of the fragmented plant cuticle from South Mountain could probably be placed within this genus.
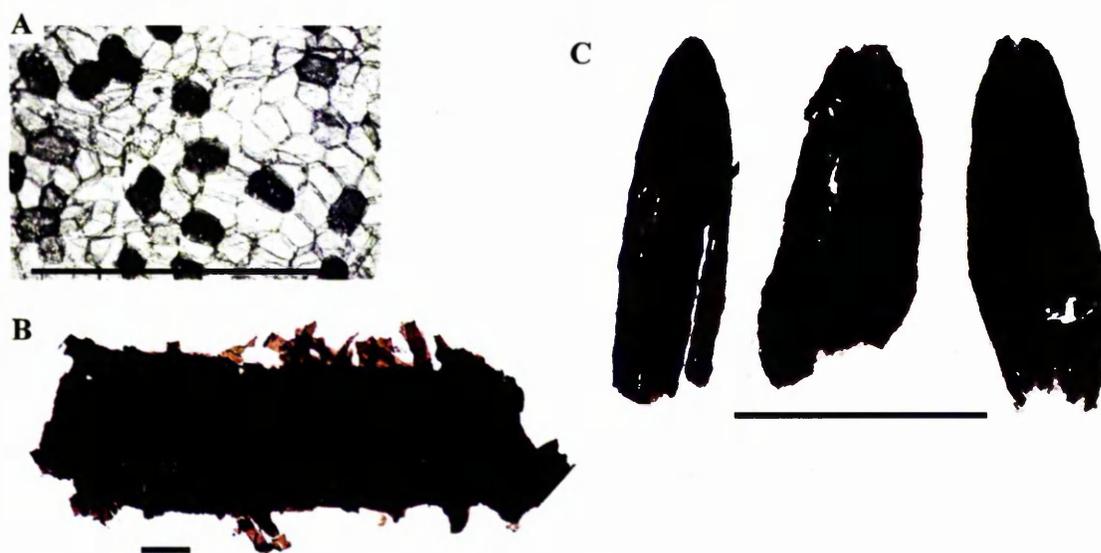
Figure 5.8 Examples of common plant fragments recovered from macerates of sediments from South Mountain and High Knob, New York. **A**, *Pallaviciniites*. Parenchyma cells. **B**, *Pallaviciniites*. Rhizomatous portion of plant formed by tubular structures. Scale bar represents 0.1mm. **C**, fibrous, fusiform sporangia, ?*Archaeopteris*. Scale bars represents 1mm.

Fossil arthropods at SM-1 are preserved in lenses of dark grey, fine-grained mudstone at the foot of sandy foresets. These include arthropleurids, centipedes, scorpions, spiders, trigonotarbids and possibly hexapods, and are described fully in chapters 6–9. The clam *Archanadon catskillensis* (figure 5.9) was observed in close proximity, slightly lower than the arthropod bearing horizon, and the conchostracan *Euestheria* was observed in sediments from SM-2 (Landing *pers. comm.*). Ostracodes were not observed at South Mountain, despite their relative abundance elsewhere in the region (*pers. obs.*).

The concentration of vertebrate material seen in SM-2 consists largely of placoderm plates with a tuberculate texture (see chapter 10). Fish scales and dermal bone are evident in thin section. Many of the fish scales exhibit a bulging base of acellular bone with a crown of layered dentine and are interpreted as acanthodian fish scales (figure 5.10A, D, E). Larger vertebrate fragments consist of dermal bone plates attributed to placoderms (figure 5.10A, B, C, E). Some of the tubercles appear to be made of semidentine, which is a characteristic feature of arthrodires (Burrow and Turner, 1999).

Figure 5.9 Large clam, *Archanadon catskillensis* from South Mountain quarry, Schoharie County, New York. Camera lens cap measures 60mm.
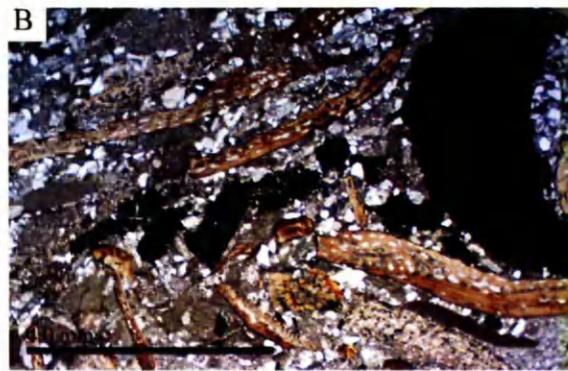
SMB2.3   **SMB2.3**
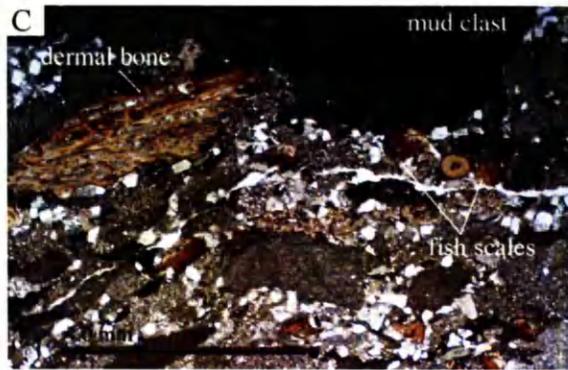
SMB2.2   **SMB2.1**

SMB2.1

Figure 5.10 Thin sections from fish bearing strata of Brink quarry (SM-2). Sections show acanthodian fish scales and placoderm (?arthrodire) dermal bone. See sedimentary log for exact horizon. **A**, placoderm (?arthrodire) dermal bone in centre with tubercles composed of semidentine. Acanthodian fish scales below. **B**, large mud clast in upper right. Elongate dermal bone in centre. **C**, lithic clasts, fish scales and dermal bone. **D**, fish scales including acanthodian scales. **E**, dermal bone in matrix of lithic clasts and quartz grains.

5.2.4   Depositional environment

Sediments at South Mountain are dominated by thick sequences of red, root-churned mudstones and sandstones, cross-bedded sandstones, and grey mudstones. Plant fossils are relatively common and there is an aquatic fauna of clams and conchostracans. Terrestrial arthropod fossils are preserved amongst fragmented plant material in organic-rich lenses, and vertebrate fossils occur in a poorly sorted bed of fish plates and lithic clasts at the base of a cross-bedded sandstone.

These sediments are interpreted as alluvial floodplain deposits, with larger sand bodies representing fluvial channels. The concentration of poorly sorted vertebrate material indicates periodic flooding of the channels, and at SM-2 it appears to have collected behind a large branch as part of a logjam. Red, oxidised, root-churned sandstones and mudstones are interpreted as palaoesols formed on a predominantly well-drained alluvial plain. Localised lenses of grey fissile mudstones represent relatively rapid deposition in abandoned channels and lakes on the floodplain, or at the foot of sandy foresets.

Root traces reveal an autochthonous community of plants inhabiting the riverbanks. The fossil evidence shows that the community would have been structurally diverse, ranging from small herbaceous plants and bushy shrubs through to large trees. *Archaeopteris* appears to have grown on well-drained sites adjacent to rivers where they formed dense gallery forests (Meyer-Berthaud *et al.*, 2000; Fairon-Demeret *et al.*, 2001), and eventually on drier parts of the floodplain (Driese *et al.*, 1997). *Archaeopteris* would have afforded dense shade by the efficient arrangement of leaves to trap all available sunlight (Fairon-Demaret *et al.*, 2001).

Archanadon catskillensis and *Euestheria* are traditionally considered to indicate freshwater conditions (Vanuxem, 1842). However, Knox and Gordon (1999) argued that a brackish-water environment should be re-examined for *Archanadon*. In the Catskill magnafacies of New York and Pennsylvania *Archanadon* has only been reported from deposits very near to the palaeoshoreline and is also seen to be associated with a brackish ostracod fauna. No ostracods were observed at South Mountain, although they were relatively abundant at other sites within the Catskills.

The palaeoenvironment at South Mountain is therefore interpreted as a freshwater to brackish fluvial system, close to the palaeoshoreline. Repeated stacks of red and grey mudstones and cross-bedded sandstones represent fluvial channel deposits flowing over a well-drained floodplain with an autochthonous community of trees and shrubs.

5.3 *High Knob*

High Knob quarry is situated approximately 3km north along Shale Pit Road in Schoharie County (see figure 2.3 for exact location). It is a low-relief shale quarry once employed for road surfacing and now apparently disused (figure 5.11). High Knob quarry lies within the New York State Forest Reserve.

5.3.1 *Sedimentology*

A sedimentary log for High Knob is illustrated in figure 5.12. The overall lithology is similar to that at South Mountain and consists largely of purple and grey mudstones, and lenses of dark organic-rich mudstone overlain by a thicker sequence of cross-bedded sandstones. Sediments from above and below the arthropod-bearing horizon are generally much finer grained than those at South Mountain, with a lower quartz content and enrichment of organic matter. They are frequently root-mottled and show bleached areas where post depositional reduction of sediments has occurred around decaying organic material (figure 5.13B). Mudstones show fine, parallel laminae (figure 5.13A, D) and two scales of sediment mixing (figure 5.13E).

High Knob quarry lies approximately 5km to the northwest of South Mountain at approximately the same altitude (about 700m above sea-level). Since no major faults are known to run through the area, the regional dip is relatively low and to the east, and the overall lithologies are similar, the sediments at High Knob are assumed to lie within the same Oneonta Formation. No palynological work has been conducted on these sediments to confirm this.

Figure 5.11 High Knob Quarry (HK3.2) view north. Shale pit road, Schoharie county, New York State, USA. Log corresponds to exposed sediments in the photograph, arthropod-rich horizon is indicated with an arrow. See figure 5.3 for key.

HIGH KNOB FOREST RESERVE

High Knob Quarry
HK3.2

GR: 741906 422607

8m

Feldspathic sandstone with trough cross bedding and rare sandstone pebbles

Green root-churned sandstone overlain by fine-grained red sandstone

Purple-red sandstone with thin muddy layers. Reduction mottling

6m

Red sandstone with low angle cross sets. Changes laterally to root churned sandstone in west end of quarry

Cobble sized clasts up to 50mm

Pink-grey laminated mudstone cut by cross-bedded sandstone

4m

HKQ5

Dark grey, fissile mudstone with abundant pyritised plant material up to 0.8m. Arthropods.

HKQ4

Green sandstone overlying red sandstone with roots

HKQ3

Sample Nos.

HKQ2

Purple silty sandstone with reduction mottling and horizontal roots

2m

HKQ1

No exposure

Fine grained red sandstone with reduction mottling and dessication cracks

mud
f. sand
m. sand
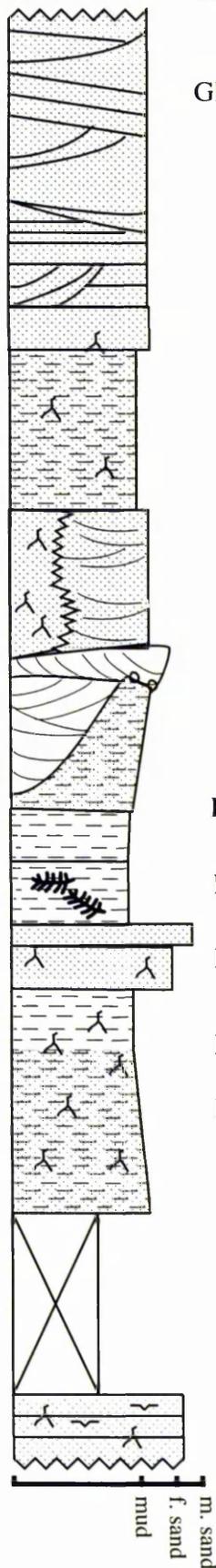
Figure 5.12 Sedimentary log of High Knob quarry (HK3.2) in Schoharie County, New York State, USA. ?Oneonta Formation. Additional information provided by Ed Landing (NYSM). See figure 5.3 for key.
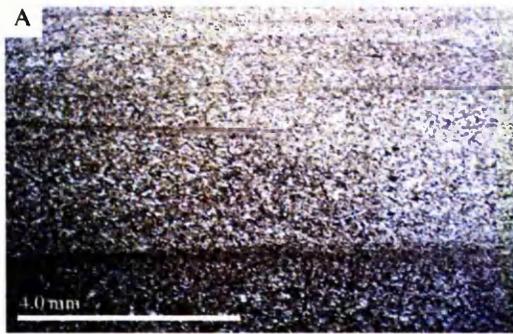
HKQ1

Purple and grey-green mottled sandy siltstone. Well sorted with millimetre scale laminae (0.2mm) of silt sized material. 80% quartz, grains subangular to subrounded. 5-10% organic material.
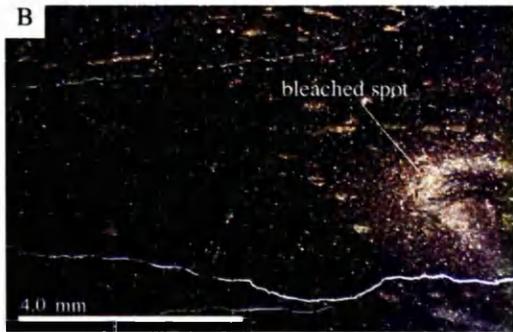
HKQ2

Purple to grey fissile mudstone. Enriched in organic content, low quartz (5%). Bleached spot towards right of image caused by post-depositional reduction of sediments around organic material, probably a root.
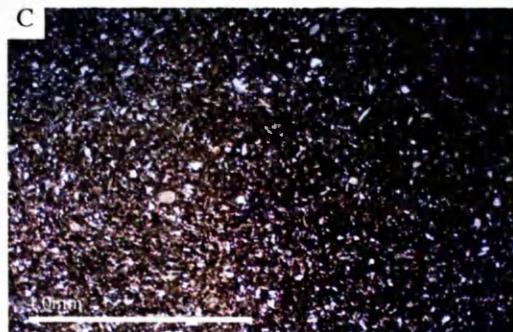
HKQ3

Purple to grey massive blocky, sandy mudstone. 60% quartz, grains subangular to subrounded, up to 0.2mm. Root churned, moderately sorted.
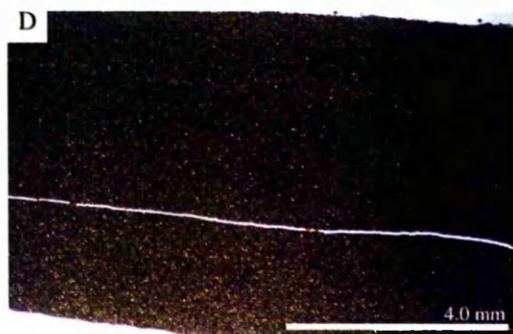
HKQ4

Dark grey well sorted mudstone weathering to orange and yellow. Fine parallel laminae in hand specimen.
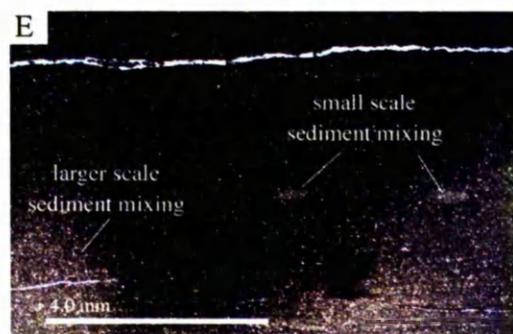
HKQ5

Purple to grey mudstone. Enriched in organic content, low quartz (5%). Two scales of bioturbation— millimetre scale and submillimetre scale.

Figure 5.13 Thin sections from High Knob quarry, Schoharie county, New York. See sedimentary log for exact horizons.

5.3.2 Fossil flora of High Knob

On the floor of the quarry at High Knob is a several tens of millimetres thick lens of densely packed plant fossils. The plants are much larger and more complete than those at South Mountain, and consist of layers of stems and branches ranging from less than 10mm to more than 50mm wide. Pyrite permineralisation has preserved much of the plant material and the compressed stems still retain a degree of three-dimensionality so that vascular tissue can be observed. Identifiable fragments include lycopods (figure 5.14G), and the larger stems and branches can be attributed to *Archaeopteris*. A nearly metre-long branch was uncovered here and taken back to the New York State Museum (figure 5.14H). The smaller stems can be roughly divided into two groups. Stems up to 10mm wide show a monopodial growth habit with smaller lateral branches and scalariform thickenings on the main axis (figure 5.14F). These are attributed to trimerophytes, which typically possess either completely fertile or completely sterile lateral branches (Taylor and Taylor, 1993).

Smaller, dichotomously branching stems up to 5mm wide are also present. The overlapping nature of the plants makes it difficult to follow axes and lateral stems to their ends without further preparation. Lateral stems appear to dichotomise repeatedly and terminate in curved tips. These specimens are interpreted as zosterophylls. Several complete sporangia were uncovered (figure 5.14A, B, C). The sporangia occur singly as elongate, slightly rectangular structures measuring up to 10mm long. They are frequently curved into a kidney-shape and appear to be borne terminally, although there are no clear examples showing the mode of attachment to the stem.

5.3.3 Fossil fauna of High Knob

Ostracods and specimens of *Euestheria* (Landing *pers. comm.*) were the only conspicuous macrofauna observed at High Knob. However, maceration of the plant rich mudstones resulted in the recovery of well-preserved arthropod material including probable trigonotarbids and scorpions. These are illustrated and described in chapter 7.
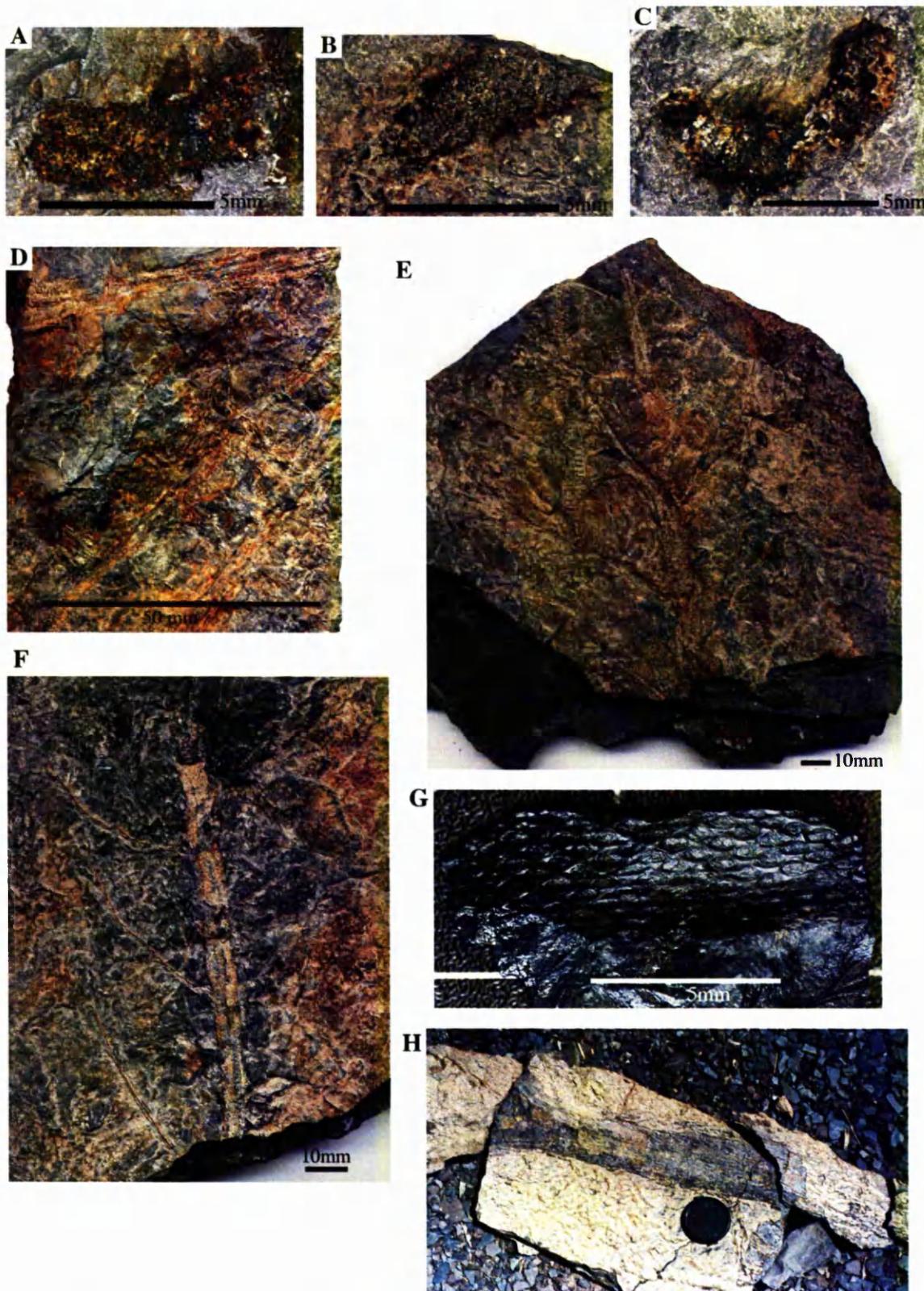
Figure 5.14 Plant macrofossils from High Knob quarry, Schoharie County, New York State. **A**, **B**, and **C**, kidney-shaped sporangia. **D**, typical texture of randomly oriented, layered plant material. **E**, complete specimen showing central stema and lateral branches. **F**, trimerophyte with scalariform tracheids on central stem. **G**, lycopod stem showing spirally arranged leaf bases. **H**, large branch of ?*Archaeopteris*, camera lens cap is 60mm.

5.3.4   Depositional environment

High Knob quarry is dominated by red, root-churned sandstones and mudstones with desiccation cracks, and cross-bedded sandstones. Pyrite permineralised plant fossils are common and there is an aquatic fauna of ostracods and conchostracans. Terrestrial arthropod fossils are preserved amongst the plant stems and no vertebrate fossils were observed.

These sediments are interpreted as alluvial plain deposits with laterally discontinuous sand bodies eroding downwards into more mud-rich sediments. The presence of desiccation cracks indicates aerial exposure of the sediments, and periodic drying. The contiguous nature of channel sands and red, root filled sediments indicates that there was an autochthonous community of plants, probably living alongside river channels. The thick layers of plant material may have resulted from periodic heavy flow or floods that flattened the plants living along the stream banks; however, the mix of different plant fossils and the absence of any kind of alignment does not support this. An alternative explanation is that the plants were eroded from the riverbank and transported a short distance before sudden deposition, possibly during a flood phase. *Archaeopteris* is generally considered to have had a deciduous habit and dropped whole branches rather than individual leaves, which were attached directly to the branches in *Archaeopteris* rather than by a stem as in true leaves. This deciduous habit may have been an adaptation to combat water stress, and would have resulted in a thick layer of litter accumulating during the dry season (Scheckler, 1978). Pyrite permineralisation is common amongst Devonian plant fossils and is characteristic of those in a marine setting swept into a basin by rivers.

The palaeoenvironment at High Knob is therefore interpreted as a brackish to marine fluvial floodplain with an autochthonous community of vegetation dominated by *Archaeopteris*, growing along the banks of rivers. Well-drained, terrestrial palaeosols are indicated by the presence of roots and desiccation cracks, and the red, oxidised nature of the sediments.

5.4   Dutton Ridge

Samples from Dutton Ridge were collected by Linda Hernick and Sharon Mannolini (NYSM) during summer 2002 and sent to Manchester for analysis. The Dutton Ridge samples came from a quarry off Anderson road in Dutton Ridge State Forest near the town of Broome in Schoharie County (figure 2.3). No photograph is available for Dutton Ridge, and its precise stratigraphic location is unknown.

Sedimentary details are illustrated in figure 5.15. The sediments comprise grey and red sandstones with sparse root casts, grey, bedded sandstones and massive grey root churned mudstones. Sediments generally fine upwards, and towards the top of the section there are small lenticular sands within a brown-grey siltstone.

Plant-rich sediments at Dutton Ridge are pyritised. They overlie a thinly bedded red sandstone with sparse root casts, and underlie a dark grey bedded sandstone. Macerated samples from the plant rich horizon did produce some fragmented arthropod cuticle, most of which is illustrated in figure 5.16. The vast majority of cuticle pieces exhibit a characteristic lunate cuticle sculpture and are interpreted as eurypterid cuticle. Only specimens DR2, DR4b and DR4c (figure 5.16N, O, P) do not fit with this identification and may represent different arthropod taxa.

The overall picture at Dutton Ridge is of a marine transgression, with sediments ranging from red terrestrial palaeosols to siltstones with brachiopods at the top suggesting fully marine conditions. The dominance of an aquatic fauna at Dutton Ridge contrasts with those observed at South Mountain and High Knob. The coarser sediments at Dutton Ridge may mean that currents were flowing too quickly for the deposition of fragile terrestrial arthropod material, which settled out in finer sediments deposited under quieter conditions, or that they were deposited farther inland where there was less vegetation and hence fewer arthropods.

No exposure

6m

Brown-grey siltstone
with lenticular sand
bodies. Fine bedding,
rare branches, spiriferids
and *Leio*

Massive, grey, root-churned
siltstone

4m

Dark grey sandstone
with cm scale bedding

Dark grey, coarse to
medium grained
sandstone. Bedding 5–10cm.

2m

Abundant, partially pyritised
plants and some arthopod
material, mostly eurypterid

Red, finely bedded medium
to fine grained sandstone
with sparse root casts

mud

f. sand

m. sand

Figure 5.15. Sedimentary log for Dutton Ridge State Forest Quarry, redrawn from an original sketch by Ed Landing, NYSM. See figure 5.3 for sedimentary log.
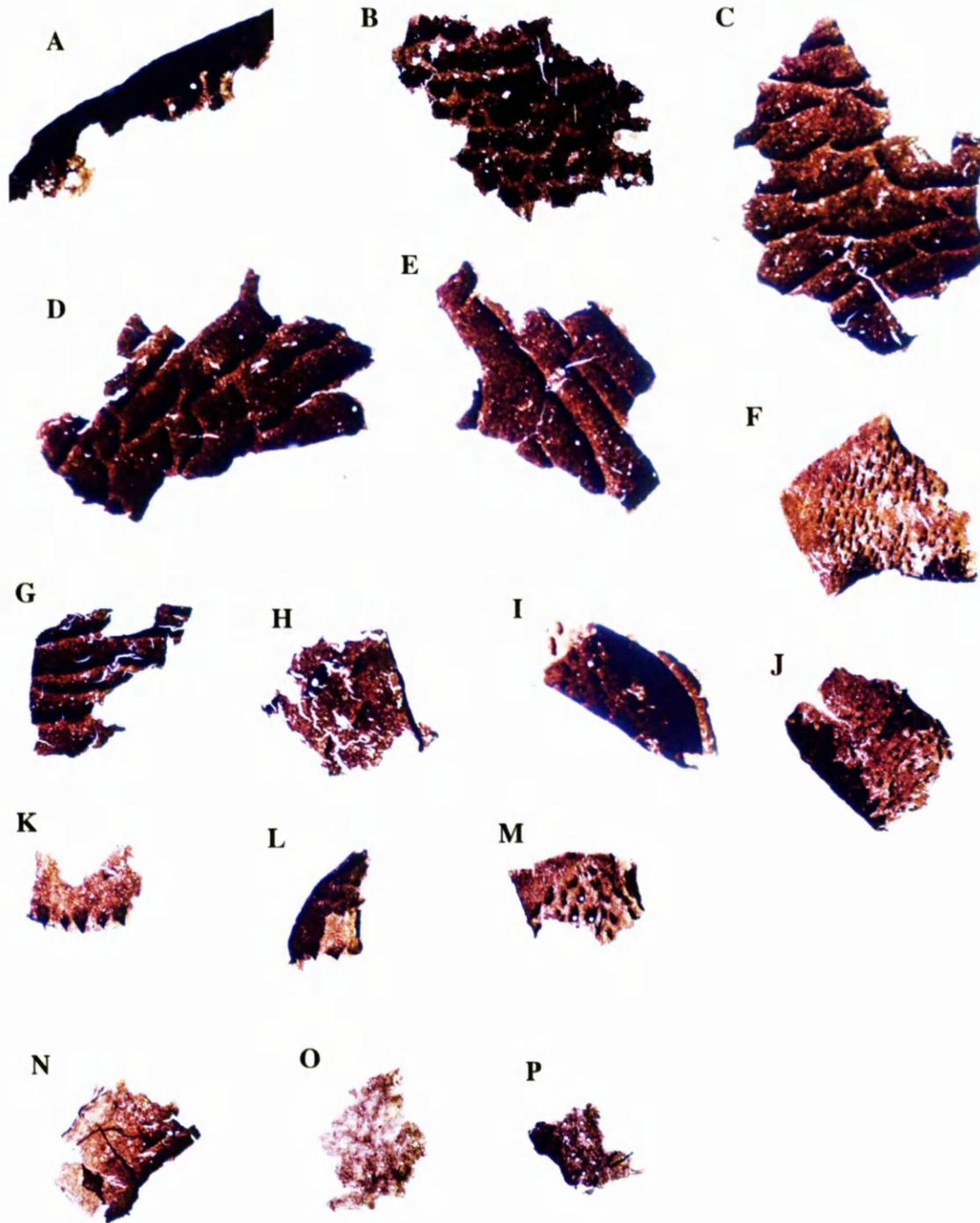
Figure 5.16 Arthropod cuticle from Dutton Ridge. **A**, DR4d. **B**, DR6. **C**, DR3. **D**, DR7. **E**, DR4. **F**, DR10. **G**, DR6c. **H**, DR4a. **I**, DR8. **J**, DR6d. **K**, DR10a. **L**, DR6b. **M**, DR6a. **N**, DR2. **O**, DR4b. **P**, DR4c. A–M are identified as eurypterid cuticle. N, O and P are unidentified but probably represent a different arthropod. Magnification x100

5.5   Other sites

Further samples were collected from a number of other plant-bearing exposures across New York State and macerated for potential arthropod material. Unfortunately, most of the sediment samples were coarser than those from South Mountain and High Knob, and this may have contributed to the dearth of useful material recovered.

Sediments from Cairo quarry (off route 145, 7.2km from East Durham) were collected from immediately below a weathered bone bed from which a small shark tooth was recovered. Maceration of these sediments repeatedly failed to produce any recognisable arthropod material. A few cuticle fragments perforated with circular holes were recovered and are illustrated in figure 5.17. Although the holes in the cuticle fragments could potentially represent setal sockets, their density and size variation is less suggestive of arthropod cuticle and they are interpreted as plant cuticles. Sediments from Cairo quarry were particularly difficult to macerate (quartz rich?) and took weeks and even months to digest.

Sediments from Kropp Road in Albany county (figure 2.3) contained finely disseminated pieces of coalified plant material and not much else. The sediments were too coarse to preserve fine detail and caused cuticles to fragment into very small, unidentifiable pieces. Similarly, samples from Hilltop Road quarry near the town of Waterlo in Albany County and Haverly Hollow Road quarry, east of Middleburgh on the Schoharie-Albany county border, also failed to produce any significant plant or arthropod material after maceration.
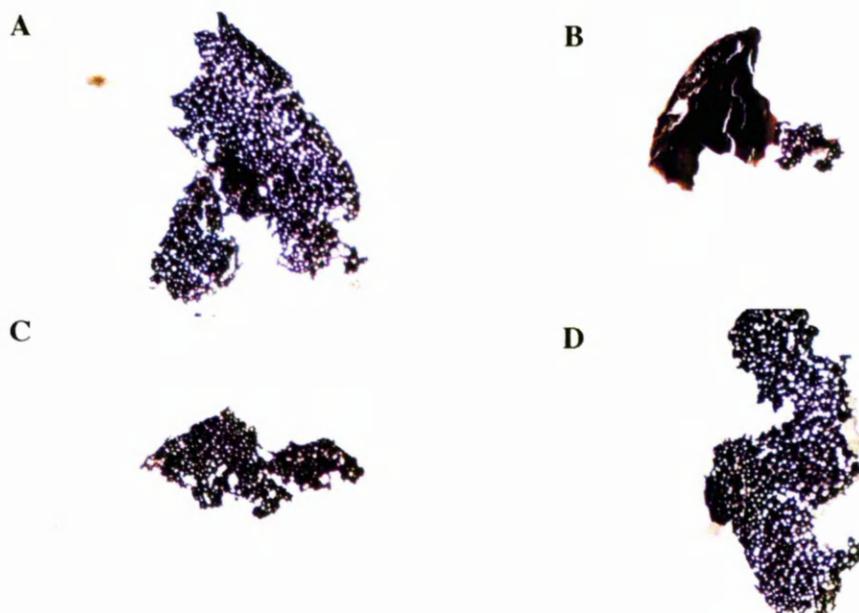
Figure 5.17 Scraps of cuticle from Cairo quarry, Albany County, USA. **A**, CB2. **B**, CB2b. **C**, CB2d. **D**, CB2c. Magnification x100

5.6 Summary

Evidence combined from sedimentological, palaeontological and palaeomagnetic data indicate that the Catskill delta region was situated within a palaeolatitude of 5–20° during the Middle and Late Devonian (Woodrow *et al.*, 1973; Woodrow, 1985), whilst palaeomagnetic data obtained directly from Catskill sediments in New York State suggest a palaeolatitude of only 1° (Kent and Opdyke, 1978). The climate was tropical and rainfall was seasonal. The Catskill alluvial systems were dominated by low-gradient, high-sinuosity, meandering rivers close to the coast, and wider (up to hundreds of metres), deeper, higher gradient channels carrying coarser sediment further inland. Muddy floodplain areas were more extensive near the coast such that the proportion of channel deposits increased up-valley (Bridge, 2000).

Sediments exposed in south-central New York and described above, consist largely of red and green-grey root-churned palaeosols, mudstones, and sandstone channel deposits. The lateral discontinuity of channel deposits could suggest that the rivers were meandering or part of a braided system, and the rapid deposition of large plant fragments and vertebrate material suggests periodic flooding. Large expanses of red palaeosols are suggestive of well-drained floodplains with an autochthonous community of vegetation. The development of large root systems was coincident with an increase in plant stature and permitted anchorage to the soil substrate, nutrient and water uptake, and facilitated soil gas exchange (Driese *et al.* 1997). The large systems of bifurcating roots seen at South Mountain are not associated with any other plant remains, but may represent the roots of *Archaeopteris*, which appears to have been a dominant arborescent floral element of the Catskill delta (Banks *et al.*, 1985). Driese *et al.* (1997) described root and stump casts of early trees preserved in Middle and Late Devonian sediments in Pennsylvania and New York. They described horizontal, strap-like roots, 50–20mm wide, associated with stumps with distinctly flared bases, which they interpreted as probably representing *Eospermatoperis*. Vertical root casts measuring 100–150mm in diameter and up to 1.5m long, were associated with weakly flared to corm shaped stumps and interpreted as *Archaeopteris*. The roots at South Mountain measure between 5 and 30mm wide and are predominantly horizontal, occurring on bedding planes and cutting across relict ripple structures in the sediment. They bifurcate and can be seen extending for several metres. Using the descriptions and interpretations given by Driese *et al.* (1997) these would be interpreted as the root systems of ?*Eospermatoperis*. However, the roots at South Mountian are not very strap-like, and specimens of *Eospermatoperis* described by Driese *et al.* were associated with gleyed soils and a high water table, whereas those at South Mountain clearly lived in a well-drained soil. Casts of *Eoaspermatoperis* are known to occur in the Upper Manorkill Formation near Gilboa (Driese *et al.*, 1997; Goldring, 1927), however it is

possible that the roots observed at South Mountain are not *in situ* and instead represent the washed out roots of *Archaeopteris*. Reduction mottling of sediments occurs at both South Mountain and High Knob and, although no root casts are preserved, is evidence of vertical root penetration. Vertical penetration of roots up to 20mm in diameter was described by Elick *et al.* (1998) from the Lower Devonian Battery Point Formation in Gaspé, Canada and attributed to plants similar in morphology and stature to the lycopsid *Drepanophycus* and the trimerophytes *Pertica* and *Psilophyton*.

The overall environment was one of relatively continuous sedimentation on an alluvial plain with fluvial channels and dense gallery forests. Thick layers of litter, (produced by *Archaeopteris* in particular) would have provided moist, sheltered microhabitats that were ideal for the emergence and protection of early terrestrial animal life. Periodically this litter of plant stems and arthropods was eroded from the riverbanks and deposited downstream in abandoned channels and lakes. Both South Mountain and High Knob are interpreted as brackish water environments, possibly with more marine influence at High Knob as indicated by the permineralised plant stems. In selecting future sites for early terrestrial arthropod material, lenses of fine-grained, organic rich mudstones associated with red beds and root traces around the margin of the Appalachian basin should prove to be rewarding.

CHAPTER 6   EOARTHROPLEURA

Cuticle fragments forming distinct plates and bearing double spines surrounding small setal sockets form the largest fraction of any cuticle type recovered from South Mountain. Many of these distinctive plates are identical in morphology and cuticle pattern to specimens from South Mountain that were originally described as scorpions (Kjellesvig-Waering, 1986) and later as the arthropleurid *Eoarthropleura hueberi* (Shear and Selden, 1995).

The Arthropleuridea *sensu* Shear (1997) comprises of three monogeneric orders spanning from the late Silurian to the early Permian—Arthropleurida, Eoarthropleurida and Microdecemplicida. The giant Arthropleurida ranged from the Viséan through to the early Permian of Europe and North America and consisted of a single genus, *Arthropleura.* The remaining orders, Eoarthropleurida and Microdecemplicida were considerably smaller and ranged from the Pridolí through to the Frasnian and also had a Euramerican distribution. Eoarthropleurida contains a single family and genus, *Eoarthropleura,* which has been described from the Upper Silurian and Lower–Middle Devonian of Germany, Shropshire, New York State and New Brunswick (Størmer, 1970; Shear and Selden, 1995; Shear *et al.*, 1996). A single family and genus, *Microdecemplex,* similarly represent the arthropleurid order Microdecemplicida. The single known species was described from Blenheim-Gilboa and South Mountain in New York State (Wilson and Shear, 1999) and is the only microarthropleurid for which details of the cephalic region are known. Kraus and Brauckmann (2003) argued that small millipedes from the Order Pselaphognatha are living relatives of Arthropleurida, and that Microdecemplicida differs from Arthropleurida and Eoarthropleurida sufficiently to render the monophyly of Arthropleuridea unjustified. They recommended that Arthropleuridea should therefore be dissolved into the Penicillata ((Arthropleurida (Eoarthropleuridae + Arthropleuridae) + Pselaphognatha)) and a possible separate unit formed by Microdecemplicida and Chilognatha.

Three species of *Eoarthropleura* are currently recognised—*Eoarthropleura devonica* from Alken-an-der-Mosel and sites in eastern Canada, *E. ludfordensis* from Ludford Lane, and *E. hueberi* from New York State. Differences between the three species are not great, and a general paucity of material and differing preservational contexts makes direct comparison of specimens difficult. Current knowledge of the three species is summarised in table 5.

Table 5 Comparison of common eoarthropleurid plates from three descriped species

		Eoarthropleura devonica	*Eoarthropleura ludfordensis*	*Eoarthropleura hueberi*
Dorsal morphology	**Cuticle type**	Unknown. Preserved as impression and compression fossils within the sediment	Irregular rows of small, jagged tubercles superimposed on a polygonal pattern	'W' shaped ornamentation consisting of small setal sockets flanked on either side by two tubercles
	Tergites	Rectangular outline with slightly prolonged posterolateral corners	Unknown	No true tergites known
	Paratergal lobes	Curved anterolateral corner. Flat rim bordering anterior and lateral margins	Unknown	'Type 3' Roughly rectangular with curved anterolateral corner. Concentric sculpture line. Double-lamellate
Ventral morphology	**Sternite**	(Cordate plate-labrum) Symmetrical, rounded plate with gently bilobed posterior margin. Transverse terrace lines	Unknown	'Type 1'- sternite Symmetrical, rounded plate with gently bilobed posterior margin. Transverse terrace lines
	Subquadratic plate	(Sternite) Anterior margin bilobed with a median notch. Posterior rim narrowing anteriorly	Unknown	Unknown
	K plate	Four marginal setae—two posterior and two lateral. Concentric terrace lines	Two posterior marginal setae.	'Type 2' Four marginal setae—two posterior and two lateral. Concentric terrace lines
	B plate	Straight medial border, rounded distal margin with broad lateral rim	Unknown	'Type 4' Straight medial border, curved posterior border with characteristic flange
	Appendages	Two, maybe three, poorly preserved podomeres with rectangular to subquadratic outline	Unknown	Rectangular podomeres with crenulated posterior margin and large setal sockets bearing stout spines
	Age	Emsian	Pridoli	Givetian–Frasnian
	Reference	Størmer, 1976	Selden and Shear, 1995	Shear and Selden, 1995 Kjellesvig-Waering, 1986

The most diagnostic feature of the arthropleurid group is the ventral plate complex, which differs from genus to genus (Shear and Selden, 1995). Within *Eoarthropleura* the rosette plate is absent from the ventral plate complex and only sterna, K and B plates are found. Dorsally each tergite has a trilobate structure consisting of an axial portion delineated from the lateral paratergal folds by a distinct suture (Shear and Selden, 1995). The total number of trunk segments is unknown, although Størmer (1970) reconstructed *E. devonica* with thirteen trunk tergites and a telson. From slight variations in the width of tergites, Wilson (1999) concluded that the trunk narrowed both anteriorly and posteriorly. Morphology of the head and mouthparts are largely unknown.

Eoarthropleura is the only fossil at South Mountain to be identified from both cuticle compression and body fossils and a full description and discussion of the material is provided below. Since there has historically been some ambiguity over the correct identification of the various associated sclerites, the type numbers used by Shear and Selden (1995) are continued here in order to prevent confusion and to facilitate discussion and interpretation. Previous nomenclature and interpretation of *Eoarthropleura* sclerites are summarised in table 6.

Table 6 Comparison of nomenclature used in the description of *Eoarthropleura*. Names in bold are referred to in the text.

Shear and Selden (1995)	Størmer (1976)	Kjellesvig-Waering (1986)	Wilson (1999)
Type 1 Sternite	Cordate plate Labrum	Rounded scorpion gill	?Pleurite
Type 2 K plate	K plate. Cover for gills or ventral sac	Irregular scorpion gill	B plate
Type 3 Paratergum	Paratergum	Scorpion abdominal plates	Paratergum
Type 4 B plate	B plate. Cover for basal part of appendage	Irregular scorpion gill	?K plate
Tergite	Subquadratic plate Sternite	Not described	Sternite
Type 6 Labrum?	Not described	Not described	Labrum?

6.1   Cuticle topography

One of the most characteristic features of this cuticle type is the presence of setal sockets, which are flanked on either side by two slightly curved triangular projections, forming a 'W' type ornamentation. This pattern is clearly visible in both transmitted light images and electron micrographs of the cuticle. Figure 6.1 shows electron micrographs of this pattern at different scales. In between this ornamentation, and on sclerites where this ornament is absent, the cuticle has a granular texture consisting of numerous minute denticles. These two cuticle patterns may occur independently of each other or concurrently on the same sclerite. They are clearly related since plates bearing both cuticle patterns are found in direct association.

A second characteristic feature of this cuticle type is the presence of dark terrace lines. These appear as thickened, sclerotised lines in the cuticle, producing distinctive patterns on many of the individual sclerites. Patterns of terrace lines associated with particular plates are discussed in the relevant sections below.

6.2   Cuticle morphology

Most of the cuticle fragments bearing this pattern can be identified as one of a number of distinctively shaped plates, descriptions of which are given below. Although much of this cuticle type is set with a dense pattern of setal sockets, very few setae are preserved, suggesting that the setae were either very small and / or fragile in life, or detached from the cuticle during moulting. Short, stout setae gently curving towards a sharp point are occasionally preserved, housed in conspicuous marginal sockets. Other plates are found with small spines (no associated sockets) flattened onto their cuticle surface during burial and compaction. No other sensory organs are known to be associated with this cuticle type.

6.3   Dorsal morphology

True tergites have been described from specimens of *Eoarthropleura devonica* but are unknown from other species of *Eoarthropleura*. Only the paratergal lobes have been described from South Mountain, reinforcing their demarcation from the central axis. The most complete dorsal morphology from amongst the 'microarthropleurids' is seen in specimens of *Microdecemplex rolfei*, which bears ten tergites with undifferentiated paratergal folds.
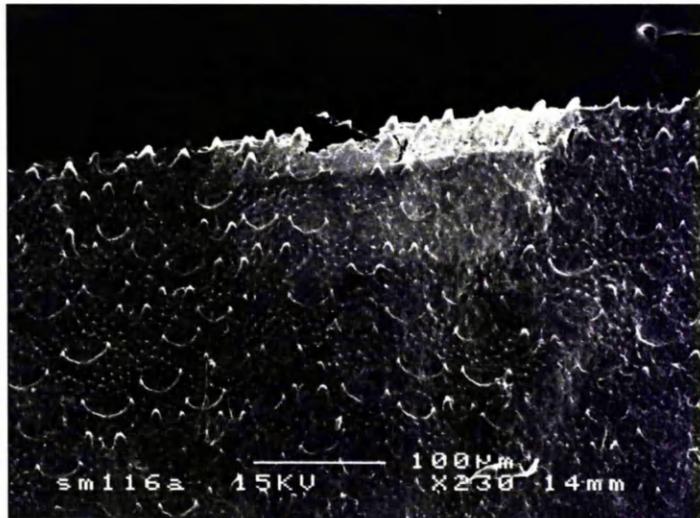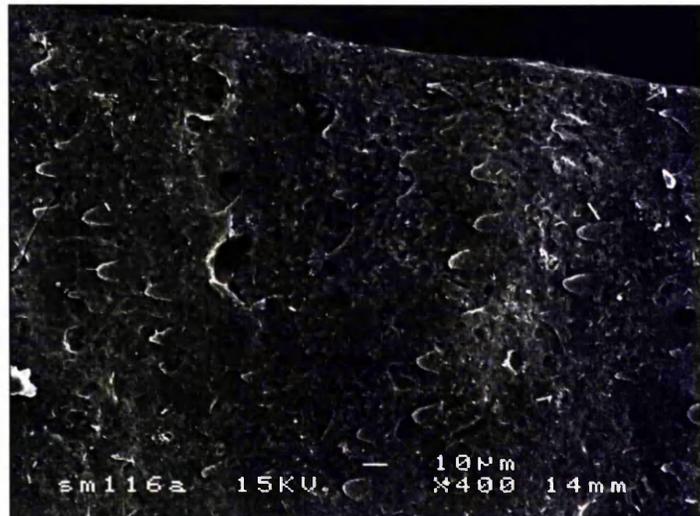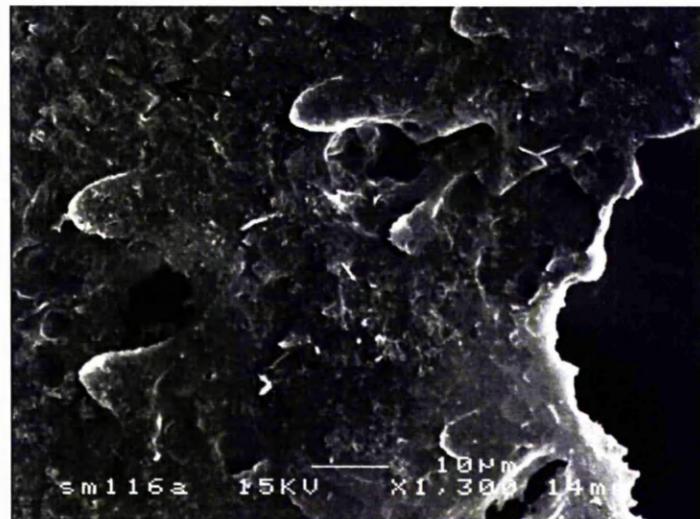
Figure 6.1 Scanning electron micrographs of large opaque fragments of *Eoarthropleura* cuticle from South Mountain, New York State. **A**, characteristic 'W' shaped ornamentation formed by double peaks with minute denticles between, x230. **B**, larger scale ornamention with setal sockets flanked by double spine, x400. **C**, Detail of double spine and setal socket. Note small dents caused by compression of sedimentary grains onto the cuticle surface marked by an arrow, x1,300.

6.3.1 Tergites

A featureless piece of cuticle attached to a paratergal lobe in specimen SM1.115.V31 (figures 6.2 and 6.3C) probably represents part of a true tergite. Two other possibilities for tergites are specimens SM1.115.V10 (figure 6.2E) and SM1.130.8a (figure 6.4A). This latter specimen appears similar to some of the paraterga but has no rounded corners and no marginal zone of ornamentation, hence its interpretation as a tergite. The cuticle has a wrinkled surface, which could be the result of flattening an originally convex structure, or could indicate that this specimen represents a moult.

Specimen SM1.115.V10 also has two straight margins angled at ninety degrees to one another, but differs in that it is entirely covered with the 'W' shaped ornamentation and (assuming the spines are oriented approximately posteriorly) has a crenulated posterior margin. The cuticle is a single layer and is the only specimen of its kind known from South Mountain.

6.3.2 Type 3 plates

Type 3 plates are square to rectangular shaped with a broadly rounded anterolateral corner, interpreted by Størmer (1970), Shear and Selden (1995) and Wilson (1999) as parterga (synonyms are paratergal lobes or paratergal folds). The most complete plate is 1.3mm wide and 1.1mm long. Previously described type 3 plates from South Mountain measure 2–2.5mm wide and are approximately square (Shear and Selden, 1995). A keel runs parallel to the anterior and lateral margins of the plates, gradually narrowing and disappearing just before reaching the posterior border. The double nature of the cuticle suggests that these are true paraterga *i.e.* outgrowths from the tergites, and not tergal plates (Shear and Selden, 1995).

Paraterga are preserved at South Mountain as both impression and compression fossils (figures 6.2–6.5). All specimens of paraterga exhibit ornamentation of the narrow zone of cuticle formed between the keel and the anterior and lateral margins (figures 6.2 and 6.3 C, D, F; figure 6.4 B, C, D). Whilst the interior of the paraterga generally has a granular texture, the characteristic 'W' shaped ornamentation found on other parts of *Eoarthropleura* is restricted the lateral and anterior margins. Specimen SM1.115.V12 (figure 6.4 C, D) clearly illustrates the two layers of cuticle seen in the paraterga. In this specimen the marginal ornamentation is restricted to only a single (dorsal?) layer of cuticle and does not occur on the ?ventral surface. Some of the paraterga also bear small marginal spines associated with the ornamented cuticle zone (SM1.115.V38 and SM1.115.V45, figure 6.2 D, F). The spines have a rounded base and gently curve towards a sharp tip. They are not associated with conspicuous setal sockets and are therefore interpreted as spines rather than articulated setae. A single spine figured by Shear and Selden (1995; their figure 7h) is very similar

to the spine seen on specimen SM1.115.V38 (figure 6.2F) and may have a similar origin. However, it is considerably larger than other observed spines and measures 2.16mm long. This could indicate the presence of much larger paraterga at South Mountain that are going unnoticed because they fragment into smaller, unidentifiable pieces. None of the paraterga previously described from South Mountain and Alken-an-der-Mosel, and attributed to *Eoarthropleura,* are associated with spines or setae of any sort. This apparent absence of paratergal spines may simply reflect the relatively small number of specimens examined, and the fact that there is no conspicuous socket to mark the site of attachment when the spine is absent. *Microdecemplex,* on the other hand, has two obvious setal sockets set just in from, and slightly anterior to, the posterolateral corner. However, these setae are striated and moveable, the cuticle of the paratergum is smooth, and the paratergal folds are not clearly demarcated from the central axis and do not readily detach as they do in *Eoarthropleura.*

Paratergal folds described from Alken-an-der-Mosel are almost identical to those seen at South Mountain but are considerably larger. The paraterga of *Eoarthropleura devonica* measure 9–11mm in length and 6.5–8.5mm in width, whereas those from South Mountain, assigned to *E. hueberi,* measure 2–2.5mm and are approximately square. The smallest specimen from Alken-an-der-Mosel is 5.8mm long and 4.3mm wide, which Størmer (1970) attributed to a juvenile. The width of the paratergal folds varies with the position on the body, resulting in a slight narrowing of the body both anteriorly and posteriorly (Wilson, 1999) and explains the variation in shapes observed in the plates from South Mountain. The marginal ornamentation seen on the paraterga from South Mountain is not referred to in Størmer's description of *E. devonica,* which he states has smooth paraterga, but is clearly evident in the compression fossil in figure 6.5. Since both are preserved in the same context, it could be argued that these represent real differences between the specimens.

Collum segments were reported from specimens of *Eoarthropleura* with a small, raised anterior rim and lateral embayments, similar to those in *Arthropleura* and *Microdecemplex* (Wison, 1999). Differences occur in the intersection of the posterior of the lateral embayments with the margin of the collum segment, occuring posteriorly in *Eoarthropleura* and anteriorly in *Arthropleura* and *Microdecemplex.* Collum segments are currently unknown from South Mountain.

Figure 6.2 *Eoarthropleura* par27terga and ?tergites. **A**, SM1.115.V38.a **B**, SM1.115.46. **C**, SM1.115.V31. **D**, SM1.115.V45. **E**, SM1.115.V10. **F**, SM1.115.V38. Note spines on lateral margins of D and F. See text for explanation. Magnification x50.

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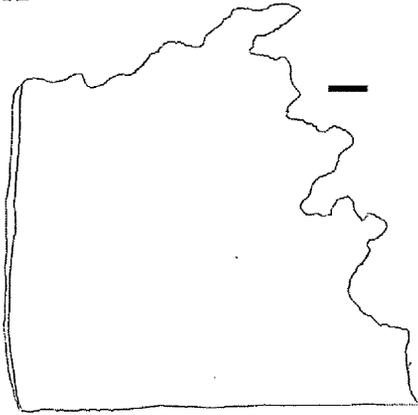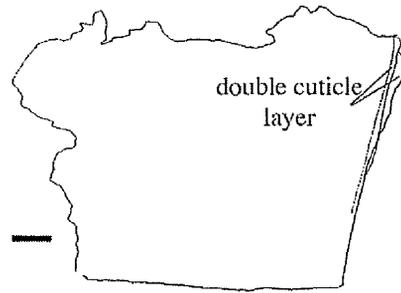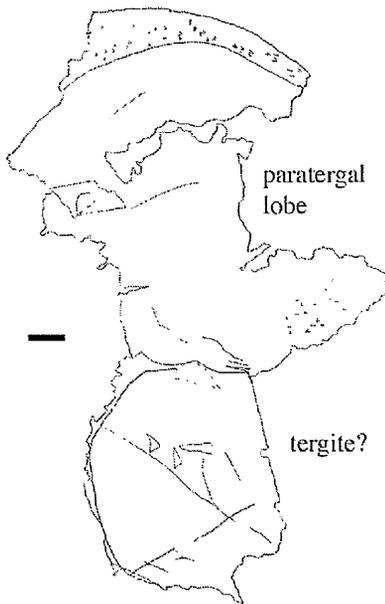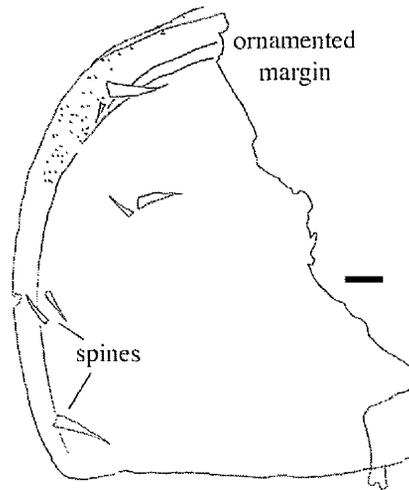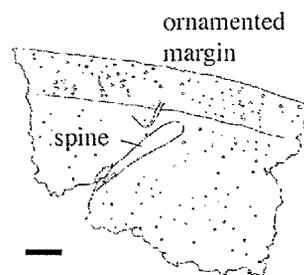
Figure 6.3 Interpretative drawings to accompany figure 6.2. *Eoarthropleura* paratergal lobes. **A**, SM1.115.V38a. **B**, SM1.115.46. **C**, SM1.115.V31. **D**, SM1.115.V45. **E**, SM1.115.V10. **F**, SM1.115.V38. Scale bars represent 0.1mm.
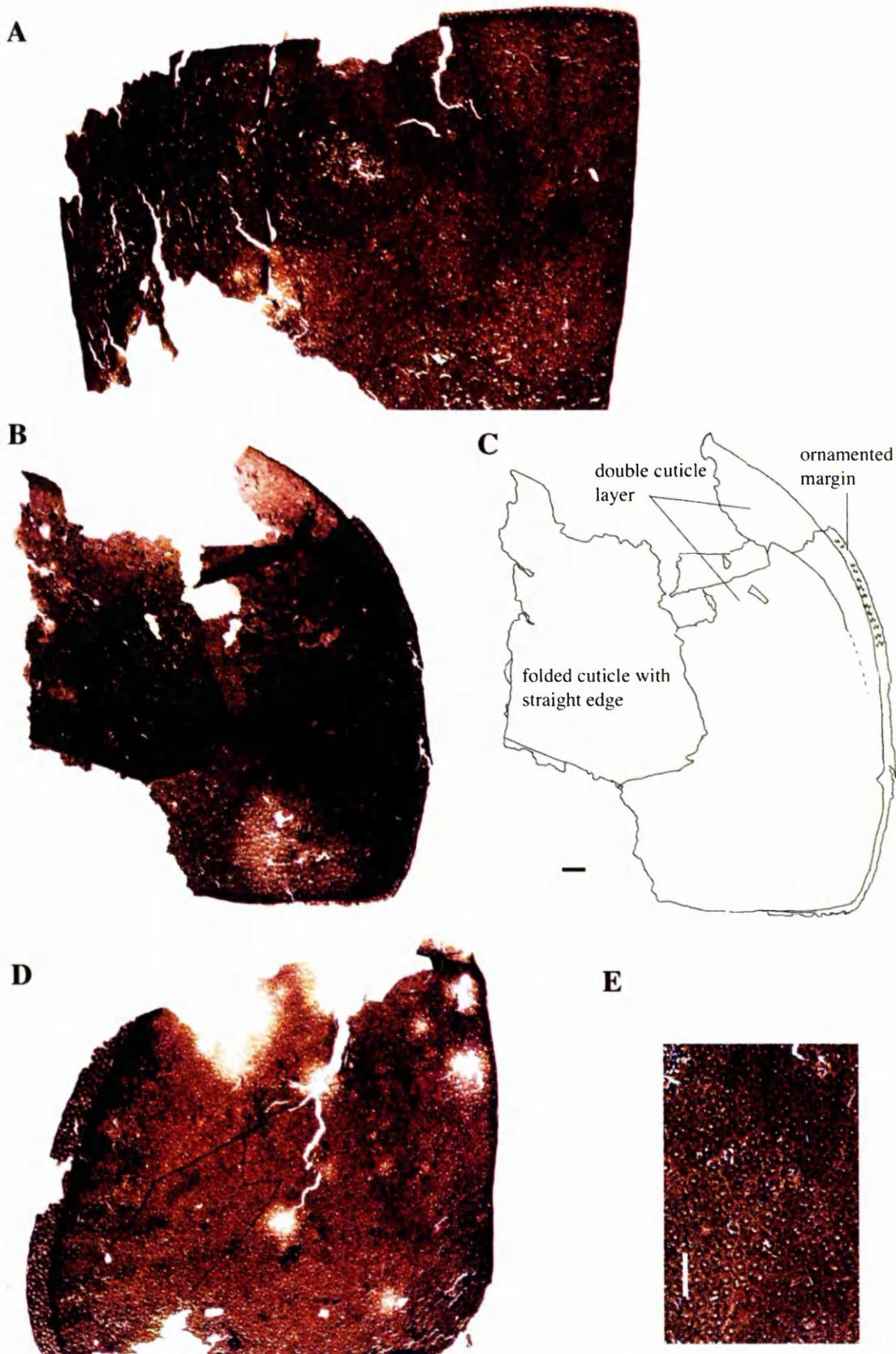
Figure 6.4 *Eoarthropleura* paraterga and ?tergite. **A**, possible tergite, SM1.130.8a. **B**, paratergal lobe showing double layer of cuticle and marginal ornamentation of dorsal surface, SM1.115.V12. **C**, interpretive drawing to accompany B, SM1.115.V12. **D**, paratergal lobe, SM1.130.8b. **E**, detail of tuberculate cucticle - SM1.130.8a. Magnification x37.5, scale bars represents 0.1mm.
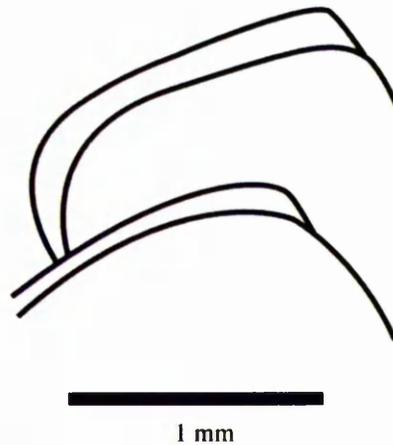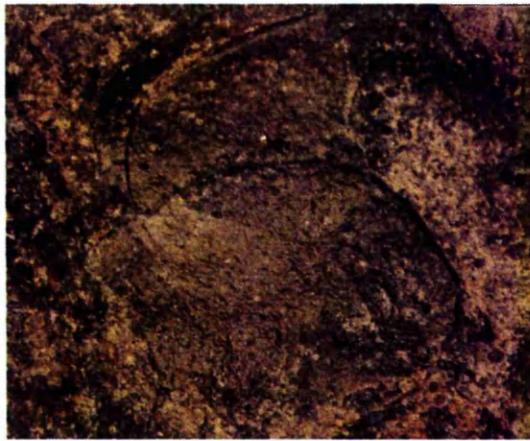
Figure 6.5 Impression fossil of *Eoarthropleura* from South Mountain, New York State. Two overlapping left paratergal folds. Scale bar represents 1mm.

6.3.3 Cephalon

Specimens SM1.122.7 and SM1.133.1 (figure 6.9A, K) may represent plates from the cephalic region of *Eoarthropleura*. The cuticle piece forms a broadly suboval shape with a curved posterior border and a notched anterior edge. There is a double layer of cuticle and the notch is formed by two triangular outgrowths of cuticle surrounding two smaller and more pointed projections (absent in SM1.133.1). Shear and Selden (1995; figures 6a and 8k) described a similar piece of cuticle from South Mountain, which they called a type 6 plate. This piece is also elliptical with a curved posterior margin and a deeply indented anterior edge. It appears to have a single rounded process in the middle of the indentation, but a second process could be obscured behind another layer of cuticle covering the right hand side of the plate. All Diplopoda have a median notch in the anterior margin of the labrum, which may contain a median tooth, sometimes with additional teeth on either side. The labrum of *Microdecemplex* bears three teeth in the labral notch (Wilson and Shear, 1999).

A third cuticle piece from South Mountain (SM1.119.46, figure 6.9B) may also belong to the head region of *Eoarthropleura*. The cuticle is crumpled and torn, but two pieces can be made out with a broadly rounded outline unlike any of the other described fragments from South Mountain. On the left hand side of the fragment the cuticle is very thin and pale and this is overlapped by a darker cuticle fragment, the rounded margin of which has been pinched out into a subtriangular process with the apex missing. Clearly further material is required before any firm conclusions can be drawn, but this cuticle piece could be analogous to the flared lateral processes observed in *Microdecemplex*. Both of the type 6 plates described above have an extra layer of cuticle folded over on one of the side suggesting a wider lateral extension of this plate.

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6.4   Ventral morphology

The ventral morphology of *Eoarthropleura* is somewhat better understood, largely due to the higher number of serially homologous plates that occur in the ventral plate complex and which are consequently more frequently recovered. The rosette plate is absent from the ventral plate complex (present in *Arthropleura*) and only sterna, K and B plates are found. The precise arrangement of these sclerites, however, is unclear due to the scarcity of articulated material.

6.4.1   Type 1 plates

Symmetrical suboval plates with a raised sculpture running subparallel to the lateral and anterior margins occur frequently in macerates from South Mountain (figures 6.6 and 6.7). One margin is always torn, frequently into a roughly bilobate shape, and is assumed to occur anteriorly where the cuticle merges into the body wall (Shear and Selden, 1995). The posterior margin may also be gently bilobate. The morphology of the plates is variable and they can be broadly subdivided into two morphotypes (figure 6.8). Type A plates have a gently bilobed posterior margin and curved terrace lines that flex and gradually shallow towards the anterior (figures 6.6 and 6.7 C, ,E; Shear and Selden's figure 7 a, b, c, e). The terrace lines begin approximately one third of the way up the plate, leaving a small posteriormost section that is scattered with setal sockets and double spines. Type A plates are generally wider then they are long. In contrast type B plates are generally longer than they are wide and have much straighter posterior and lateral margins that describe an almost octagonal outline. The terrace lines run parallel to the lateral margins, but begin further forward on the plate, occurring only in the anterior half of the plate, and gently flex posteriorly in the centre (figure 6.6, A, B, D; Shear and Selden's figure 7d).

The symmetry of the plates suggests that they occupy a medial position on the animal and the range in sizes suggests that they represent several forms of the same structure (Shear and Selden, 1995). Identical plates with the same pattern of terrace lines were described from Alken-an-der-Mosel as cordate plates by Størmer (1976) who interpreted them as labra. The identity of sternites, on the other hand, was assigned to subquadratric plates as yet unknown from South Mountain. This discrepancy was addressed by Wilson (1999) who suggested that these type 1 plates might represent pleurae, based on the observed medial position of ventrally situated subquadratic plates in compression fossils of *Eoarthropleura* from Gaspé. However, these specimens were poorly preserved and in the light of a complete absence of any such structure at South Mountain, and the presence of well-preserved articulated ventral material the interpretation of type 1 plates as sternites seems most likely. See section 6.5 for discussion.
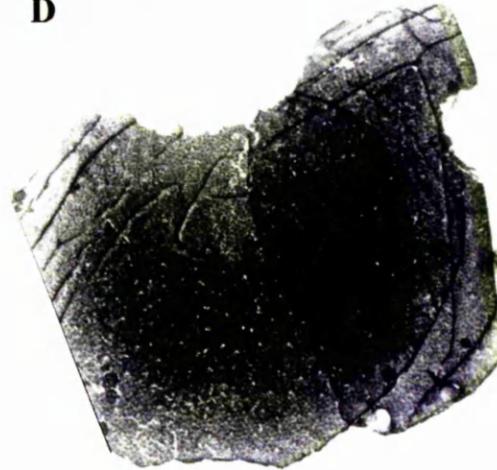
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Figure 6.6 *Eoarthropleura* cuticle fragments from the ventral plate complex. **A**, sternite - SM1.213.2a. **B**, sternite - SM1.119.32. **C**, sternite - SM1.213.13. **D**, sternite and K plate in connection - SM1.112.6. **E**, sternite, K plates and B plate - SM1.213.2. **F**, sternite and K plate - SM1.213.3. All speciments orientated with anterior to top. Magnification x50.
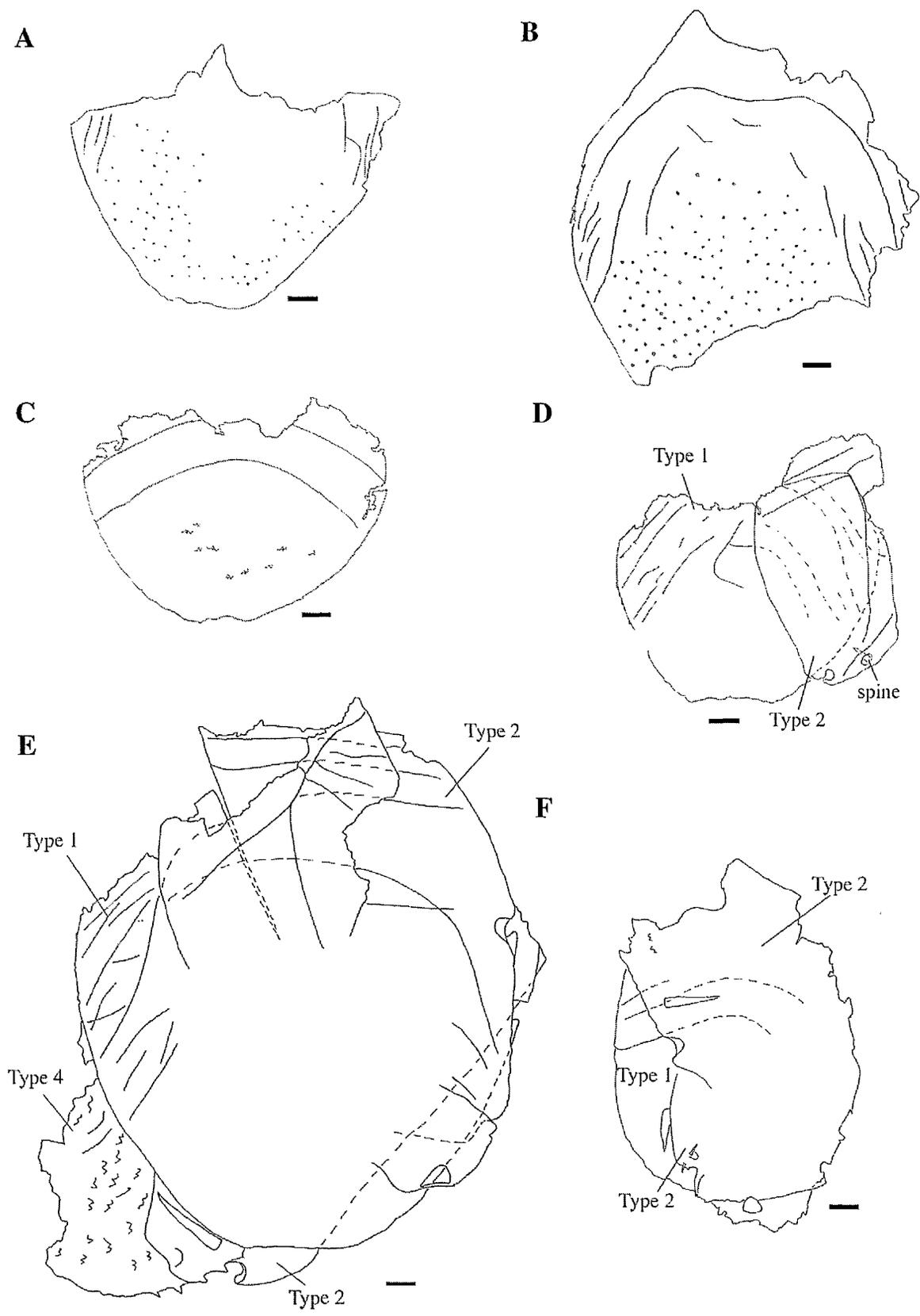
Figure 6.7 Interpretative drawings to accompany figure 6.6. *Eoarthropleura* cuticle fragments from the ventral plate complex. **A**, sternite - SM1.213.2a. **B**, sternite - SM1.119.32. **C**, sternite - SM1.213.13. **D**, sternite and K plate in connection - SM1.112.6. **E**, sternite, K-plates and B plate - SM1.213.2. **F**, sternite and K plate - SM1.213.3. All speciments orientated with anterior to top. Scale bars represent 0.1mm.

A   B

1.0 mm
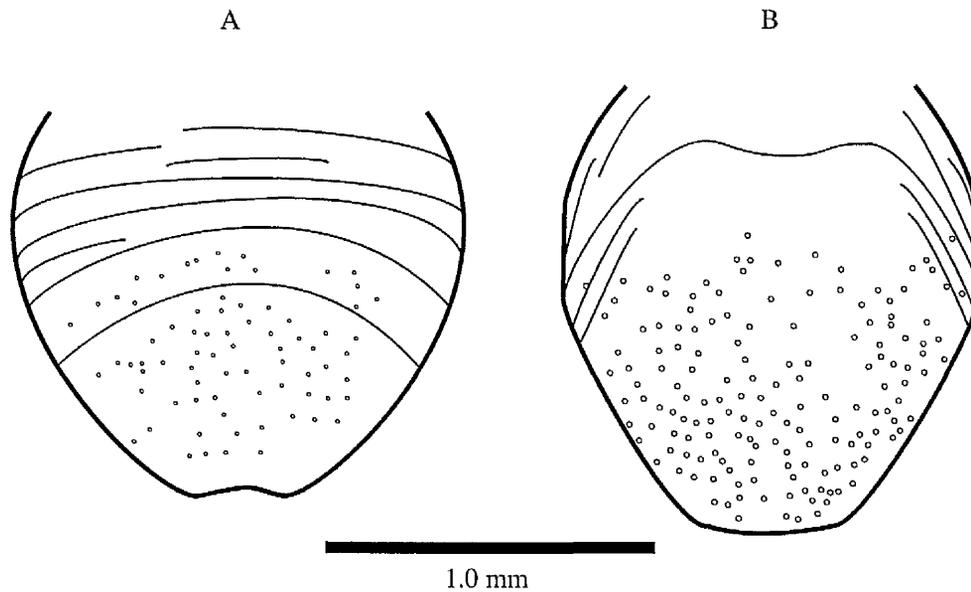
Figure 6.8 Variation in sternite morphology of *Eoarthropleura* specimens from South Mountain, New York State. Drawings approximately to scale.

6.4.2   Type 2 plates

These are subrectangular plates that broaden anteriorly and bear a number of large setal sockets on the lateral and posterior margins occasionally bearing stout, curved spines (figures 6.6 and 6.7 D, E, F, 6.9J; Shear and Selden's figure 8 e, j). Terrace lines run concentrically and parallel to the anterior and lateral margins. Once again the anterior is taken to be towards the torn margin where the cuticle presumably reduced to a thin membrane. The plates are asymmetrical and have a straight medial edge and a broadly curved lateral margin. Type 2 plates are known from impression fossils of Alken-an-der-Mosel and New Brunswick, and from compressed cuticle fossils of South Mountain.

Type 2 plates are presumed to be paired, ventral structures associated with the sternite (Shear and Selden, 1995). They were designated K plates by Størmer (1976), an identification that was upheld by Shear and Selden (1995) but questioned by Wilson (1999) who argued that the K plate should be renamed as a B plate in keeping with potentially homologous structures in *Microdecemplex* and *Arthropleura*.
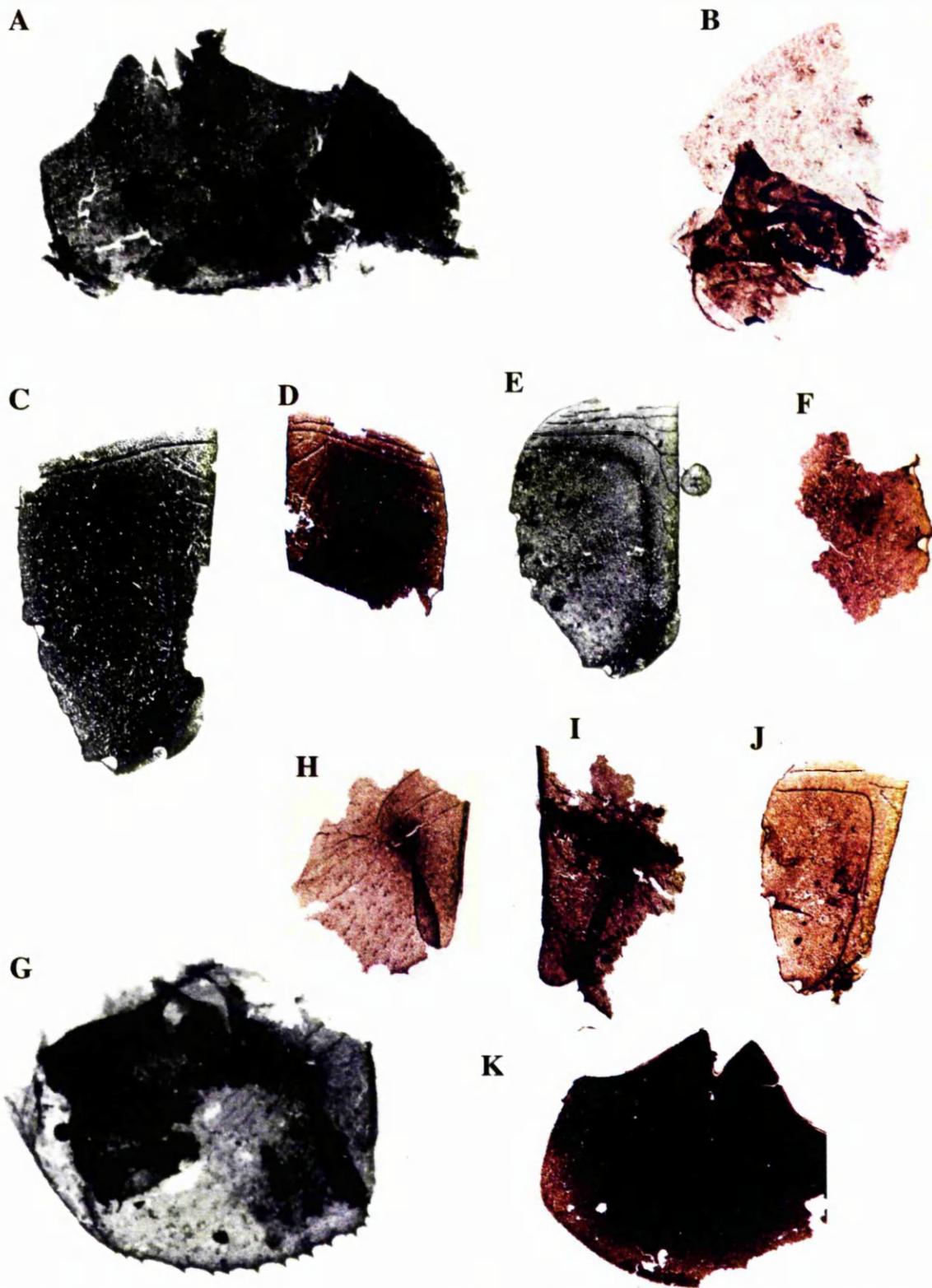
Figure 6.9 *Eoarthropleura* cuticle plates from South Mountain, New York. **A**, possible labrum with median notch - SM1.122.7. **B**, possible cuticle from cephalic region - SM1.119.46. **C**, K plate with single lateral setal socket - SM1.112.6a. **D**, folded K plate with at least one lateral setal socket - SM1.4.8. **E**, large, complete K plate - SM1.118.9. **F**, K plate fragment with two lateral setal sockets - SM1.115.V51. **G**, B plate - SM1.113.3. **H**, B plate fragment - SM1.115.V27. **I**, B plate fragment - SM1.115.V40. **J**, K plate - SM1.130. **K**, labrum - SM1.133.1 All plates orientated with anterior to top. Magnification x50.
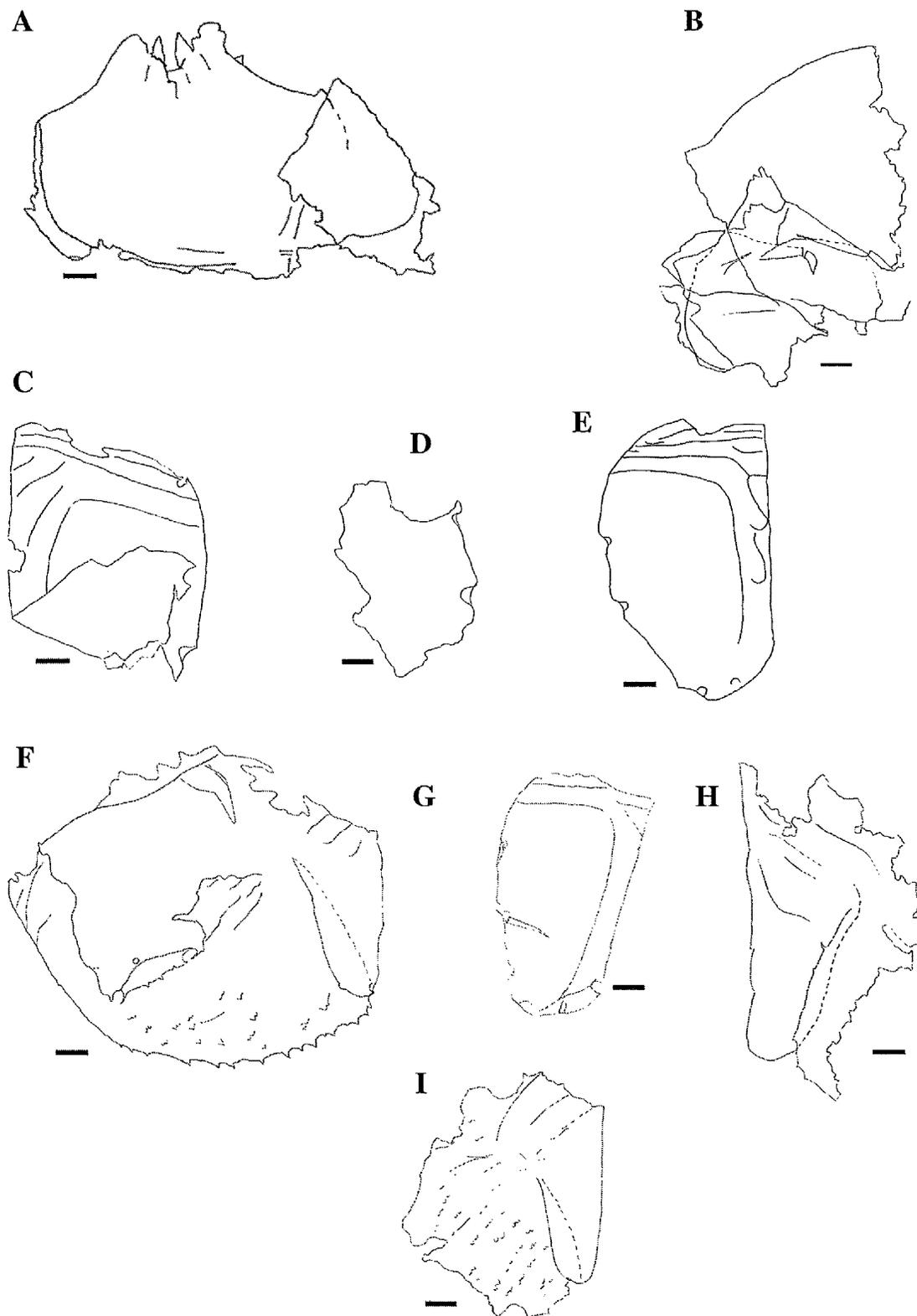
Figure 6.10 Interpretative drawings to accompany figure 6.9. **A**, possible labrum with median notch - SM1.122.7. **B**, possible cuticle from cephalic region - SM1.119.46. **C**, folded K plate with at least one lateral setal socket - SM1.4.8. **D**, K plate fragment with two lateral setal sockets - SM1.115.V51. **E**, large, complete K plate - SM1.118.9. **F**, B plate - SM1.113.3. **G**, K plate with preserved spine - SM1.130. **H**, B plate fragment - SM1.115.V40. **I**, B plate - SM1.115.V27. All plates orientated with anterior to top. Scale bars represent 0.1mm.
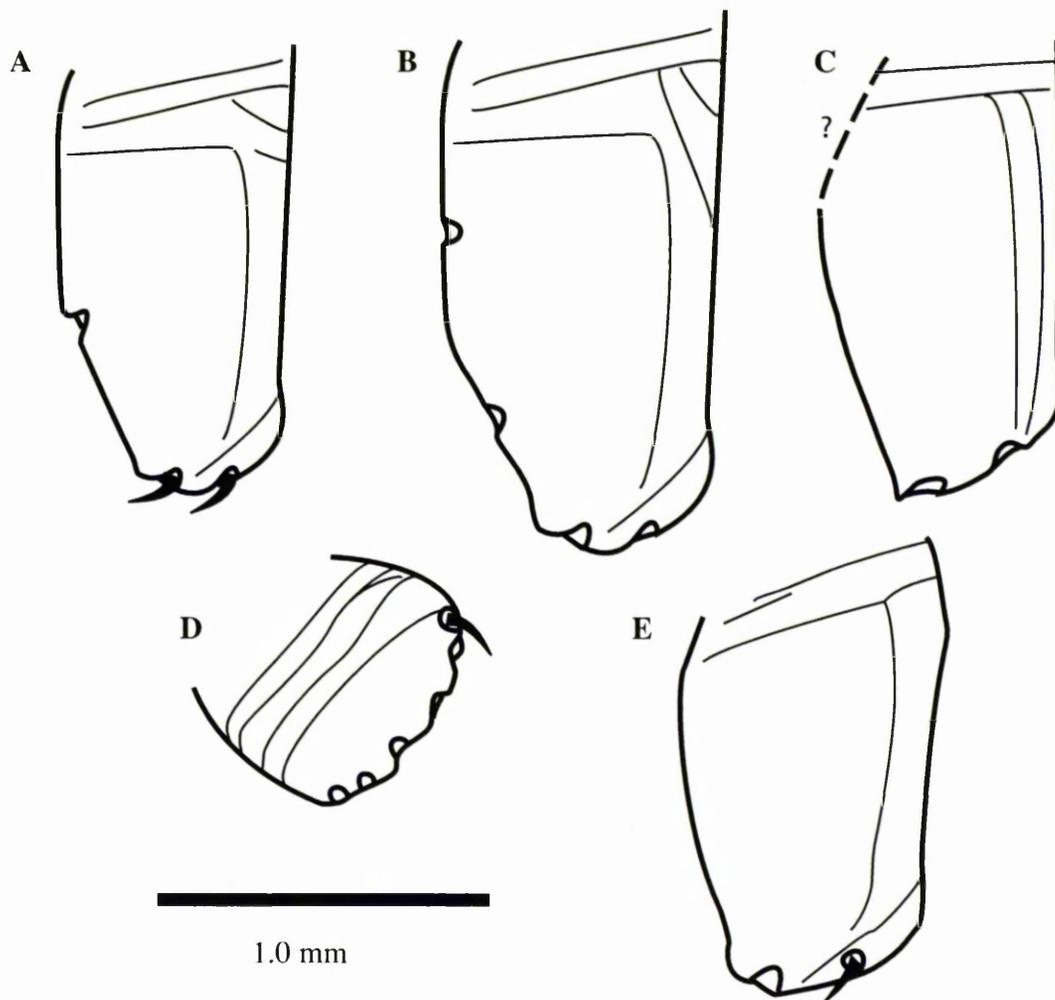
Figure 6.11 Variation in type 2 plate (K plate) morphology amongst compressed cuticle specimens of *Eoarthropleura*. **A**, single lateral setal socket, terrace lines parallel to margins. **B**, two lateral setal sockets, terrace lines parallel to margins. **C**, lateral setae absent, longitudinal terrace lines intersect lateral terrace lines (*Eoarthropleura ludfordensis*). **D**, Possible K plate with six marginal setal sockets and transverse terrace lines. Asssociated with samples of *E. hueberi*. **E**, lateral setae absent, intersecting terrace lines but lacking the distinctive cuticle pattern of *E. ludfordensis*. Found in association with specimens of *E. hueberi* at South Mountain. All drawings approximately to scale, variations in size occur.

Although the general shapes of type 2 plates are broadly consistent, there is a degree of variation in the patterns of terrace lines and number of setal sockets. These are illustrated in figure 6.11 and here termed morphotype 2A, 2B *etc*. The pattern of terrace lines broadly subdivides type 2 plates into two categories. The first is characterised by K plates with two straight transverse terrace lines anteriorly, the posteriormost of which is perpendicular to and intersected by a gently curved longitudinal terrace line occurring towards the medial margin.

This includes morphotypes C and E. The second category includes K plates with one terrace line running parallel to the medial and anterior margins, two or three transverse terrace lines anteriorly and short diagonal terrace lines running across the anteromedial corner. This group includes morphotypes A and B. The former group includes K plates that only bear two setal sockets on the posterior margin, which is generally broader than those of the latter. There are no setal sockets on the lateral margins, and the only real difference between these two plates is their cuticle pattern. The second group of K plates may bear one or two lateral setal sockets in addition to the two posterior ones. In both types, the setal sockets house stout, slightly curved spines (figure 6.6 D, E, F). The morphotype 2D plate (figure 6.11) was reported by Shear and Selden (1995, figure 4a and 8j) and is the only specimen of its kind. The significance of this plate is unknown but it is included here for the sake of completeness.

Previously, the absence of lateral setal sockets and presence of perpendicular, intersecting terrace lines were cited as diagnostic features for the single K plate described from Ludford Lane and attributed to *Eoarthropleura ludfordensis*. In contrast those described from South Mountain and attributed to *E. hueberi* were described as possessing at least four (and in one case six) marginal setal sockets and a different pattern of terrace lines (Shear and Selden, 1995). However, a K plate (SM1.112.6, figure 6.6D) almost identical to that described from Ludford, but with a different cuticle pattern, also occurs at South Mountain. This raises several possibilities. Firstly, two of the diagnostic features cited by Shear and Selden (1995) for *E. ludfordensis* may be void, and the species should be diagnosed on its cuticle pattern alone; the type E morphotype occurring at South Mountain would then represent either a new species or morphological variety (sexual dimorphism, ontogenetic variation) within a species. Secondly, the cuticle pattern is insignificant and *E. ludfordensis* occurs at South Mountain.

Shear and Selden (1995) described *E. hueberi* as possessing at least two lateral setal sockets. Other K plates recovered from South Mountain are superficially similar to those of *E. hueberi*, but only have one lateral setal socket (SM1.213.2, figure 6.6E; SM1.112.6a and SM1.4.8, figure 6.9 C, D). Either these K plates belong in a different taxon, or the original diagnosis of *E. hueberi* needs amending. In specimens of *E. hueberi* two lateral sockets occur well before the first transverse line appears towards the anterior margin of the plate. Taken with the second posterior socket they effectively divide the lateral edge of the plate between the first terrace line and the posteriormost point into thirds. In SM1.112.6 and SM1.4.8, however, only one socket occurs laterally and there is no such division. In specimens of *E. devonica*, K plates are identical in the number of setal sockets and pattern of terrace lines, and only really differ in their size. Those from Alken-an-der-Mosel measure up to 6.6mm long whereas the maximum length of a K plate recovered from South Mountain is 2.95mm.

The K plate from Ludford Lane measures 1.25mm long. Although type 2 plates do vary in size, there is no direct correlation between size and number of setal sockets or pattern of terrace lines. Thus it is unlikely that the variations in morphology are a function of age, but are more likely to reflect sexual dimorphism or interspecific variation.

6.4.3   Type 4 plates

Type 4 plates rarely occur as complete specimens and the presumed anterior margin is always absent (figure 6.9G, H, I). These are asymmetrical plates with a broadly rounded posterior margin fringed with short spines, and a straight medial edge (figure 6.12). The characteristic feature of these plates is a posteriorly directed medial lobe, which emanates from a dark area of cuticle and overlaps onto the main body of the plate. The lobe also bears short spines along its posterior margin. Terrace lines occur towards the anterior of the plate and the characteristic cuticle pattern of *Eoarthropleura* is conspicuous over a large part of the posterior area. The terrace lines appear to radiate from the dark area of cuticle and run diagonally from the lateral to median margin. The lobed portion of these plates is more frequently preserved since it overlaps to form a double thickness of cuticle.

Shear and Selden (1995) interpreted these plates as homologous with Størmer's B plate. The B plate described by Størmer, however, forms 'an elongate rather flat lobe with a rounded distal margin,' and 'a broad lateral rim that extends as far as to the transverse posterior border.' Both plates have a straight medial border and are assumed to be lateral paired structures abutting the K plate as part of the ventral complex (Shear and Selden, 1995). Specimen SM1.113.3 (figure 6.9G) shows a podomere compressed onto the surface of a type 4 B plate suggesting that it represents the coxa of the walking leg in *Eoarthropleura*.
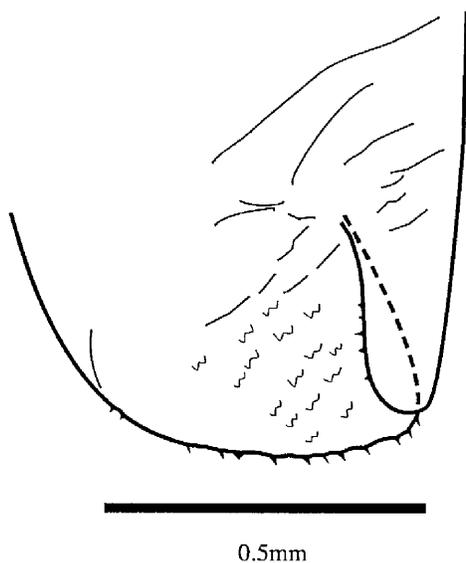
Figure 6.12 *Eoarthropleura* B plate (type 4) drawn as a composite of fragmented pieces from South Mountain. Approximately to scale, plates vary in size.

0.5mm

Little is known of the appendages of *Eoarthropleura* and despite the large numbers of podomeres that should theoretically exist amongst the debris, there has been no formal description of the appendicular morphology. During this research, however, podomeres have been relatively abundant in macerates from South Mountain (figures 6.13–6.17) and a detailed description is set out below.

Most of the material occurs as isolated podomeres, but occasionally two or three are found articulated (figure 6.13A, C, E). The most complete leg, consisting of four podomeres with well developed spines and a terminal claw, is illustrated in figures 6.13A and 6.14A. *Eoarthropleura* had a seven segmented leg and, in keeping with the terminology applied to *Microdecemplex* these are designated the coxa, trochanter, prefemur, femur, postfemur, tibia and tarsus. The podomeres are generally short and broad, and the distal margins are ornamented with large, moveable spines and smaller spines that occur as outgrowths of the cuticle on the distal margins of some podomeres (figure 6.17). Some podomeres bear longitudinal rows of tubercles on their lateral surfaces.

Tarsus

The only known example of a tarsus is specimen SM1.3.20 (figure 6.13A). It is a long podomere measuring 500μm long and is approximately five times long as it is wide. The margins of the tarsus are subparallel and the podomere narrows distally where it articulates with a smooth, curved claw. Proximally it articulates with the tibia via a dorsal hinge. The leg structure contrasts with that of *Microdecemplex,* where the postarsal claw apparently fuses with the tarsus (Wilson and Shear, 1999).

The tarsus is set with a dense pattern of setal sockets, one of which appears to contain a very long setae measuring 275μm. This is the only podomere with no ornament of spines on the distal margin.

Tibia

The tibia is shorter and broader than the tarsus, and measures approximately 300μm long and 220μm wide in specimen SM1.3.20 (figure 6.13A). The dorsal margin is straight and the podomere narrows proximally by a gentle flexing of the ventral margin towards the dorsum. There is a slight emargination of the proximal margin on the ventral side, to about one fifth of the length of the tibia (figure 6.13B, D). The tibia articulates dorsally with the ?postfemur (SM1.4.10, figure 6.13E).

Setal sockets are generally smaller and less dense than those occurring on the tarsus. Some occur on raised tubercles in longitudinal rows on the lateral surface. Distally at least two, possibly three, macrosetae occur dorsally and one ventrally. These spines are

long and striated, and are housed in conspicuous sockets (SM1.115.V48, figure 6.13F). Between these large spines lie either one or four smaller spines, giving the appearance of a crenulated margin. It is assumed that the four spines occur retrolaterally and the single spine prolaterally, since their presence may inhibit flexure of the leg in the horizontal plane. This pattern of smaller spines is repeated on many of the other podomeres.

Postfemur?

The postfemur has a characteristic flared shaped and is considerably broader distally than it is proximally. In specimen SM1.3.20 (figure 6.13A) it measures 300μm long, and is 300μm wide across the distal margin and 230μm across the proximal margin. Two other examples of postfemora are illustrated in figures 6.13 and 6.14C and E, and two further possible postfemora in figures 6.15 and 6.16A and C.

Two rows of setal sockets on raised tubercles occur laterally, but other setae are sparse. Distal macrosetal sockets indicate the presence of one dorsal macroseta and two ventral macrosetae. Four small spines occur retrolaterally and one prolaterally. The postfemur articulates proximally with the femur, which is seen to rotate through almost ninety degrees in both specimens SM1.3.20 and SM1.128.4 (figure 6.13A and C). The proximal margin is either obscured or missing in the articulated specimens; however, specimens SM1.213.4 and SM1.213.7 exhibit emargination of the proximal margin (figure 6.15A, C).

Femur?

Only the distal portion of the femur is preserved in the two specimens SM1.3.20 and SM1.128.4 (figure 6.13A, C). The dorsal margin is straight and forms an acute angle with the distal margin, which gently curves ventrally. The distal margin lacks the macrosetae seen on other podomeres but retains the pattern of one small prolateral and four small retrolateral spines.

Prefemur?

The identification of podomeres SM1.116.1 and SM1.115.V52 (figure 6.14B and F) is somewhat ambiguous since they have not been found in association with any other podomeres. At a first glance these podomeres resemble the tarsus described above, but on closer examination they differ in a number of ways. The dorsal and ventral margins are subparallel and both flex towards the centre producing a podomere that appears slightly bulbous both proximally and distally. The one complete specimen (SM1.115.V52) measures approximately 1200μm long and is about four times as long as it is wide. This is considerably larger than the tarsus, although it is not possible to directly compare the two podomeres since they may have originated from different sized legs.

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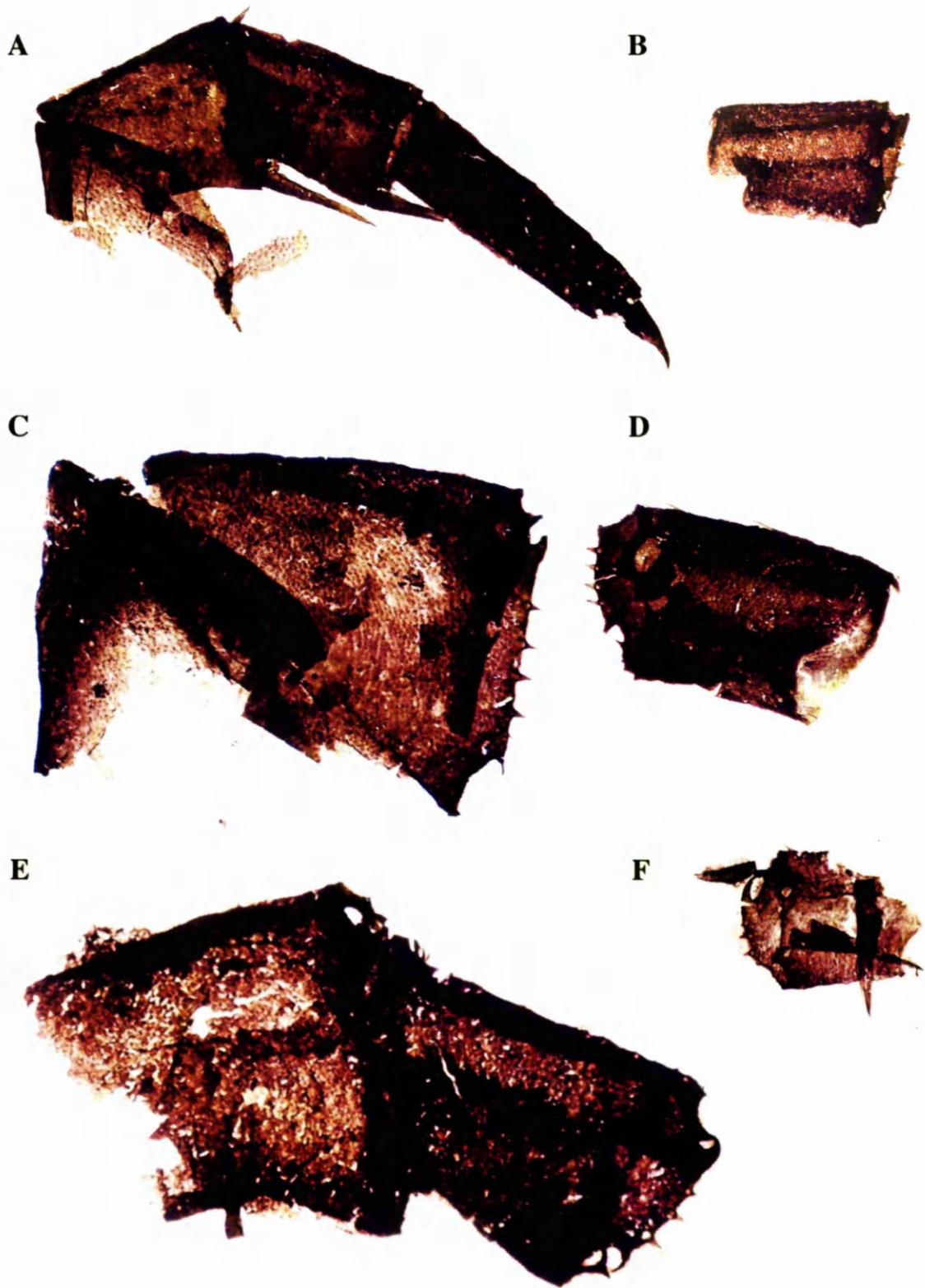
Figure 6.13 *Eoarthropleura* podomeres from South Mountain, New York State. **A**, four articulated podomeres with macrosetae and terminal claw - SM1.3.20. **B**, small podomere showing small distal spines and proximal emargination - SM1115.V37. **C**, two articulated podomeres - SM1.128.4. **D**, single podomere - SM1.4.10. **E**, two articulated podomeres - SM1.119.7. **F**, small isolated podomere with large, articulated macrosetae - SM1.115.V48. All podomeres oriented with dorsal surface uppermost. Magnification x100.
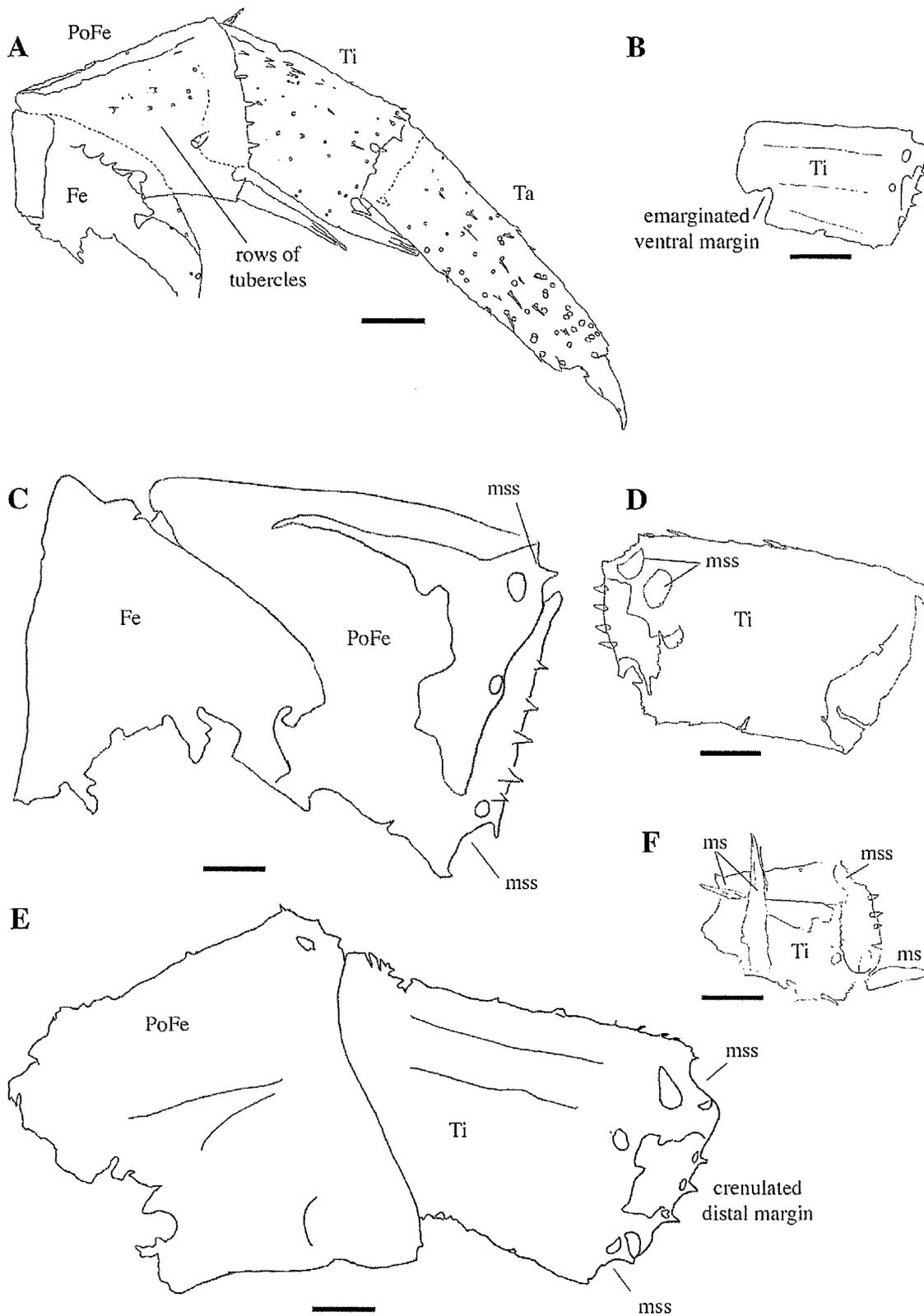
Figure 6.14 Interpretative drawings to accompany figure 6.13. **A**, four articulated podomeres with striated macrosetae and terminal claw - SM1.3.20. **B**, small podomere showing small distal spines and proximal emargination - SM1115.V37. **C**, two articulated podomeres - SM1.128.4. **D**, single podomere - SM1.4.10. **E**, two articulated podomeres - SM1.119.7. **F**, small isolated podomere with articulated macrosetae - SM1.115.V48. All podomeres orientated with dorsal margin uppermost. Scale bars represent 0.1mm.
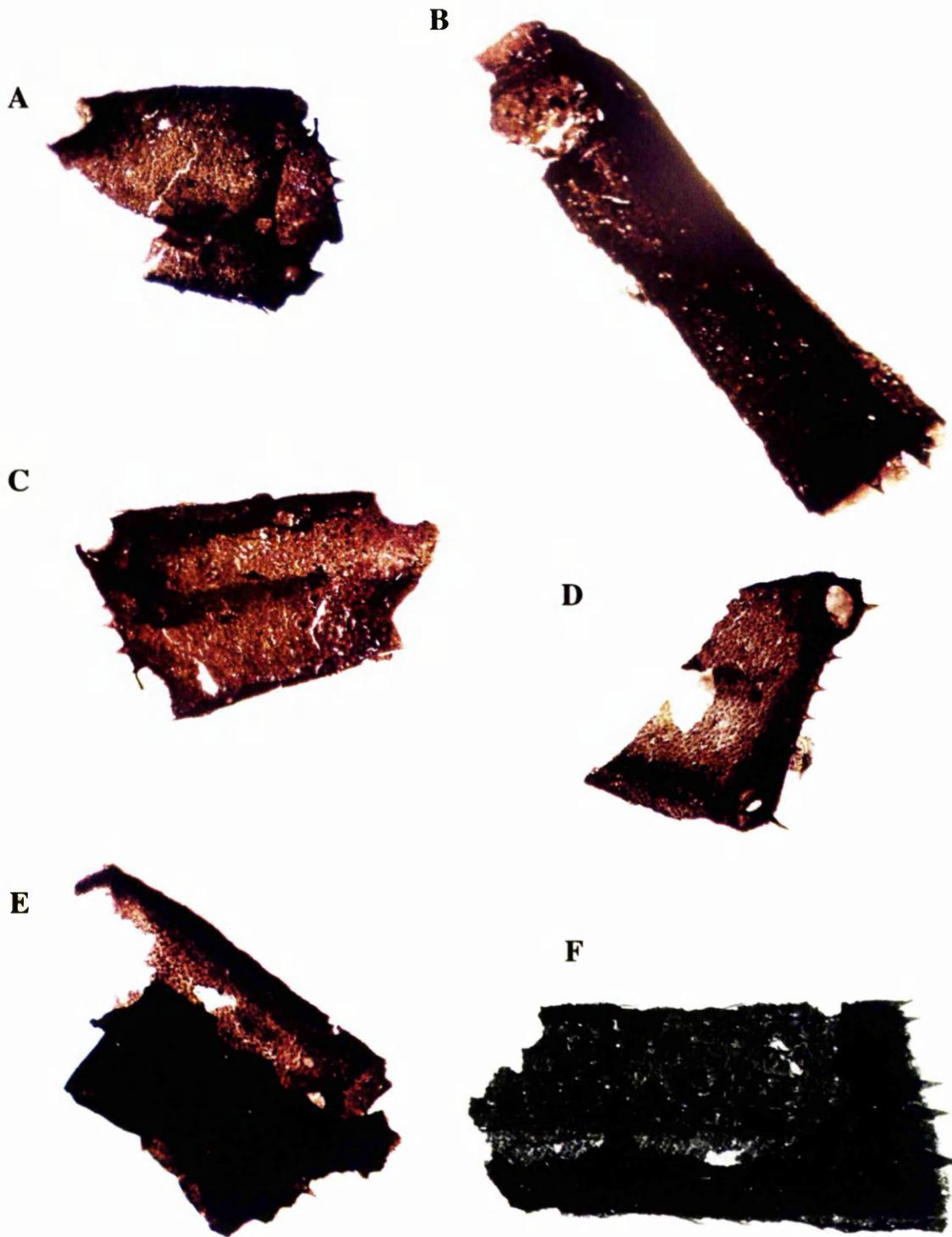
Figure 6.15 *Eoarthropleura* podomeres from South Mountain, New York State.
A, isolated podomere - SM1.213.4. B, elongate, setose podomere - SM1.115.V52.
C, isolated podomere - SM1.213.7. D, distal portion of podomere - SM1.213.4b.
E, isolated podomere, partially obscured by amorphous organic matter - SM1.213.4a.
F, distal portion of setose podomere - SM1.116.1. All podomeres oriented with dorsal
margin uppermost. See text for explanation. Magnification x100, except for C which is
x75.
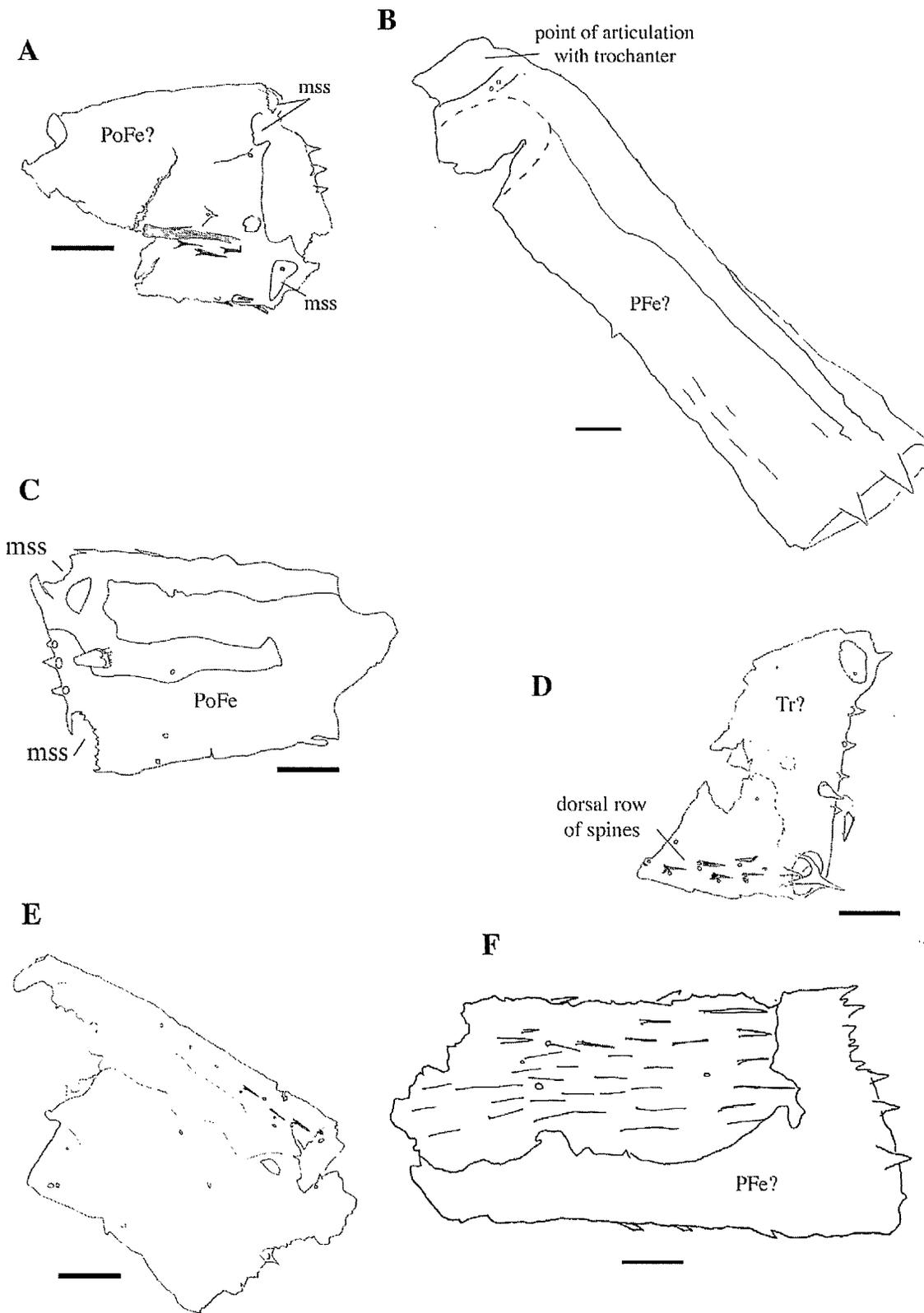
Figure 6.16 Interpretative drawings to accompany figure 6.15. **A**, isolated podomere
- SM1.213.4. **B**, elongate, setose podomere - SM1.115.V52. **C**, isolated podomere -
SM1.213.7. **D**, distal portion of podomere - SM1.213.4b. **E**, isolated podomere, partially
obscured by amorphous organic matter - SM1.213.4a. **F**, distal portion of setose podomere
- SM1.116.1. All podomeres oriented with dorsal margin uppermost. Scale bars represent
0.1mm.
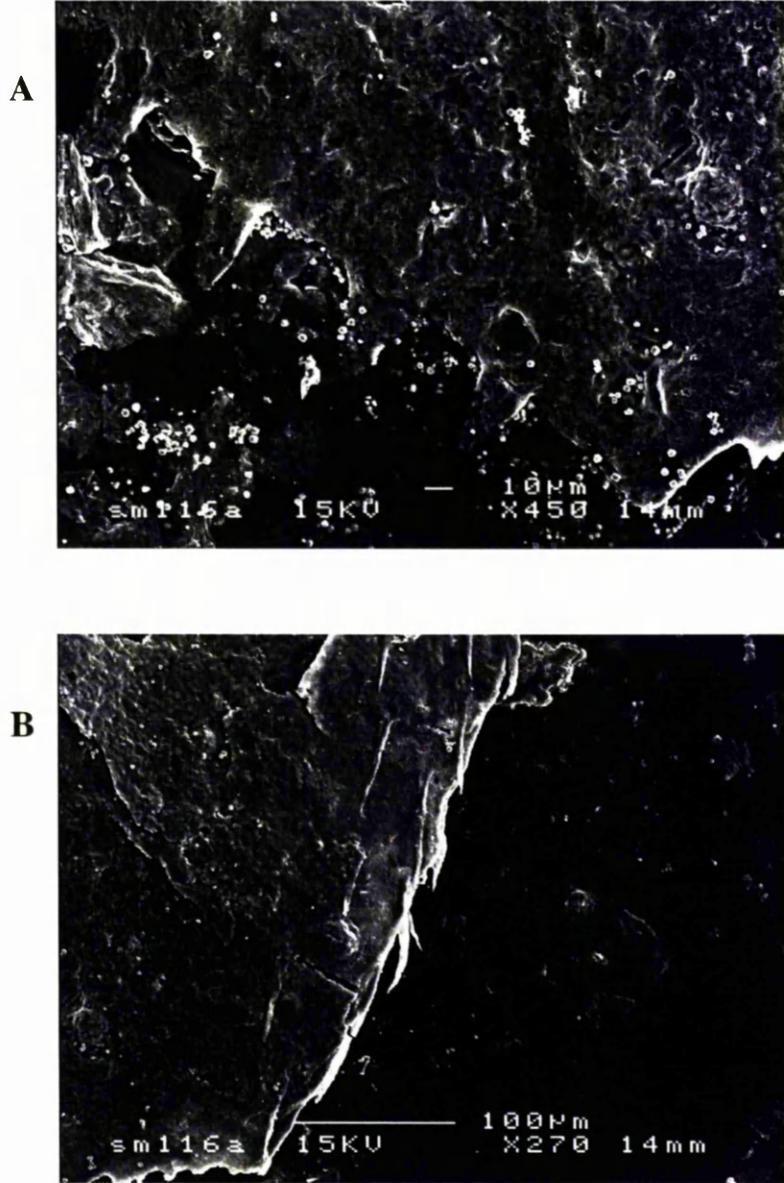
Figure 6.17 Scanning electron micrograph of cuticle from *Eoarthropleura* podomeres. **A**, distal margin of ?tibia showing four small spines occuring as outgrowths of the cuticle. Magnification x450. **B**, small distally directed setae on surface of podomere. Magnification x270.

The ?prefemur is densely setose and the distal margin is adorned with small spines. It has no macrosetae and is approximately symmetrical about the long axis, making it difficult to ascertain dorso-ventral orientation. Proximally there is a small protrusion, which occurs slightly off centre. If the podomere was oriented so that the distal margin was higher than the proximal margin in life, then this protrusion would occur ventrally.

Trochanter

Specimen SM1.113.3 (figure 6.9G) shows a small podomere compressed onto the surface of a type 4 plate (B plate). The morphology of this podomere also matches that of specimen SM1. 213.4b (figure 6.14D) and also a cuticle piece described by Shear and Selden as a type 4 plate (their figure 7f). The presumed ventral margin of the trochanter is straight and the dorsal margin dips down at a gentle angle towards it. Distally there are two short, socketed setae, one ventrally and one dorsally, with smaller spines in between. The margins of the two large sockets are themselves ornamented with two small spines and a number of small setae occur on the ventral surface.

From specimen SM1.113.3 (figure 6.9G) it appears that the proximal margin of this podomere adjoins the B plate (coxa) towards the anterior of the plate where the cuticle is often absent. Exactly how the two podomeres articulate is unclear.

Coxa

In both *Arthropleura* and *Microdecemplex* the distal end of the B plate articulates with the trochanter, and Wilson and Shear (1999) suggested that the B plate in *Arthropleura* and *Microdecemplex* be referred to as the coxa to bring arthropleuridean anatomy in line with the rest of the Myriapoda. Based on other similarities with the arthropleurids Wilson (1999) suggested that either the K or B plates of *Eoarthropeura* should represent the coxa, and from the evidence given above it would appear that it is the B plate. The mode of articulation, however, remains unclear unless cuticle from the trochanter merged into cuticle from the coxa.

In some respects the legs of *Eoarthropleura* resemble those of *Microdecemplex*. They both have seven segments and are conspicuously ornamented with large socketed spines. In *Microdecemplex* these occur on the prefemur, femur and postfemur whereas in *Eoarthropleura* they occur on the tibia and femur. *Eoarthropleura* podomeres are much more setose than those of *Microdecemplex*, which appears to have a much smoother cuticle surface and also lacks the cuticle patterning seen in *Eoarthropleura*. Finally, the distal claw or posttarsus, is fused to the tarsus in specimens of *Microdecemplex* but is articulated in *Eoarthropleura*. A possible reconstruction of a walking leg of *Eoarthropleura* is illustrated in figure 6.18.

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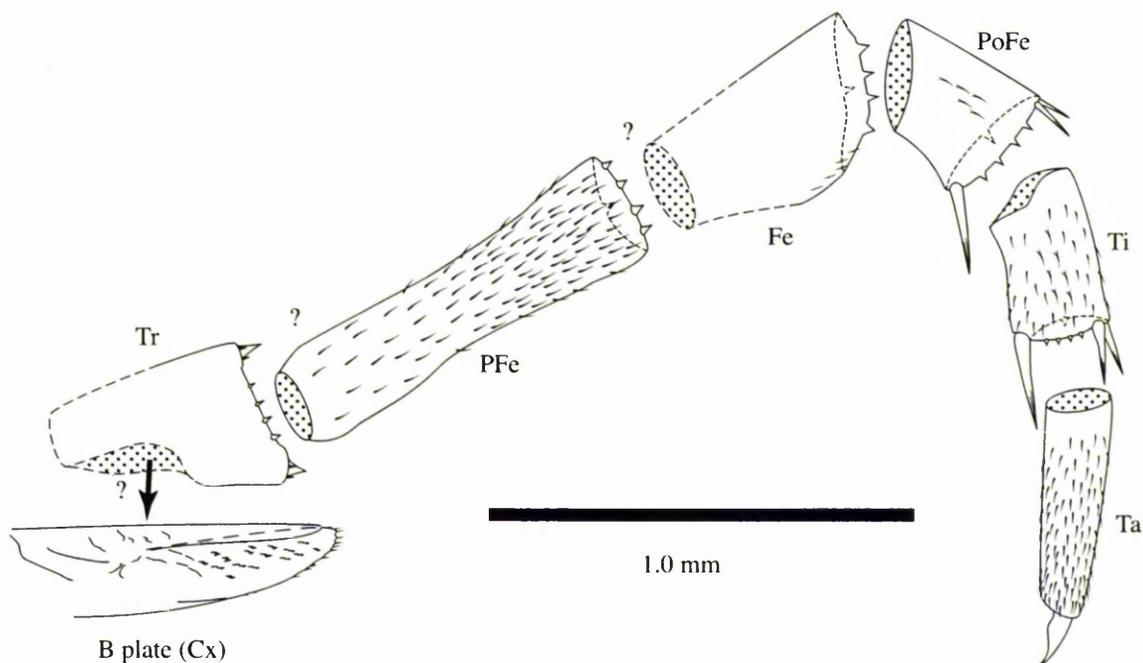
Figure 6.18 Possible reconstruction of a typical walking leg from *Eoarthropleura*, posteriormost aspect. Long dashes represent congecture where material is absent or poorly preserved. Question marks indicate uncertainty over position or articulation.

6.5   *Association of sclerites*

The dorsal morphology of *Eoarthropleura* is relatively well understood. The ventral morphology, however, is more ambiguous. Størmer (1970) originally interpreted the ventral plate complex of *Eoarthropleura* as a medial sternum (subquadratic plate) flanked on either side by a K and B plate, which abutted via their straight lateral margins. Shear and Selden (1995) reinterpreted the complex, placing the sternite (Størmer's cordate plate) in medial position and situating the K plates towards the anterior and the B plates towards the posterior (figure 6.19). The subquadratic plates described by Størmer remain elusive at South Mountain. This could be a result of the different preservational modes (compression versus impression) as Wilson (1999) also reported the presence of a medially located subquadratic plate in rather poorly preserved impression fossils from eastern Canada.

Clearly the sternites, *sensu* Shear and Selden (1987), K and B plates were all closely associated in *Eoarthropleura* and specimen SM1.213.2 (figures 6.6E, 6.7E) shows a symmetrical sternum (type 1 plate) overlapping two opposite facing K plates and at least one B plate. Two K plates overlapping a sternum are also evident in specimen SM1.213.3 (figures 6.6F, 6.7F). The question then arises as to whether the sternite overlaps the K and B plates (as in Shear and Selden's ventral reconstruction) or whether the K and B plates over the sternite as in Størmer's reconstruction. From the available specimens it is impossible to

tell either way, but in both *Arthropleura* and *Microdecemplex* the K and B plates overlap the sternite and this may well also be the case in *Eoarthropleura* (Wilson, 1999).

Two sternite morphotypes occur at South Mountain and it is difficult to assess their association with other cuticle plates since articulated material occurs so infrequently. The only articulated type B sternite, however, is associated with a type E K plate, which has only two distal setal sockets and bears a similar terrace line pattern to the *Eoarthropleura ludfordensis* specimen. Articulated type A sternites are only found associated with type A or B K plates. It is tempting to speculate that the two cuticle associations represent different species of *Eorthropleura*, but for now there is insufficient material to draw any firm conclusions.
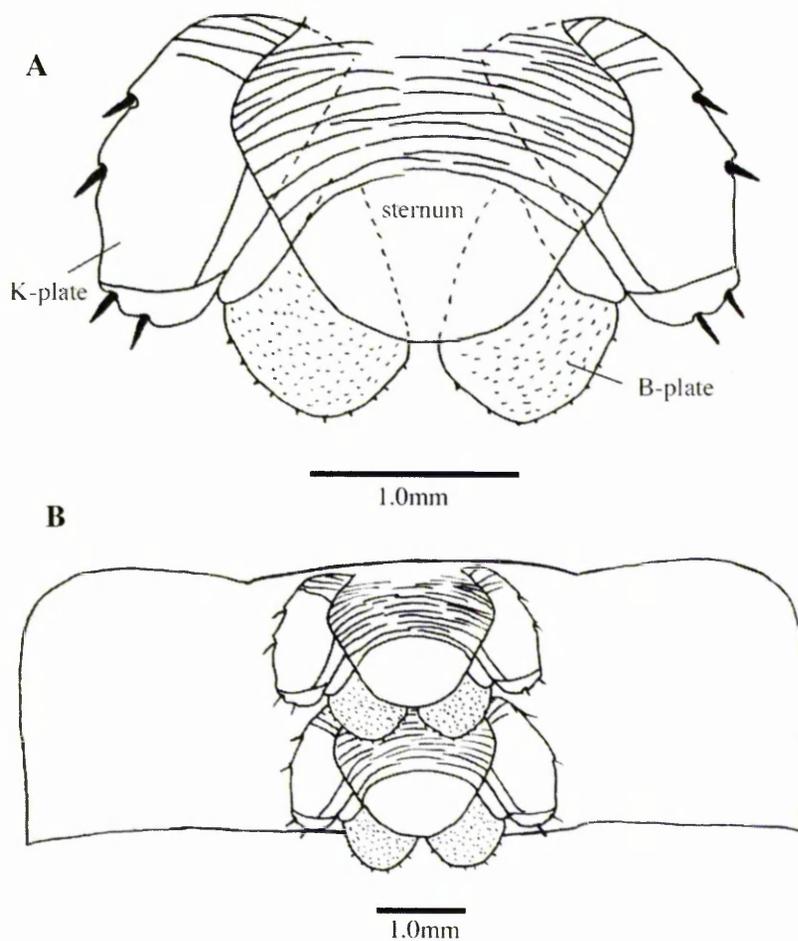
Figure 6.19 *Eoarthropleura hueberi* (Kjellesvig-Waering, 1986) possible reconstruction based on re-orientation of B and K plate complex so that the setose margin of K plate is lateral in position, and probable diplosegmentation. **A**, relationship between B and K plates and sternite; **B**, position of the complex in relation to tergite. Modified from Shear and Selden (1995).

Since so much of the *Eoarthropleura* material from South Mountain is fragmented and dispersed within the sediment, it is difficult to assess relative sizes of cuticular plates. It is clear that there is considerable variation in size and shape, which is to be expected if the preserved material is representative of an entire population. Accurate observations on relative sizes can therefore only be made on either articulated material or material preserved *in situ*. Shear and Selden (1987) suggested that the ventral plates of *E. devonica* were about half the length of associated tergites preserved on the same slab and that *E. devonica* was therefore probably composed of diplosegments. This is much harder to prove from the dispersed material available at South Mountain and many of the ventral plates are approximately the same length as the paraterga although there is no evidence to directly associate these sclerites. Diplosegmentation would be further supported by a 1:1 ratio of sternites, and 2:1 ratio of K and B plates to paraterga amongst the recovered sclerites. Out of interest, 6 sterna, 7 paraterga, 9 K plates and 4 B plates are reported in this chapter. If these are combined with the specimens figured by Shear and Selden (1995) this brings the total number of plates from South Mountain to 13 sterna, 15 paraterga, 22 K plates and 10 B plates. Of course the ratios are unreliable in such a small and poorly constrained data set, but it is interesting to note that the ratio of paraterga to the sterna and K plates does support diplosegmentation of *Eoarthropleura* at South Mountain.

6.6   *Summary*

The following points concerning *Eoarthropleura* arise from material presented in this chapter:

1   The paraterga of *Eoarthropleura heuberi* had dorsal spines.

2   Two different morphotypes of B plate are found at South Mountain.

3   Several different morphotypes of K plates occur at South Mountain.

4   There appear to be distinct associations of K and B plate morphotypes.

5   The walking legs had seven segments, terminated in a curved claw and attached to the body of *Eoarthropleura* via the B plate.

The implication of these findings is that amongst the material from South Mountain there are at least two morphpotypes of *Eoarthropleura*. The first has type A sternites and type A or B K plates, which bear either one or two lateral setae. The second type has type B sternites and K plates with no lateral setae (types C and E). According to the diagnosis of *E. hueberi* this would represent a new species. However, the cuticle pattern on both morphotypes is identical and until more complete specimens come to light, these should be maintained as *Eoarthropleura hueberi*, possibly representing male and female morphologies. The

diagnosis of *E. heuberi* should be amended appropriately. Accordingly, it is predicted that similar plates will be found at Ludford lane and the diagnosis for *E. ludfordensis* should also be amended.

It is interesting to speculate on whether arthropleurid material from South Mountain would have been assigned to a new species had it been preserved as compression fossils alone. The confusion over the identity of the sternite seems to have arisen over differences in the interpretation of plates preserved in different contexts, and different characters are naturally used for identification in each case. The principal differences between *E. heuberi* (compression fossils) and *E. devonica* (impression fossil) lie in the cuticle pattern and ambiguity over the identity of certain plates. It is entirely possible that these two species are the same.

Morphological information from the cephalic region of *Microdecemplex* suggests the inclusion of arthropleurids within the Diplopoda, which are now known to have been truly terrestrial by at least Wenlock times (Wilson and Anderson, 2004). This information, combined with anatomical features and preservational context, suggests that Eoarthropleurids were probably also terrestrial although no respiratory organs have yet been described. However, the total absence of spiracles or tracheae from amongst arthropleurid material is problematic and Kraus and Braukmann (2003) proposed that arthropleurids were semiaquatic and achieved gas-exchange by plastron-breathing *via* the ventral K plates, which were essentially haemolymph filled sacs. Whether or not this is true for *Eoarthropleura* remains to be seen, but they were certainly small enough to respire using a typical diplopod tracheal system (Wilson, 1999). In support of a semiaquatic habitat Kraus and Brackmann (2003) argued that the cuticle of *Arthropleura,* and probably also of *Eoarthroplera,* was 'paper thin' and weak and supported by musculature and antagonistic hydraulics of the body cavity. Evidence cited in support of this was the presence of wrinkles across the surface of some specimens. The mode of preservation and abundance of specimens of *Eoarthropleura* at South Mountain contradicts this and indicates that the cuticle was relatively strong and well sclerotized.

Cuticle with a granular surface topography forms the second largest fraction (next to arthropleurid cuticle) of recovered fragments from South Mountain. The preservation of pectines (midventral sensory appendages unique to scorpions) amongst this cuticle type gives an unambiguous identification, and other characteristic scorpion sclerites (metasomal body rings, chelae *etc*) are also preserved.

Classification of living scorpions is based upon internal and external morphology including cheliceral dentition, numbers and patterns of trichobothria, shape of coxapophyses and sternum, leg spination, telson shape, venom glands and male and female reproductive systems. Classification of fossil scorpions, however, is largely based upon the arrangement of the coxosternal region—a scheme initiated by Petrunkevitch (1955) and utilised extensively by Kjellesvig-Waering (1986). Despite a comprehensive review of fossil scorpion sytematics by Kjellesvig-Waering (1989) who recognised twenty-one superfamilies, the scheme was revised and largely rejected by Stockwell (1989) and later by Jeram (1994).

Since the fragments included here are largely fragmentary and disarticulated, and scorpion classification relies on using a number of character states ((no autapomorphies have been identified for the Mesoscorpionina (Jeram, 1994)), they are mostly placed *incertae sedis*. Many of the features used to identify both modern and fossil scorpions are unavailable for consideration amongst dispersed scorpion cuticle, and it is difficult to relate fossil taxa from whole specimens to those from dispersed cuticle assemblages. Useful taxonomic characters are, to a large degree, mutually exclusive and characters that are useful in the identification of dispersed scorpion cuticle are only of marginal use with whole scorpion fossils. Variations in cuticle patterns and sclerite morphology can be a powerful diagnostic tool and Jeram (1989) successfully classified and identified dispersed cuticles on the basis of cuticle patterns and topography in his thesis on Carboniferous scorpions.

The nomenclature used in the following descriptions adheres to that of Stahnke (1970) who presented a comprehensive overview of scorpion nomenclature and mensuration including comparative nomenclature, English synonyms, and equivalents in French, German and Spanish.

7.1 *Cuticle topography*

Scorpion cuticle from South Mountain has a characteristic granular appearance with small triangular thickenings scattered sporadically across the surface (figure 7.1A). The cuticle does exhibit a degree of variation in the density of the 'granules' and may on

occasion merge into cuticle with a reticulate pattern (figure 7.1B). The colour ranges from a pale golden to dark brown or black, and is often ornamented with lines of dark, sclerotised cuticle. The colour probably reflects the mode of preservation and the original cuticle state (moult or living specimen) rather than the age of the specimen, since there is no apparent correlation between size and colour, which would be expected otherwise (see chapter 3 for discussion of cuticle taphonomy).

7.1.1 Sensory organs

Many of the scorpion fragments from South Mountain are covered with setal sockets; the setae themselves, however, are often absent. The cause of this may be physical (longer residence time in the litter, transportation prior to burial), or it might reflect the delicate nature of the setae, which were easily disarticulated from the exoskeleton upon death or ecdysis. Generally the cuticles are less hirsute than those attributed to spiders and trigonotarbids, with setal sockets occurring at a much lower density. The most setose cuticles of all recovered scorpion fragments are those from the pedipalps and, where they occur, the setae are relatively short and stout (e.g. SM1.120.V5, figure 7.7F). Stahnke (1970) defined three types of setae amongst living scorpions: microchaetes—small, whitish, fine setae with a base attached to a poorly developed areolar cup, found on the fulcra of the pectines; macrochaetes—large, coloured setae, each arising from a cup-shaped areolar that is completely filled by the base of the seta, found particularly on the metasoma, on sternum 7 of the mesosoma, on the intercrestal area of the anal arch, and on the pectines; and trichobothria—long, thin setae arising from a cup-shaped areolar that is not completely filled by the base of the seta, found only on the femur, patella and tibia of the pedipalps. Amongst the fossil scorpions from South Mountain setae are found preserved on the chelae, pectines and metasoma. Those on the metasoma appear slightly longer and finer than those on the chelae, but generally there is little variation amongst them. In the classification of living scorpions, the number and position of trichobothria can be a useful taxonomic indicator, and is widely used. If they were present on the South Mountain scorpions the only specimen upon which they might appear is SM1.4.8a (figure 7.7A). There are neither setae preserved on this specimen nor characteristic bothria that might suggest the presence of trichobothria at one time.

The most conspicuous sensory organs occurring amongst the scorpion fragments are the pectines—comb-like sensory structures unique to scorpions. Lamellae, teeth and peg organs can all be distinguished. These structures are discussed in more detail in section 7.2.2. Recent scorpions bear slit sense organs on all leg segments, mostly occurring on the lateral surfaces and grouped near to the joints. Two pairs of proprioceptors were also described from each metasomal segment of a scorpion by Pampathi Rao and Murthy (1966). Although

slit sensilla are relatively commonplace in spider cuticle from South Mountain, no such organs were observed in any of the scorpion fragments.

Recent scorpions have a single pair of median eyes and between zero and five simple lateral eyes. Fossil specimens have been variously described as possessing holochroal (compound) and schizocroal eyes (Kjelleswig-Waering, 1986). No eye structures were recovered from amongst the scorpion material.

7.2   Cuticle morphology

The scorpion cuticle from South Mountain probably displays the most varied morphology amongst individual cuticle pieces. Chelate appendages are relatively common, as are body rings, which are sometimes still articulated. Occasionally the cuticle occurs as folded and compacted jumbles, providing useful information on the relative positions and associations of cuticular plates.

7.2.1   Tergites

Most of the larger pieces of granular, scorpion-like cuticles from South Mountain (e.g. figure 7.1 A,B) are attributed to tergites since this is where the largest expanse of cuticle occurs. In living scorpions there are seven tergites, which are joined to the ventral sternites by the lateral pleural membranes. Figure 7.1C, D, E, F illustrates four examples of tergites with the ventrally directed lateral margin folded underneath and part of the pleural membrane intact. By analogy with living and fossil scorpions, the anterior margin is taken to be towards the finely crenulated transverse keel. Ecdysis occurs along a line through the lateral pleurae of modern scorpions, thus it is likely that these specimens represent part of a moulted exoskeleton.

All four specimens are united by a single transverse keel, which runs right across the tergite approximately one fifth of the way in from the anterior margin. Posteriorly there is a narrow rebordered margin (doublure), and in three of the specimens there are one or two setal sockets situated towards the anterior. The plates measure between 540 and 700μm across their short axis, and specimen SM1.115.V14 measures 1450μm across the long axis. This is the widest specimen but it lacks a definite lateral edge and therefore this represents the minimum width of the tergite. The largest specimen is SM1.115.V21, which shows the greatest distance between the posterior margin and transverse keel, although the lateral portions are considerably narrower than in other specimens. Specimen SM1.115.V13 is also a larger plate with correspondingly larger lateral areas, but a considerably narrower doublure. There is no ornamentation between the anterior keel and anterior margin, and posterior to this the cuticle is slightly more granular. The development of posterior ornamentation on tergites is common amongst eurypterids and reoccurs among later scorpions, e.g. the Triassic

mesophonids, but is unknown in Palaeozoic scorpions (Jeram, 1997). Measurements for each of the plates are summarised in table 7.

Most of these differences in morphology can be explained by their relative positions on the body of the scorpion. In living scorpions the seven tergites typically reduce in length along their short axes towards the anterior. The pleural membranes tend to be narrower in the final mesasomal segment where the last (and longest) sternite and tergite come together before the start of the metasoma. This probably explains the proportions of specimen SM1.115.V21, which, by extrapolation of proportions from other plates, is the largest tergite but also has the narrowest ventrally directed lateral portion. Since all four specimens were recovered from the same sediment sample, it is probable that these were originally associated sclerites and may be representative of a single animal.

Specimen SM1.130.8c (figure 7.3C) resembles the tergites described above. A dark line towards the anterior margin could represent a transverse keel, and there is a rebordered margin with large, conspicuous setal sockets along its length. The most unusual feature of this specimen, however, is the presence of a group of setae situated towards the lateral margin. There are approximately ten long, fine setae, closely grouped together. Specimen SM1.115.V18 (figure 7.3B) shows a similar clumping of setae on a fragment of scorpion-like cuticle.

Shorter, more anteriorly positioned tergites occur on specimen SM1.130.8 (figure 7.3E). This is one of the most complete specimens, and it preserves the dorsal aspect of five articulated tergites, pectines and the coxae of the left third and fourth walking legs (coxae four and five) and the right fourth walking leg (figure 7.4D). The dorsal tergites are telescoped in on each other, which suggests that this specimen represents a moulted exoskeloton rather than a carcass. In life, the whole animal probably measured only 3-4mm long. The tergites are straight sided with parallel margins and the posterior margin of the second tergite flexes very gently towards the anterior. They range in length from 420 to 440μm and the width of the second tergite can be established as 1650μm. There is no visible ornamentation on any of these tergites, neither is a rebordered margin apparent.
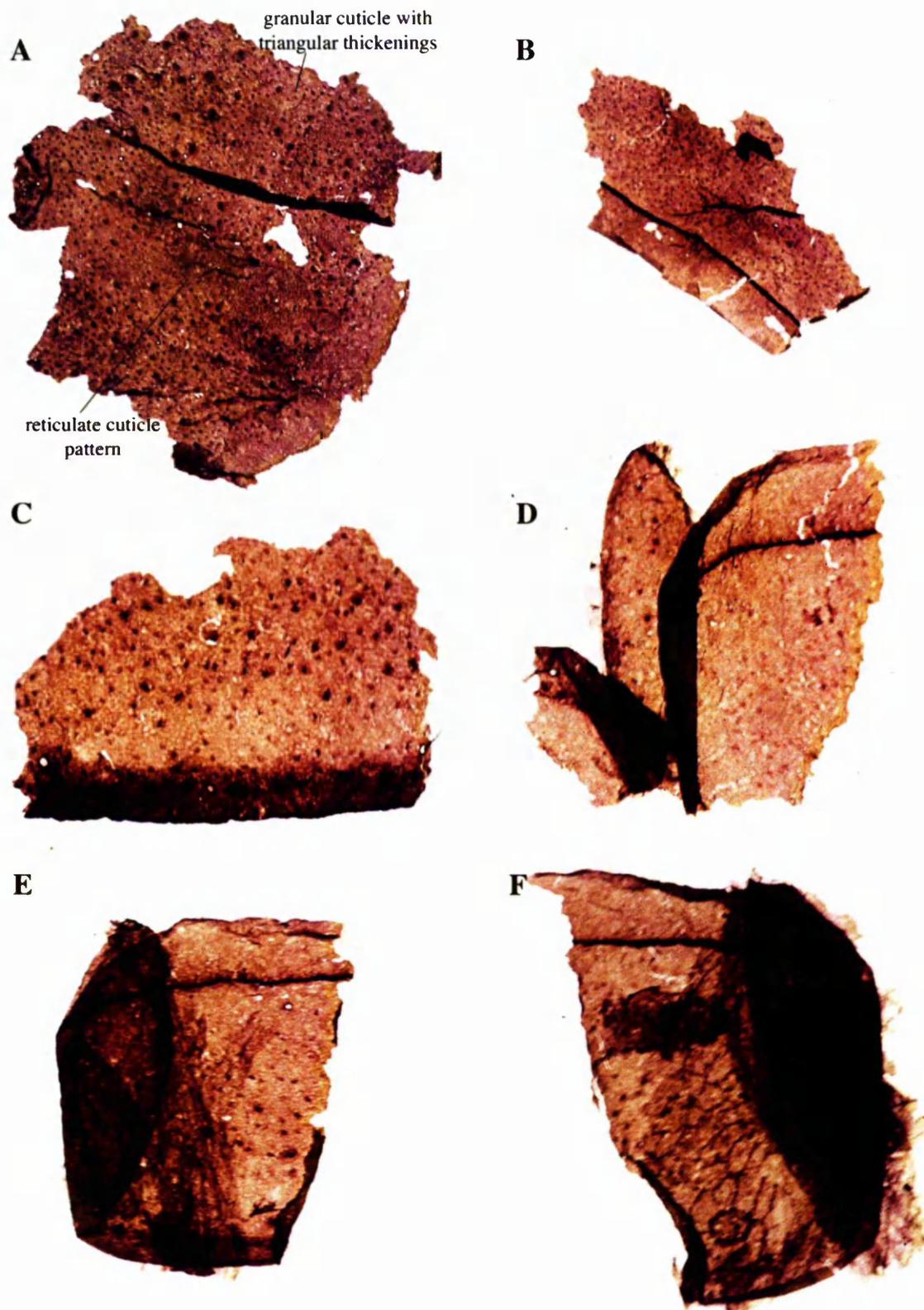
Figure 7.1 Scorpion tergites from South Mountain, New York. **A**, large piece of cuticle showing variation in topography from granular to reticulate - SM1.115.V37, x75. **B**, granular cuticle fragment with transverse keel - SM1.115.V14, x100. **C**, granular cuticle with rebordered margin and setal sockets - SM1.115.V21, x100. **D**, partial tergite with transverse keel pleural membrane - SM1.115.V21a, x100. **E**, partial tergite with transeverse keel and - SM1.115.V11, x100. **F**, partial tergite with layer of plant cuticle compressed onto surface - SM1.115.V13, x100.

A   B
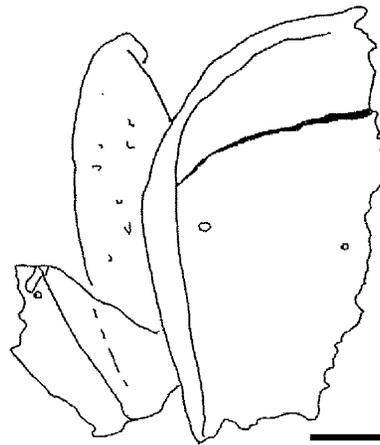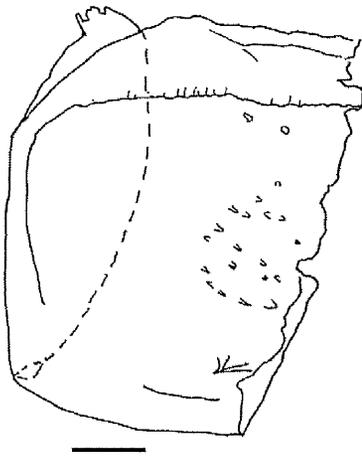
C   D
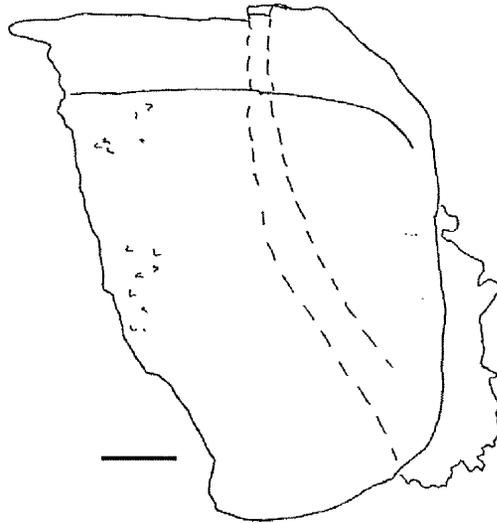
Figure 7.2 Interpretive drawings to accompany figure 7.1. **A**, granular cuticle with rebordered margin and setal sockets - SM1.115.V21. **B**, partial tergite with transverse keel - SM1.115.V21a. **C**, partial tergite with transeverse keel - SM1.115.V11. **D**, partial tergite with layer of plant cuticle compressed onto surface - SM1.115.V13. All specimens drawn with anterior towards top. Scale bars represent 0.1mm.

Mesosomal segment 2 bears the pectines, which probably extended to the edge of the body in life. The pectines have numerous rounded teeth, each of which bears a number of peg organs on its posterior facing margin. Anterior to the pectines are two wide pieces of articulated cuticle that may represent part of the first tergite. They are the only pieces bearing conspicuous setal sockets. Lying symmetrically over the apex of the pectines is a narrow strip of cuticle with the ends drawn downwards into an obtuse angle. This could be representative of the sternum, however there is nothing to suggest the presence of a genital operculum, which should lie between the pectines and the sternum. It could also represent the pectinal plate, which Kjellesvig-Waering (1986) described from several branchioscorpionid scorpions. If, however, this is the sternum then its shape does not fit into any of the superfamilies erected by Petrunkevitch (1955), which he defined by their coxosternal region. It is nonetheless reminiscent of the narrow transverse sternum that characterises the living Bothriuridae.

Specimen SM1.212.2 (figure 7.3D) is a symmetrical mass of cuticle, which has been preserved somewhat three-dimensionally. It has been less flattened and compressed than other cuticle fragments, but there are no obviously recognisable features. It may represent an oblique view of two or three mesosomal segments and part of the coxosternal region, but this is only a tentative identification.

Table 7. Comparison of measurements for tergites and pleurae from South Mountain. Measurements represent ranges or averages taken over five readings. N/A indicates measurement unavailable due to incomplete specimen.

	Short axis tergite (μm)	Long axis tergite (μm)	Anterior margin to keel (μm)	Doublure (μm)	Short axis of lateral portion of tergite (μm)	Long axis of lateral portion of tergite(μm)
SM1.115.V11	580	N/A	97–105	48–53	192	537
SM1.115.V13	700	N/A	96–115	18–24	207/260	637
SM1.115.V14	540	1450	100–120	48–53	N/A	N/A
SM1.115.V21	N/A	N/A	143–156	N/A	146	N/A
SM1.130.8						
T2	N/A	1650				
T3	440	N/A	No keel	N/A	N/A	N/A
T4	420	N/A				
T5	460	N/A				

Figure 7.3 Scorpion metasomal segements from South Mountain, New York. **A**, tergite with transverse keel and rebordered anterior margin - SM1.115.V14 x75. **B**, tuft of setae on ?scorpion cuticle - SM1.115.V18 x50. **C**, tergite, note tuft of long setae towards lateral margin - SM1.130.8c x100. **D**, scorpion cuticle. ?oblique view through metasoma - SM1.1.212.2 x100. **E**, dorsal aspect of tergites, coxae and pectines, see drawing for explanation - SM1.130.8 x50. All specimens oriented with anterior to the top.
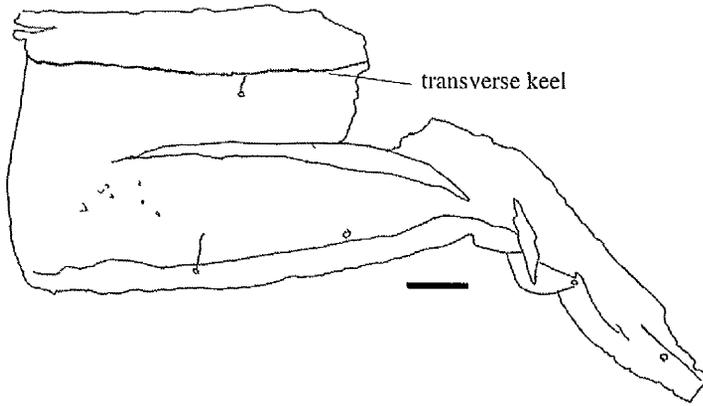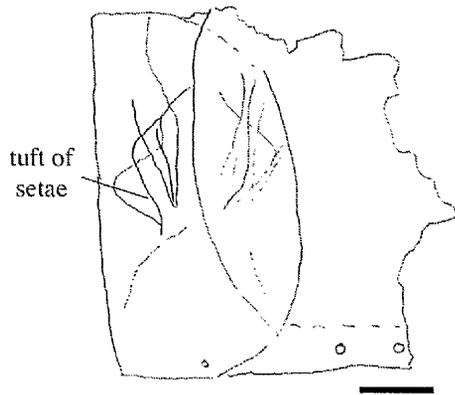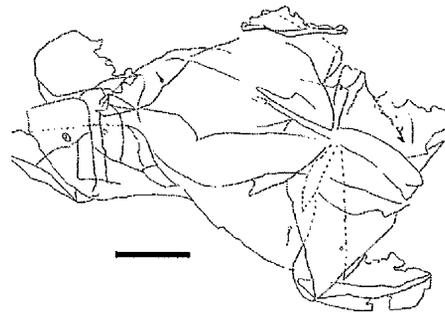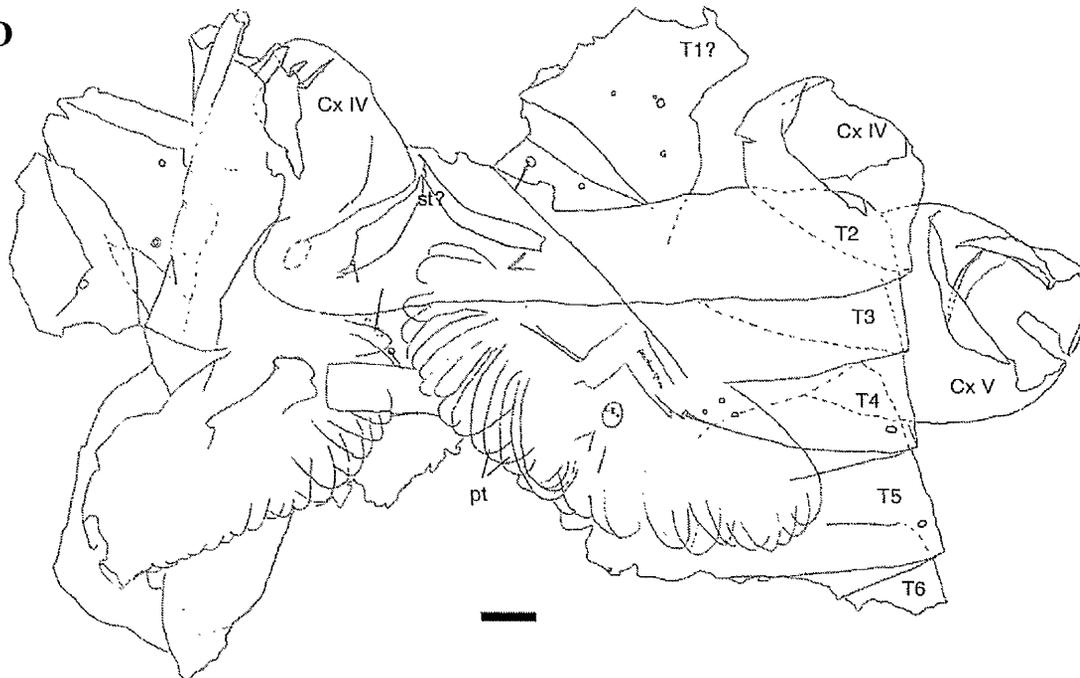
Figure 7.4 Interpretive drawing to accompany figure 7.3. **A**, tergite with transverse keel and rebordered anterior margin - SM1.115.V14 . **B**, tergite with pleural membrane? - SM1.130.8c. **C**, ?oblique view through metasoma - SM1.1.212.2. **D**, dorsal aspect of tergites, coxae and pectines - SM1.130.8. All specimens oriented with anterior to the top, scale bars represent 0.1mm.

7.2.2   Pectines

Four pectines have been recovered from South Mountain, exquisitely preserved with individual peg organs forming parallel bands on the distal margin of each pectinal tooth. Pectines are a unique feature of the order Scorpiones, and are among the most useful structures used in the identification of genera and species in all modern families. Pectines are comb-like sensory organs attached to the ventral mesosoma of scorpions. They have a mechano- and chemosensory function and brush over the ground as the animal walks. They are involved in locating mates, discerning substrate texture and identifying prey (Gaffin, 2002). In Recent scorpions they consist of three marginal lamellae and a variable number of median lamellae, fulcra and pectinal teeth (figure 7.5A). Median lamellae or fulcra are absent in some taxa and the number of pectinal teeth varies widely.

Specimen SM1.11.27 (figure 7.5B) is one of the most easily observed specimens. At least twenty-two pectinal teeth are preserved, which fan out and are attached via fulcra to the marginal and medial lamellae. Individual lamellae appear to be differentiated by thinning of the cuticle into a distal marginal lamella and a proximal medial and marginal lamella (figure 7.6A). Proximally, the presence of fulcra suggests the presence of at least six more teeth at one time. The specimen measures 1720µm along its long axis and 700µm at its widest point. The teeth are about three times as long as they are wide, and from the nature of the folding would have been fat, biconvex structures in life. Peg sensilla form thick bands along the posterior margin of each tooth. The fulcra are squat and each posses a single seta extending in the direction of the teeth. Additional setal sockets are present on the marginal and medial lamellae, which broaden proximally.

SM1.115.V12 (figure 7.5D) is part of a pectine, the two halves of which have been brought round together until they are facing each other, much like in specimen SM1.130.8 (figure 7.3E). The two halves each bear approximately fourteen pectinal teeth, arising from fulcra bearing a single seta. The pectinal teeth have been compressed in a similar fashion to those in specimen SM1.11.27 and have bands of peg organs on their proximal and posterior margins. It is impossible to say how many teeth would have belonged to this pectine in life, because both ends of the marginal and medial lamellae are missing.

Specimen SM1.130.8 (figure 7.3E) preserves an almost complete pectine in association with at least five mesosomal segments and three coxae (see section 7.2.1). The pectinal teeth number at least 32 on one side, but overlying cuticle obscures further details of their structure. These are the only pectines from South Mountain that are preserved with other body segments, and they would have extended to the edge of the body in life.
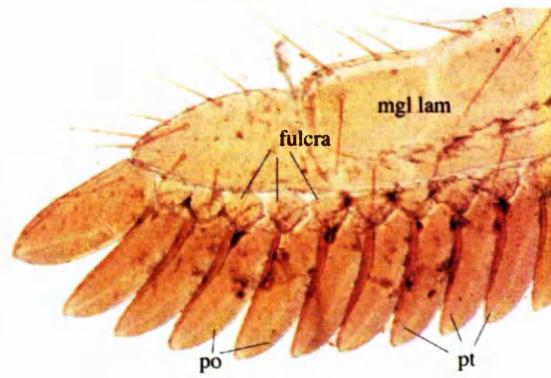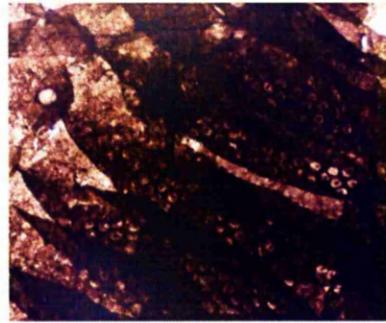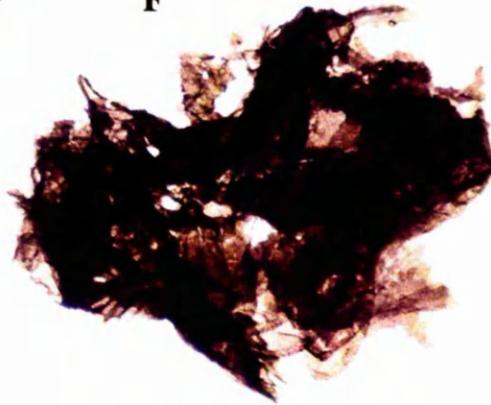
Figure 7.5 Scorpion pectines from South Mountain, New York. **A**, pectine from a Recent scorpion showing marginal lamella (mgl), fulcra (f), pectinal teeth (pt) and peg organs (po). Mangnification x25. **B**, half of a well preserved pectine - SM1.11.27. **C**, detail of SM1.11.27 to show teeth, fulcra and peg organs. **D**, opposing sets of pectinal teeth - SM1.115.V12. **E**, detail of SM1.115.V12. **F**, contorted mass of scorpion cuticle preserving pectinal teeth - SM1.213.13. All pieces oriented with anterior to the top. Magnification x50 for B, D and F.
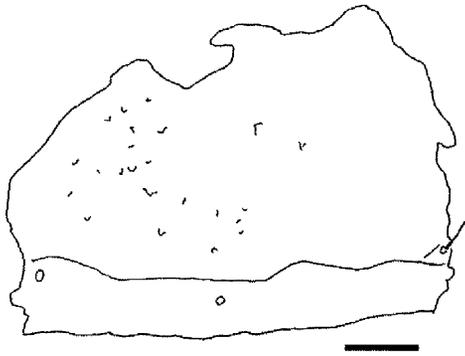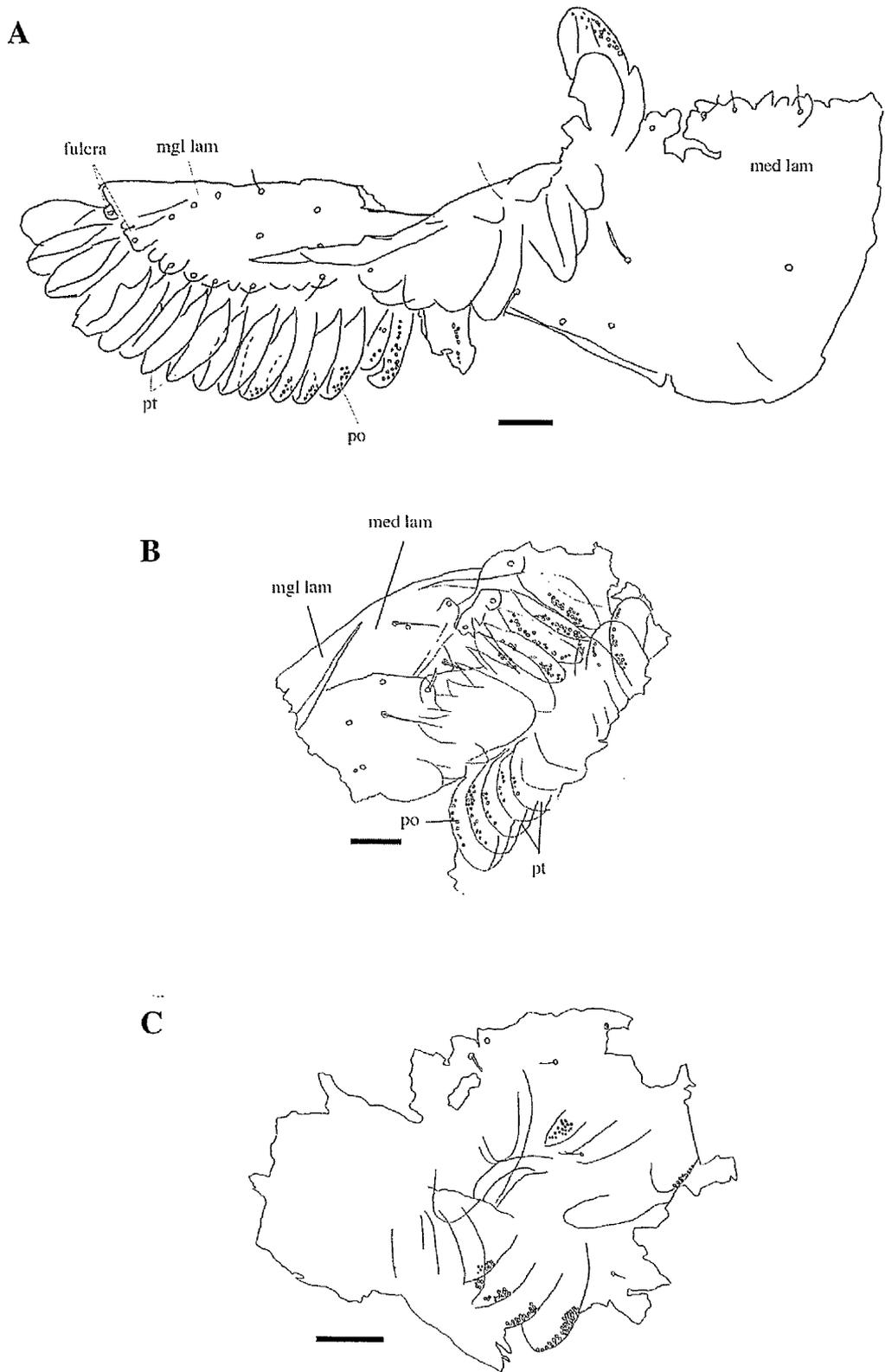
Figure 7.6 Interpretive drawings to accompany figure 7.5. **A**, half of a well preserved pectine - SM1.11.27. **B**, opposing sets of pectinal teeth - SM1.115.V12. **C**, contorted scorpion cuticle preserving pectinal teeth - SM1.213.13. All pieces oriented with anterior to the top. Scale bar represents 0.1mm.

A highly contorted jumble of scorpion cuticle (SM1.213.13; figure 7.5F, 7.6C) preserves the fourth pectine from South Mountain. The pectines have been folded around on themselves so that the teeth point in several directions and it is difficult to extract much meaningful information. The teeth are at least superficially similar to those seen in the three other specimens.

Pectinal teeth vary in shape and number inter- and intra-sexually within species, and inter-specific variation in shape and number may also be great (Stahnke, 1970). The number of peg sensilla increase as the scorpion increases in size and show inter-taxon and sometimes inter-sexual variation (Polis, 1990). With this in mind, the pectines from South Mountain show little variation, and there is no justifiable reason for suggesting that they represent more than one species of scorpion. Jeram (1989) arbitrarily set the derived state for Silurian and Devonian pectines as possessing more than 20 teeth. In practice, derived taxa possessed between 30 and 160 teeth per comb, and orthostern scorpions, including Upper Carboniferous examples, frequently had fewer than 20 teeth. The South Mountain scorpions appear to have possessed in the region of 30 fat rounded pectinal teeth, attached via fulcra to a differentiated plate. Differentiation is not easy to observe, but SM1.11.27 gives the suggestion of differentiation into marginal and medial lamellae, and SM1.115.V12 also appears to be differentiated, although it is incomplete. Kjellesvig-Waering (1986) only observed pectines divided into discrete lamellae in late Devonian and Carboniferous scorpions.

Despite poor preservation obscuring many of the details of the pectinal morphology of Palaeozoic scorpions, Kjellesvig-Waering (1986) described considerable variation and concluded that the majority of fossil scorpions had broader pectines with a more varied structure than their modern day relatives. *Proscorpius osborni* from the late Silurian, possessed pectines with an undifferentiated finlike anterior plate without rounded sclerites or areoles. Fulcra were well developed and teeth elongated but relatively stout. The Lower Devonian *Branchioscorpio richardsoni* also had a large, unjointed and undifferentiated plate, no fulcra and very large round flat teeth. From the Upper Palaeozoic, *Gigantoscorpio, Eoscorpius, Telmatoscorpio, Kronoscorpio* and many others had a well-developed jointed rachis (marginal lamella) and a greatly expanded middle lamella with areoles of irregular size and shape. In others the areoles were all consistently small and rounded throughout the middle lamella. Fulcra were well developed and the teeth were numerous, well in excess of fifty on each comb. Those that had short pectines did not develop the areoles, and in some cases the middle lamella and rachis were indistinguishable. (Kjellesvig-Waering, 1986).

7.2.3   Pedipalps

Scorpion pedipalp fragments recovered from South Mountain are illustrated in figures 7.7–7.10. The most frequently preserved parts of the pedipalp are the tarsi (moveable fingers), which have disarticulated from the tibia (manus and fixed finger), presumably prior to burial. It is possible that some of these represent the distally broken portion of a fixed finger, but in many of the specimens the finger widens proximally where it would articulate with the manus, and is not truncated by a sharp break. The only articulated pedipalp specimen is a patella and proximal part of a tibia (specimen SM1.4.8a, figure 7.7A, B). A tarsus of similar proportions, and recovered from the same shale sample, probably belongs with it. The patella is relatively short and is twisted slightly in relation to the tibia so that it is preserved in ventral aspect. The curved dorsal margin measures 400μm and is about twice the length of the ventral margin. At its deepest point the patella measures 250μm.

The tibia is incomplete but measures about 270μm at its deepest point, and approximately 300μm from its proximal edge to the point of articulation with the tarsus. The tarsus is approximately 120μm wide in its flattened state, and seven times as long as it is wide, suggesting an overall length of 1140μm for the chela of specimen SM1.4.8. Towards the dorsal margin of the manus are two dark sclerotised protrusions marking the site of articulation with the tarsus. At the base of the fixed finger is another protrusion, which may represent an apophysis (see below). The dentition of the fixed finger is cultrate with larger single teeth separating groups of single teeth along its length. The associated tarsus of SM1.4.8 and specimen SM1.115.V36 (figure 7.7C) both show similar cultrate dentition. Both tarsi have groups of 5–10 smaller teeth separated by larger single teeth and terminate in a sharp, upward curving tip. The three remaining tarsi (specimens SM1.128.10, SM1.115.V44, SM1.120.V5; figure 7.7D, E, F) have no large teeth, only very tiny denticles, and terminate in a blunt tip. These specimens can be almost exactly matched by their arrangement of setal sockets towards the tip of the finger (figure 7.9). Setae are concentrated near to the cutting margin of the finger and are fewer on interior and exterior aspects.
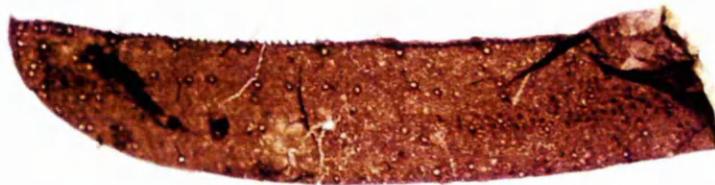
Figure 7.7 Scorpion pedipalps from South Mountain, New York State. **A**, pedipalp patella and tibia with prominant apophysis - SM1.4.8a. **B**, pedipalp tarsus associated with and possibly belonging with A - SM1.4.8. **C**, sculpted pedipalp tarsus with cultrate margin - SM1.115.V36. **D**, pedipalp tarsus with single row of denticles - SM1.115.V44. **E**, pedipalp tarsus with single row of denticles - SM1.128.10. **F**, pedipalp tarsus with single row of denticles - SM1.120.V5. Magnification x100.
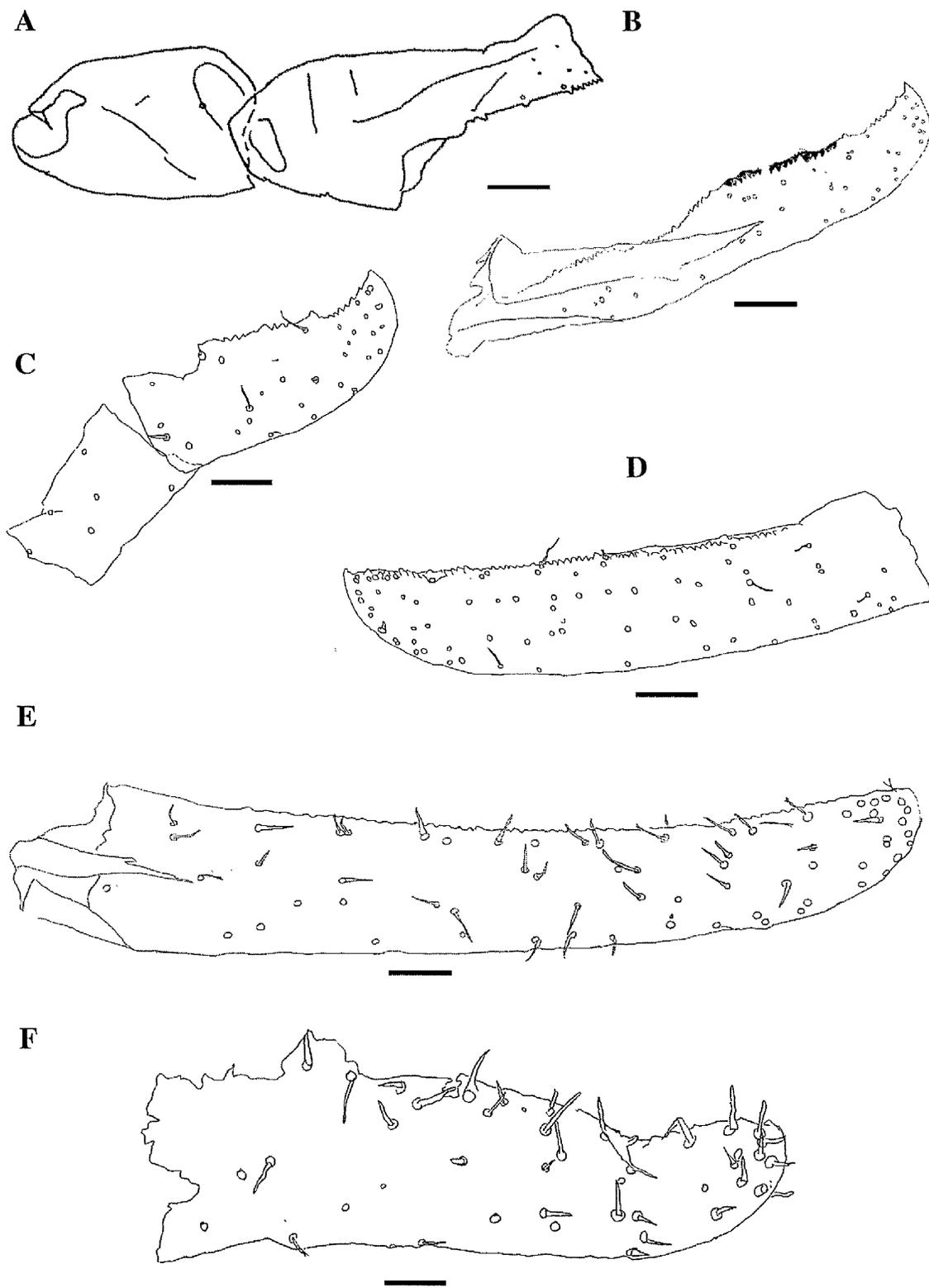
Figure 7.8 Interpretive drawings to accompany figure 7.7. **A**, pedipalp patella and tibia with prominant apophysis - SM1.4.8a. **B**, pedipalp tarsus associated with and possibly belonging with A - SM1.4.8. **C**, sculpted pedipalp tarsus with cultrate margin - SM1.115.V36. **D**, pedipalp tarsus with single row of denticles - SM1.115.V44. **E**, pedipalp tarsus with single row of denticles - SM1.128.10. **F**, pedipalp tarsus with single row of denticles - SM1.120.V5. Scalebars represent 0.1mm.

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Could these differences in dentition reflect sexual dimorphism in a single species, or do the recovered fragments represent two different taxa? Dentition does vary amongst fossil taxa, and some Silurian genera (*Palaeophonus* and *Proscorpius*) have fingers with cultrate edges, whilst others have a single file of small denticles as in the Lower Devonian *Branchioscorpio* (Kjellesvig-Waering, 1986). However, male scorpions may exhibit distinct scalloping on the inner margins of the pedipalp-chela fingers, and stronger carinae on the pedipalps and metasoma, whilst in females these margins are at most weakly scalloped (Polis, 1990). It is therefore conceivable that those pedipalp fingers displaying more sculpted margins and cultrate dentition are the male equivalents of those without. Furthermore, amongst bothriurids the male pedipalp is modified with either an apophysis or a semicircular
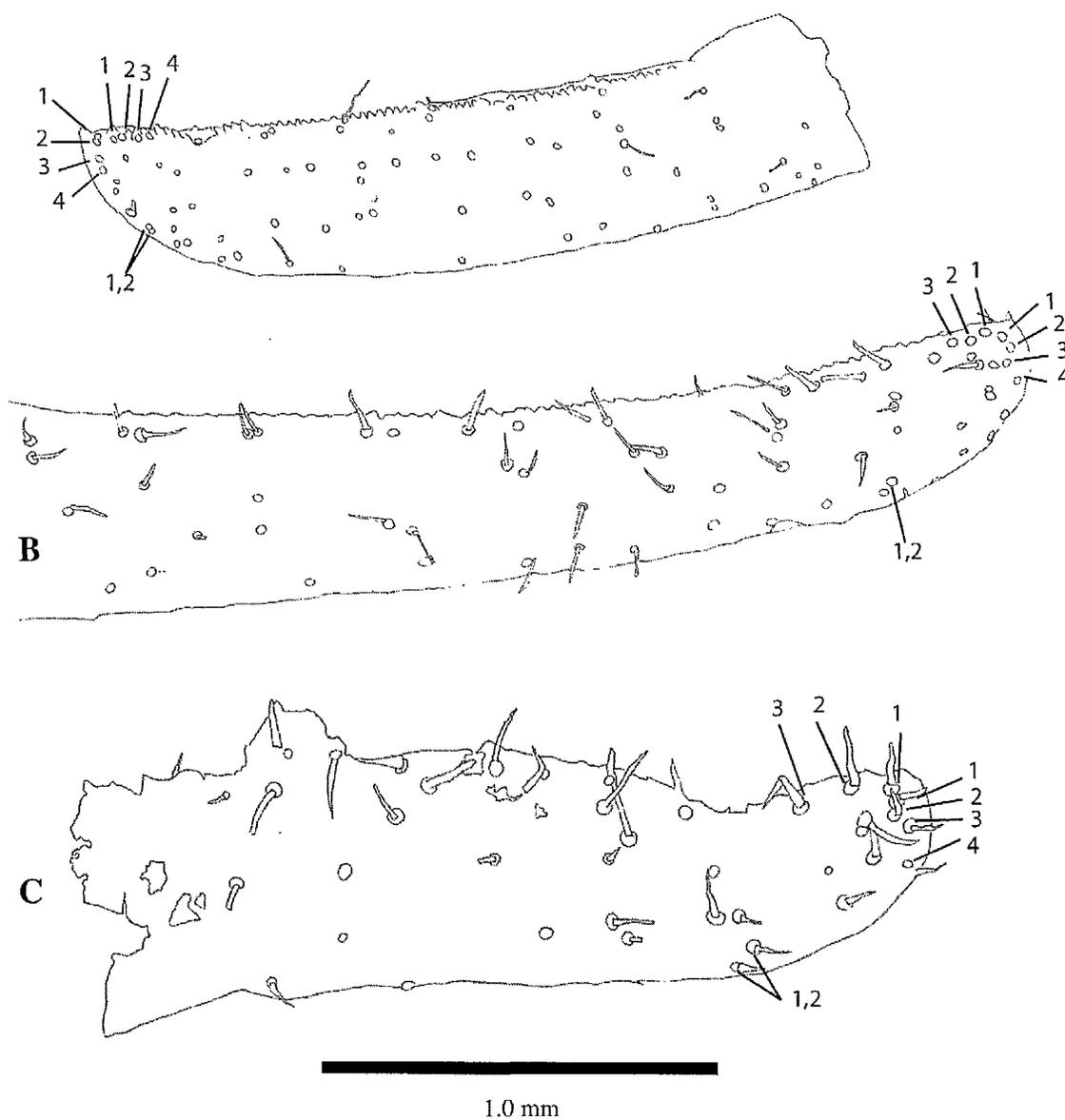
Figure 7.9 Location of setae on scorpion pedipalp fingers (tarsi) from South Mountain. **A**, SM1.115.V44. **B**, SM1.128.10. **C**, SM1.120.V5. Scale bar represents 1mm.

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depression at the base of the fixed finger, which aids in securing the female chelae during mating. Such an apophysis occurs on specimen SM1.4.8a (figure 7.7A), which also has cultrate dentition. These observations lend support to the hypothesis that the morphological variation in recovered chelae from South Mountain is a reflection of sexual dimorphism rather than species richness.

In assessing character states of Silurian and Devonian scorpions, Jeram (1989) divided the pedipalps by length. Short pedipalp fingers (not exceeding the length of the manus) were considered typical of early scorpions, and longer fingers typical of late Palaeozoic scorpions. The greatly inflated manus seen in some living scorpions is unknown in scorpions from the Palaeozoic (Kjellesvig-Waering, 1986).

7.2.4   Walking legs

There are a number of different sized and shaped podomeres recovered from South Mountain all united by their granular textured cuticle, longitudinal rows of spines and small thorns (figures 7.10–7.13). The only articulated specimen is SM1.119.50 (figure 7.10A), which, by comparison with living scorpion legs, represents the femur, tibia and the proximal portion of the basitarsus. The patella is a broad podomere with curved dorsal and ventral margins and several longitudinal rows of tiny spines or thorns. Two rows occur on the lateral face of the podomere (in its flattened state) and one each along the dorsal and ventral margins. Each row of thorns is associated with sparsely scattered setal sockets, but no setae are preserved in this specimen. The proximal margin of the patella is torn, but the distal margin is convex with the cuticle pulled out into a triangular process towards the ventral margin. A similar triangular process, but situated towards the ventral margin, is described from a similarly shaped podomere figured in Shear *et al.* (1998) and interpreted as the prefemur of a scutigeromorph centipede. The tibia of specimen SM1.119.50 is a more elongate podomere with subparallel margins. It measures approximately 280μm across the short axis and is about two and a half times as long. There are three rows of distally directed spines occurring midlaterally, ventrally and dorsally. Proximally the tibia joins the patella via prolateral and retrolateral articulations forming a transverse hinge line. Distally there is slight emargination of the ventral surface. There are no large spines or spurs on the distal margin, although in Recent scorpions (*e.g.* Buthidae) these sit within arthrodial membrane and would not necessarily remain articulated in fossil specimens. The basitarsus is narrower than the tibia (about 200μm wide), but the distal margin is missing so it is not possible to ascertain the length. Once again there are three rows of small spines associated with sparse setal sockets.
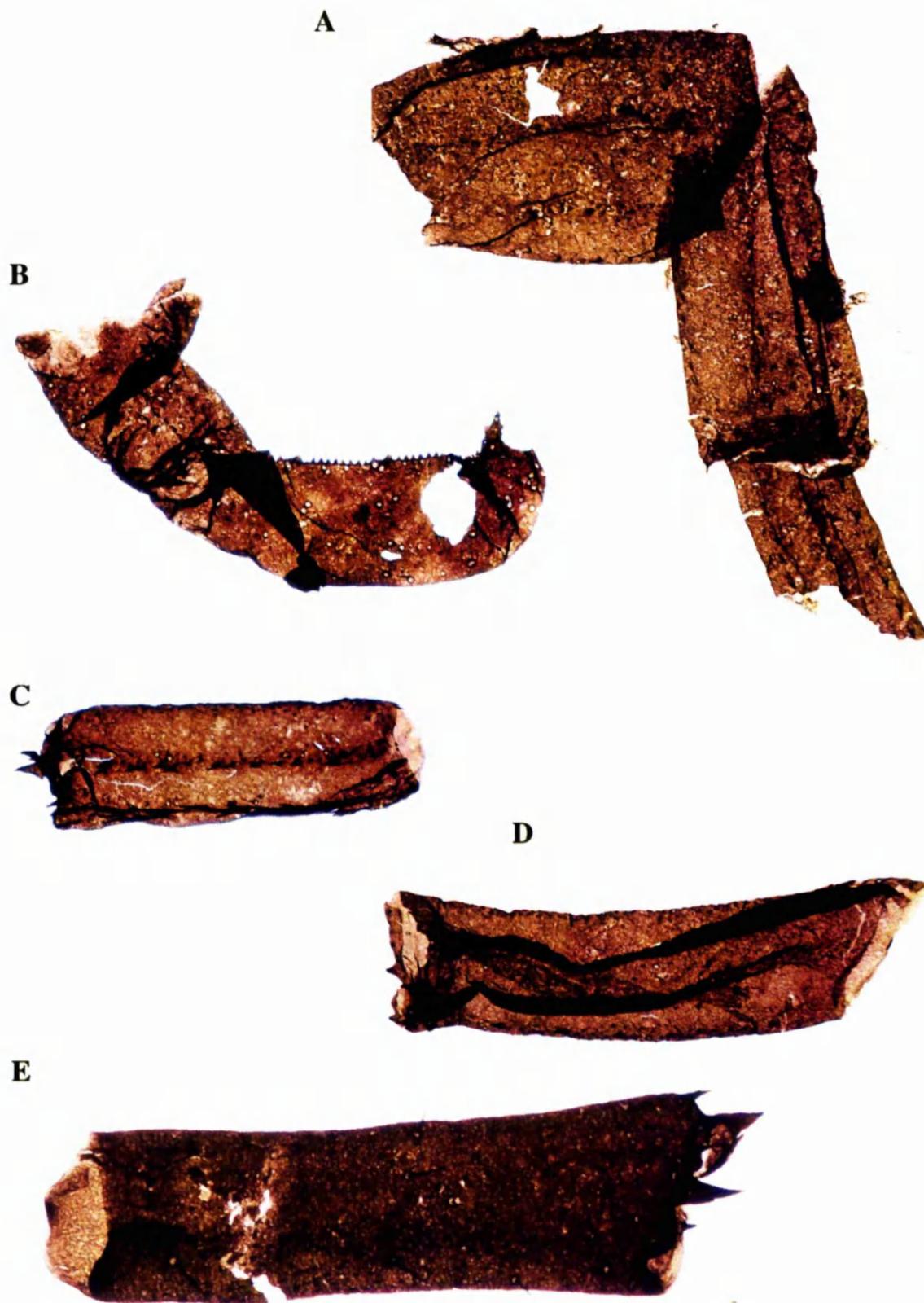
Figure 7.10 Scorpion podomeres from South Mountain, New York. **A**, articulated patella, tibia and basitarsus - SM1.119.50. **B**, pedipalp tarsus with single row of denticles - SM1.3.16. **C**, single podomere with distal spines - SM1.5.1. **D**, single podomere - SM1.120.6. **E**, single podomere with thorns and distal spines - SM1.115.V38. Magnification x100.
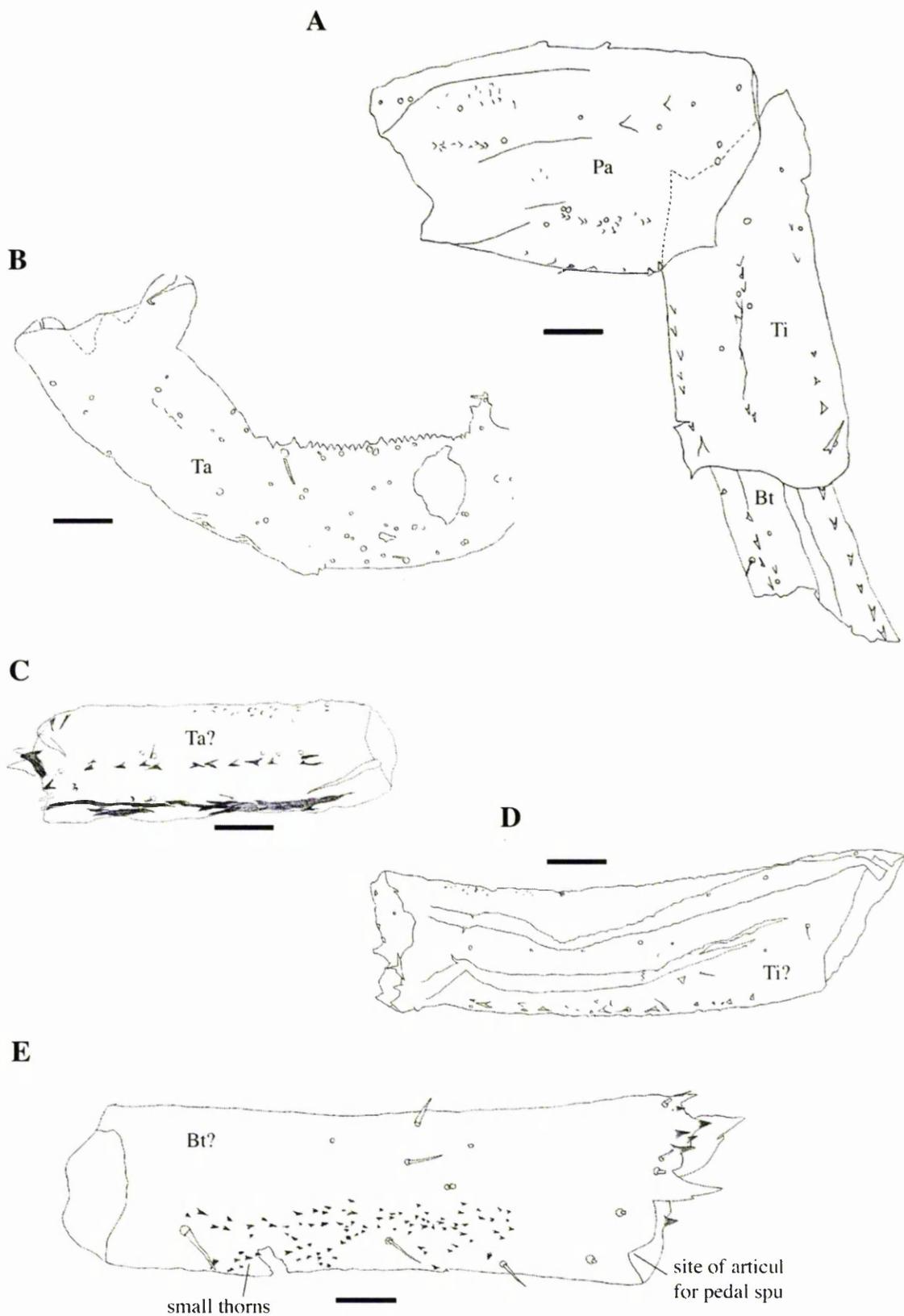
Figure 7.11 Interpretive drawings to accompany figure 7.10. **A**, articulate patella, tibia and basitarsus - SM1.119.50. **B**, pedipalp tarsus with single row of denticles - SM1.3.16. **C**, single podomere, ?tarsus, with distal spines - SM1.5.1. **D**, single podomere, ?tibia - SM1.120.6. **E**, single podomere, ?basitarsus, with thorns and distal spines - SM1.115.V38. Scale bars represent 0.1mm.
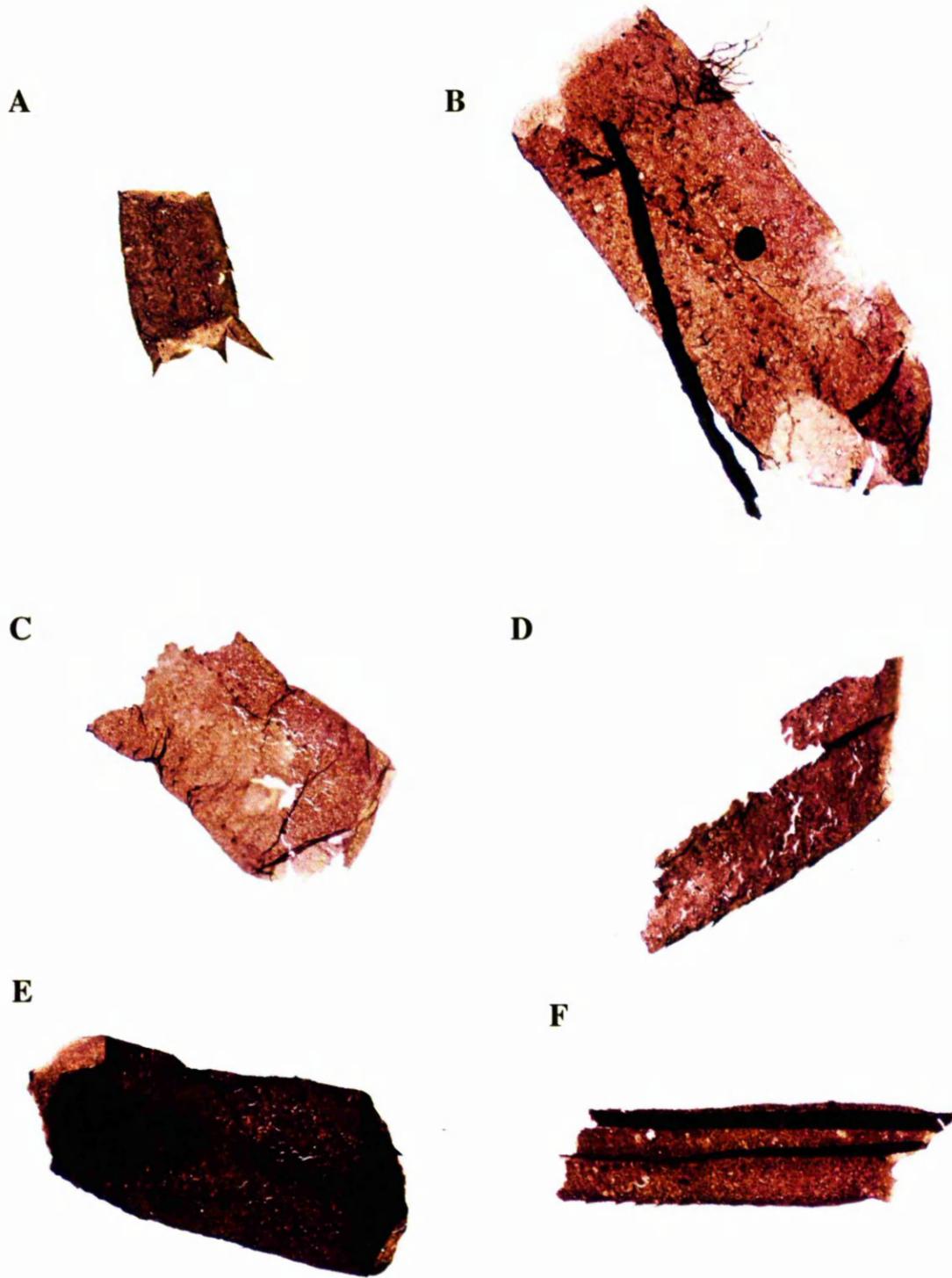
Figure 7.12 Scorpion podomeres from South Mountain, New York. **A**, short podomere (tarsus?) with distal spines - SM1.212.8. **B**, podomere with emarginated ventral surface - SM1.4.7a. **C**, small wrinkled podomere fragment - SM1.212.5. **D**, podomere fragment with serrated margin - SM1.212.6. **E**, scorpion? podomere - SM1.11.24. **F**, podomere with serrate margin - SM1.122.3. Magnification x50.

A

B

Ta?

large distal
spines

Sp

plant
fragment

emarginated
distal margin

C

D

wrinkled
cuticle surface
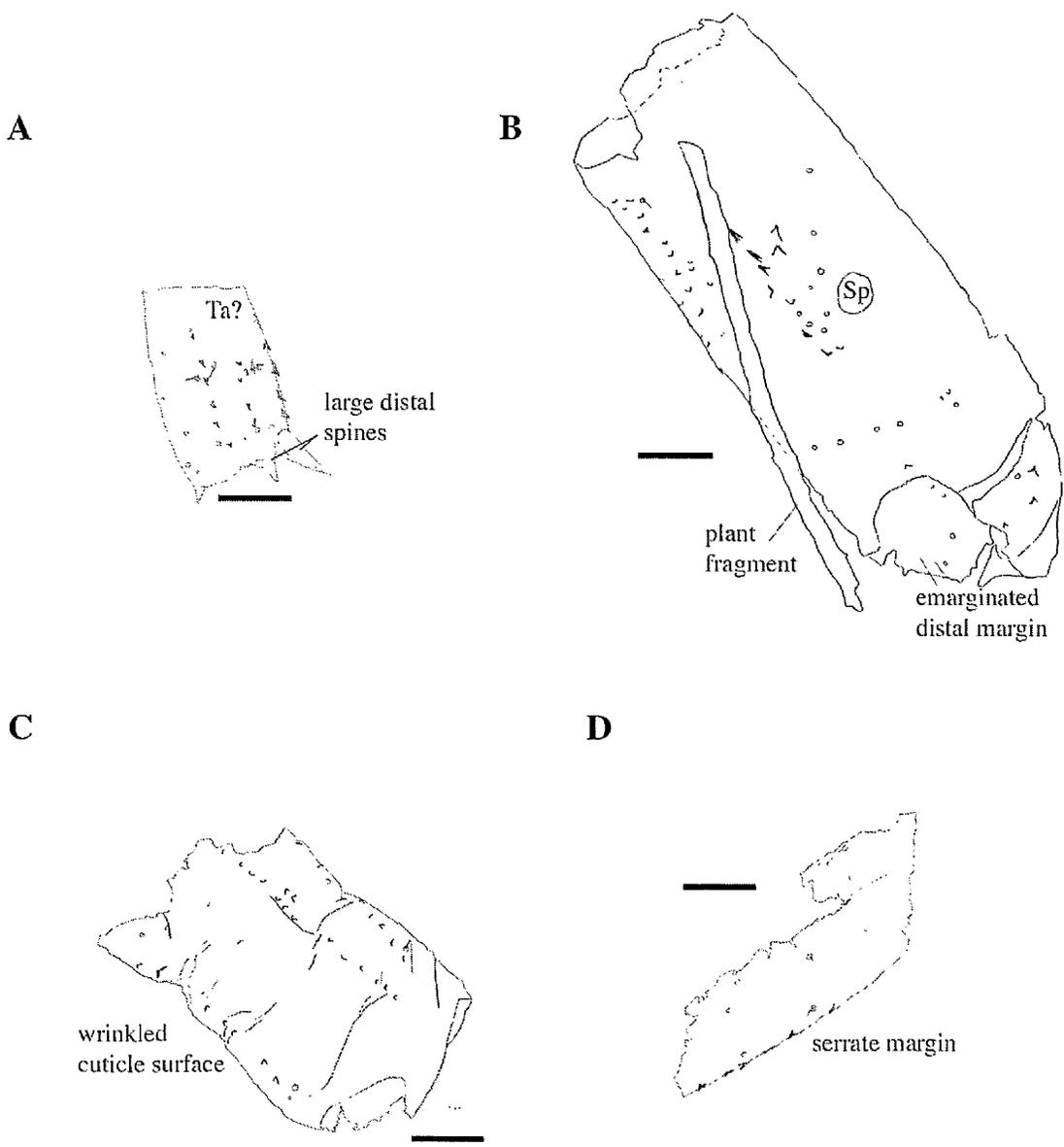
serrate margin

Figure 7.13 Interpretive drawings to accompany figure 7.12. **A**, short podomere (tarsus?) with distal spines - SM1.212.8. **B**, podomere with emarginated ventral surface - SM1.4.7a. **C**, small wrinkled podomere fragment - SM1.212.5. **D**, podomere fragment with serrated margin - SM1.212.6.Scal bars represent 0.1mm.

Two other podomeres (figures 7.10C and 7.12A) share similar characteristics with the articulated specimen described above. SM1.212.8 (figure 7.12A, tarsus?) is a short, rounded podomere with three large distal spines and three longitudinal rows of small spines. Specimen SM1.5.1 (figure 7.10C, tarsus?) similarly bears longitudinal rows of small spines, but is considerably longer and is preserved with two or three shorter processes protruding from the distal margin. All of these podomeres give the impression of a boxy construction, probably with two rows of spines occurring on the dorsal surface, one on the ventral surface and one on both prolateral and retrolateral surfaces. In a flattened specimen these may then appear as either three or four rows on either side of the podomere. Podomeres with a circular cross section are evident in some Silurian scorpions and also in eurypterids. All other scorpions show some degree of lateral compression (Jeram, 1997). Specimen SM1.115.V38 (figure 7.10E) is of similar proportions to SM1.5.1 and also bears spines on the distal margin. The longitudinal rows of spines seen on the other podomeres, however, are absent and instead there is a concentration of minute thorns along the ventral side of the podomere. Most late Palaeozoic and Recent scorpions have prominent rows of fixed cuticular thorns or stout moveable setae on the inferior surface of the basitarsus and telotarsus (Jeram, 1997). A prominent cuticular thickening combined with an embayment in the distal margin probably represents the site of articulation for a pedal spur on the basitarsus. Only three species of living scorpions are known to lack this characteristic (Polis, 1990).

SM1.120.6 (figures 7.10D, 7.11D) is a narrow podomere with longitudinal rows of spines and small processes protruding from the distal margin. These processes are much shorter than in other specimens and the emargination of the proximal margin suggest that this might represent a tibia.

Remaining podomeres are included here because of their 'scorpion-like' appearance, but until further material comes to light it is difficult to draw solid conclusions from amongst these isolated pieces. Although specimen SM1.212.6 (figures 7.12D, 7.13D) has a granular cuticle pattern, the saw-tooth margin is reminiscent of characteristic podomeres described from Ludford Lane, Rhynie and Gilboa as scutigeromorph centipede legs (Shear *et al.*, 1998).

7.2.5   *Metasoma*

Metasomal segments are easily recognisable as simple body rings with no evident sterna or terga. They are roughly rectangular and are ornamented with dark granular keels, which run longitudinally down the length of each segment. The keel is a structural thickening of the exoskeleton associated with stress points, and can be of taxonomic importance.
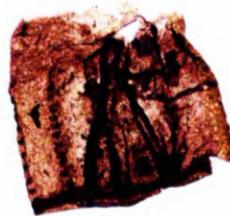
Figure 7.14 Scorpion metasomas. **A**, three articulated metasomal segments with well developed keels - SM1.119.29. **B**, two large articulated metasomal segments - SM1.19.1. **C**, elongate metasomal segment, possibly representing final segment prior to telson - SM1.16.1 x50. **D**, small metasomal segment with keels - SM1.4.7b. **E**, small metasomal segment with spore to left of picture - SM1.212.2a. Magnification x50.
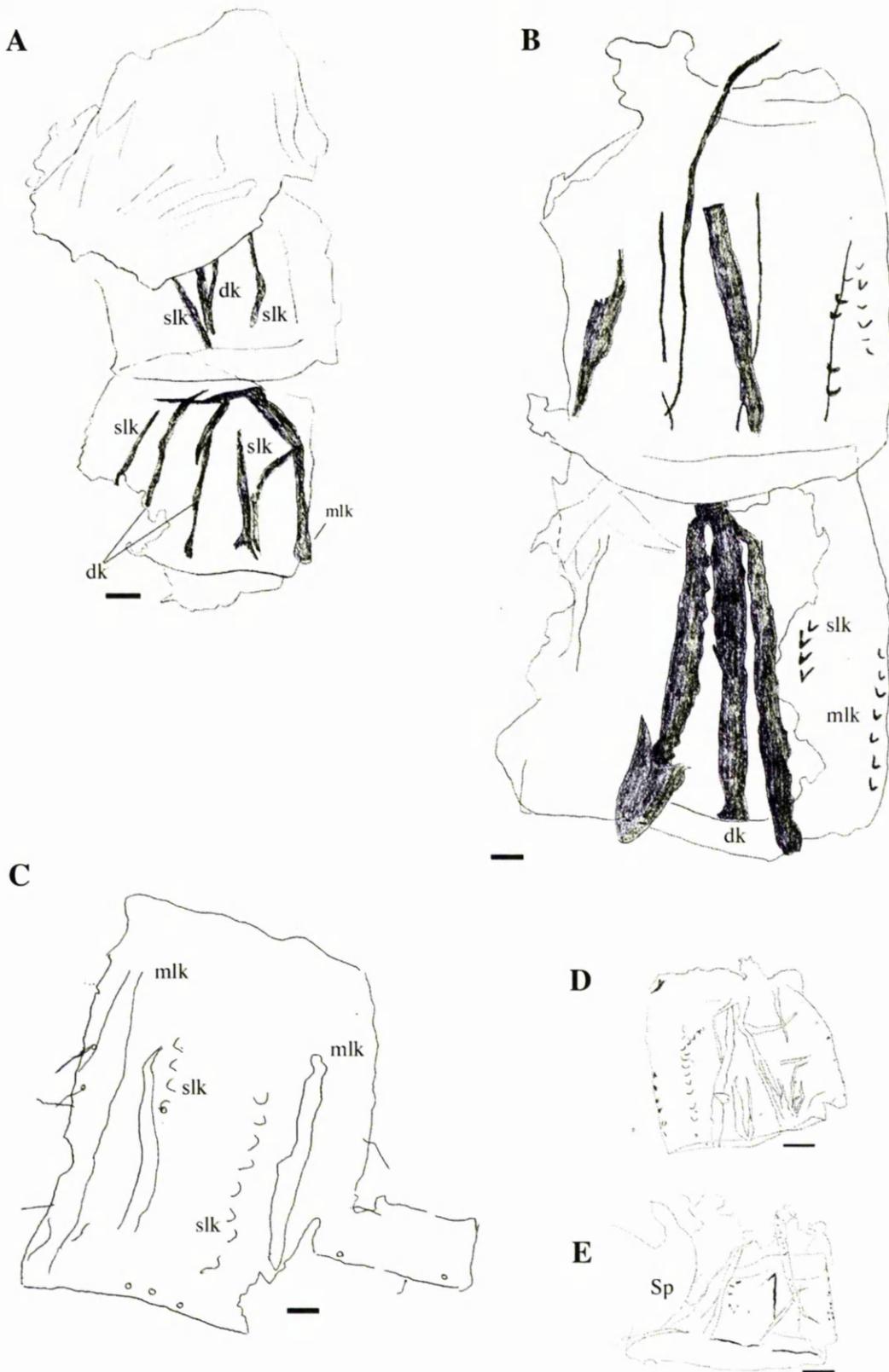
Figure 7.15 Interpretative drawings to accompany figure 7.14. **A**, three articulated metasomal segments with well developed keels - SM1.119.29. **B**, two large articulated metasomal segments - SM1.19.1. **C**, elongate metasomal segment, possibly representing final segment prior to telson - SM1.16.1 x50. **D**, small metasomal segment with keels - SM1.4.7b. **E**, small metasomal segment with spore to left of picture - SM1.212.2a. Scale bars represent 0.5mm.

In Recent and fossil scorpions there are five metasomal segments, which become progressively longer distally and terminate in a telson formed from a bulbous vesicle and needlelike aculeus. In living scorpions the fifth segment is always the longest and usually lacks dorsal keels (Stahnke, 1970). The metasoma is a fairly robust part of any scorpion and there are two examples of articulated segments from South Mountain. Metasomal segments are illustrated in figures 7.14 and 7.15.

Specimen SM1.119.29 (figure 7.14A) shows three articulated body rings from the metasoma. The segments themselves are short, and are only slightly wider than they are long. The third segment is the longest and narrowest and measures about 660μm long and 760μm wide. The first preserved segment measures approximately 550μm by 860μm. SM1.119.1 is almost three times the size of specimen SM1.119.29 but has similar proportions (figure 7.14B). The second preserved segment is longer and slightly narrower than the first. Both specimens are ornamented with at least three strongly developed, granulate keels running longitudinally down each segment. Assuming these metasomal segments are preserved in dorsal aspect, the following pairs of keels can be recognised (figure 7.15A, B): dorsals, superior laterals and median laterals.

Specimen SM1.16.1 (figure 7.14C) is the largest metasomal segment, measuring 980μm across its short axis and 1320μm along the long axis. Only the superior/inferior laterals and median laterals are preserved, which, by analogy, suggests that this might be the fifth (preanal) metasomal segment. It has the highest length to width ratio of all the metasomal segments. It is also the only metasomal segment with preserve setae. The other two pieces of scorpion metasoma (figure 7.14D, E) are considerably smaller and measure approximately 560μm long and 500μm wide. They too possess well-developed keels.

7.3   Summary

The simplest method for taxonomic grouping of dispersed arthropod cuticle, and one advocated by Jeram (1989), is to assume that all fragments belong to one species unless there is sufficient reason to believe otherwise. This assumption has reasonable basis since it is likely that at least some fragments were originally associated within the sediment, and any other method could potentially result in the erection of a new species for each sclerite.

Ventral abdominal plates are unknown from South Mountain and tergites possess a well-developed anterior transverse keel and sparse setal sockets. The presence of clumps of long fine setae on a tergite is an unusual characteristic and the significance of this is uncertain. Pectines were probably wider than the body in life and possessed around 30 fat, rounded teeth, which attached via fulcra to a differentiated plate. Each fulcra bore a single seta. The chelae are long and slender and morphological differences can be attributed to

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sexual dimorphism. Podomeres from the walking legs show a degree of variation in their ornamentation, but there are insufficient specimens to draw firm conclusions from this. It is also questionable as to whether all of these specimens represent scorpions and not centipedes. Finally, the metasomal segments are broad with strongly developed granulate keels.

Aside from obvious differences in sizes there is insufficient variation amongst all of these cuticle pieces for them to realistically represent more than one species. If all scorpion fragments are assumed to have originated from a single species then their character states can be assessed following the cladistic analysis of Silurian and Devonian scorpions by Jeram (1989). The 'South Mountain scorpion' has a mix of plesiomorphic and derived characters, which do not fit with any of the taxa included in Jeram's analysis. Derived characters include the pectines (more than 20 pectinal teeth, lamina with discrete lamellae), the long slender pedipalp tarsi, the presence of ventral thorns on the basitarsus and an elongated preanal segment. The absence of a reticulate cuticle is coded as a plesiomorphic feature (although there is evidence for some partly reticulate cuticle at South Mountain) as is the absence of tubercles on the carina of the pedipalp patella, and the relatively short length of this podomere, which is approximately equal in length to that of the manus.

It is difficult to fit character states obtained for disassociated cuticle fragments into a character state matrix that includes many characters that are unknown for many of the specimens. Naturally, the best fit tends to occur amongst taxa for which there is little overlap in available character states (i.e. taxa which include character states unknown in the South Mountain scorpion material and exclude those that are known). It may be that the material from South Mountain represents more than one taxon and therefore assuming it to be one species creates an artificial hybrid with an unrealistic set of characters. However, without further material it is difficult to speculate further. If the South Mountain scorpion material is representative of a single species, then it might be expected that the animal had long, slender pedipalps and a strong, powerful cauda not dissimilar to some genera of the modern day Buthidae. The morphology of the metasoma is broadly consistent with that described for a Cretaceous micro-buthid (only 10mm long) from Burmese amber (Lourenço and Palevol I, 2002), and the Emsian scorpion from New Brunswick in Canada also showed features consistent with extant buthids. The lamellae of the book-lungs were described with a strengthening bar of cuticle at the posterior end of each, and reticulate thickening of the lamellar surfaces (Shear et al., 1996).

CHAPTER 8   PULMONATA

The pulmonate arachnids are represented by the living orders Araneae, Amblypygi, Uropygi, and Schizomida, and the extinct order Trigonotarbida. Representatives from at least three of these groups are found in Devonian rocks of New York State, and nearly all are united by a reticulate cuticle sculpture that either covers the entire surface or is restricted to specific areas of the exoskeleton. These cuticle fragments occur as individual plates, articulated sclerites and occasionally as compressed and folded jumbles of exoskeletal elements. A high proportion of the reticulate patterned cuticle came from South Mountain, and many fragments were recovered from a single shale sample (*e.g.* SM.1.120). It is probable that these were fairly localised within the sediment and may have all originated from a single animal (see chapter 4 for a discussion on cuticle distribution within the sediment).

Cuticles with a reticulate pattern can be subdivided into three categories based upon the morphology of the reticulations and associated cuticular features. For simplicity, and to aid future identifications and reassessment of cuticle types, these are referred to here as cuticle types reticulate A, reticulate B, and reticulate C. Their defining features are described below.

8.1   Reticulate A

8.1.1   Cuticle Topography

Reticulate A cuticle bears a distinctive pattern of raised polygons forming a scale-like topography across the surface (figures 8.3–8.9). Each scale thickens distally and overlaps onto the next so that it forms the proximal border of the next polygon. Reticulations usually cover the cuticle surface entirely, but may show some variation in size and shape with position on the sclerite (*e.g.* specimen SM1.4.7 (figure 8.6E), in which reticulations diminish in size towards the distal articulation of the podomere). Minute pores, measuring 2–3 μm and scattered over the cuticle surface, are characteristic of this cuticle type. These holes have an oval to circular outline, a thickened cuticle border and do not show any internal features.

8.1.2   Sensory organs

Many reticulate A cuticle fragments are covered with numerous long fine setae. These are plain and taper gently to a slender tip, which has frequently broken off. They show no ornamentation or bifurcation. Setal sockets are numerous and show an approximately bimodal size distribution (see figure 8.1). Most setal sockets measure approximately 6 μm in diameter and certain podomeres (*e.g.* the patella) bear significantly larger (10 μm) sockets

Size frequency of setal sockets in reticulate A cuticle pieces
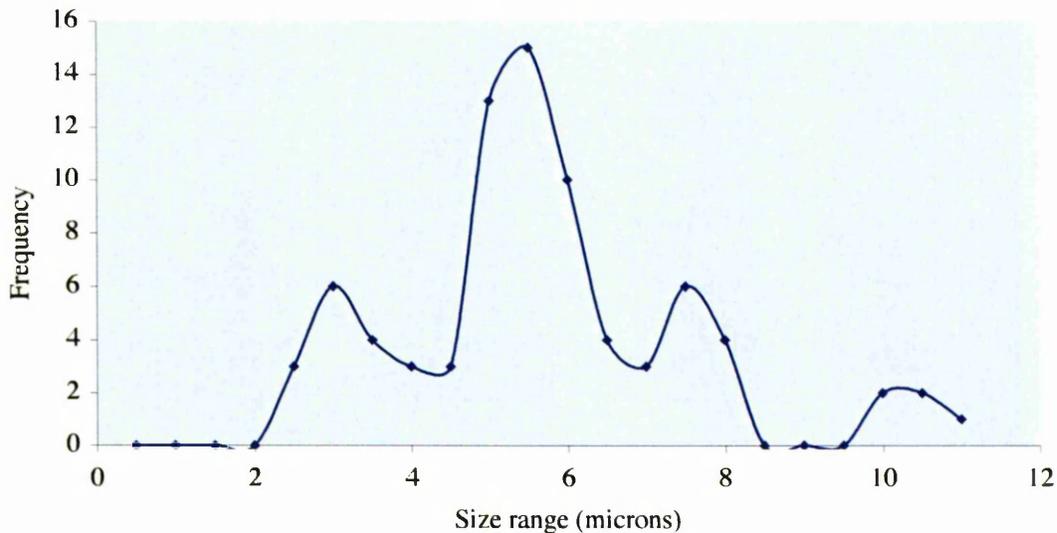
Figure 8.1 Size frequency of setal sockets in reticulate A cuticle fragments. Graph shows two partially overlapping sets of bimodally distributed data, probably resulting from variation in podomere size (see also figure 8.11). The smallest peak, representing the largest sized setal sockets, corresponds to setal sockets found on the patellae.

(see figure 8.11). The very small pores scattered over the surface of the cuticle measure approximately 2µm in diameter and are probably analogous to the single slit sense organs of Recent spiders (see figure 8.2).

Podomeres with a reticulate A cuticle pattern frequently bear slit sensilla and compound lyriform organs on their margins. In modern arachnids slit sensilla occur as isolated single slits, loose groupings of several slits, or composite arrangements of 2–29 slits arranged in parallel and commonly surrounded by a cuticular border, known as lyriform organs (Barth, 2002). Slit sensilla measure mechanical stress in the cuticle and occur in greater numbers at the distal ends of podomeres. In true lyriform organs the slit sensilla are neurally integrated to act as a single unit. Morphologically they are recognised as true lyriform organs if the slits are as close together as their individual widths, and are parallel to one another (Selden *et al*, 1991). Recent spiders have fifteen lyriform organs on each leg, orientated parallel to the long axis of the leg with the exception of the metatarsus where it is perpendicular (Barth, 2002). In other arachnids there are between zero and two lyriform organs on each leg, and where spiders have lyriform organs, scorpions and uropygids have groups of single slits (Barth, 2002). Lyriform organs occur in amblypygids and uropygids only on the distal end of the metatarsi of legs 2–4. Slit sensilla are a unique feature of arachnids, and only in spiders do lyriform organs occur on podomeres other than the metatarsi.
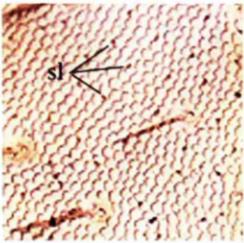
Figure 8.2 Detail of *Heptathela* femur showing scale like cuticle topography scattered with minute slit sensilla (sl) and setae.

Much of the reticulate A cuticle bears a strong resemblance to, and is often indistinguishable from, cuticle from Blenheim-Gilboa described as the spider *Attercopus fimbriunguis* (Shear and Selden, 1991). However, not all of the fragments recovered here are identical and some exhibit notable differences. These are discussed below.

8.1.3   Cuticle morphology

Podomeres form the majority of the cuticle material in this category, together with two possible examples of cuticle from the carapace and abdomen. Descriptions of individual pieces are set out below.

Carapace:

Specimen SM1.120.V2 (figures 8.3A, 8.4A) shows three distinct podomere-shaped cuticle pieces, one of which appears to be attached to a cuticle fragment with an apparently sculpted margin, possibly representing part of the carapace. The attitude of the setae, however, indicate that the longest podomere is orientated with the proximal margin to the right, therefore it seems that the two fragments are merely compressed together and were not attached to each other in life. The carapace fragment bears a large (30μm) elliptical hole towards one of the margins, which could represent an eye. Small marginal setal sockets occur nearby, but are not observed elsewhere. The cuticle sculpture and associated podomeres are identical to that of *A. fimbriunguis*, which Selden *et al.* (1991) described as possessing a carapace without sculpted margins and with setal sockets restricted to the anterior margin. Elliptical holes in the cuticle measuring approximately 100μm (maximum diameter) were interpreted as eyes. The apparent sculpture of the margins of the carapace in SM1.120.V2 is difficult to unravel but could have resulted from the cuticle having folded across an eye-hole.

All four cuticle fragments in specimen SM1.120.V2 bear an identical reticulate pattern, long, fine setae, and minute pores scattered across the cuticle surface. The longest podomere measures about 200μm wide and at least 520μm long, although the distal margin is missing, and is interpreted as a femur. The shortest fragment is interpreted as a patella and the remaining piece as part of a tibia (see below).
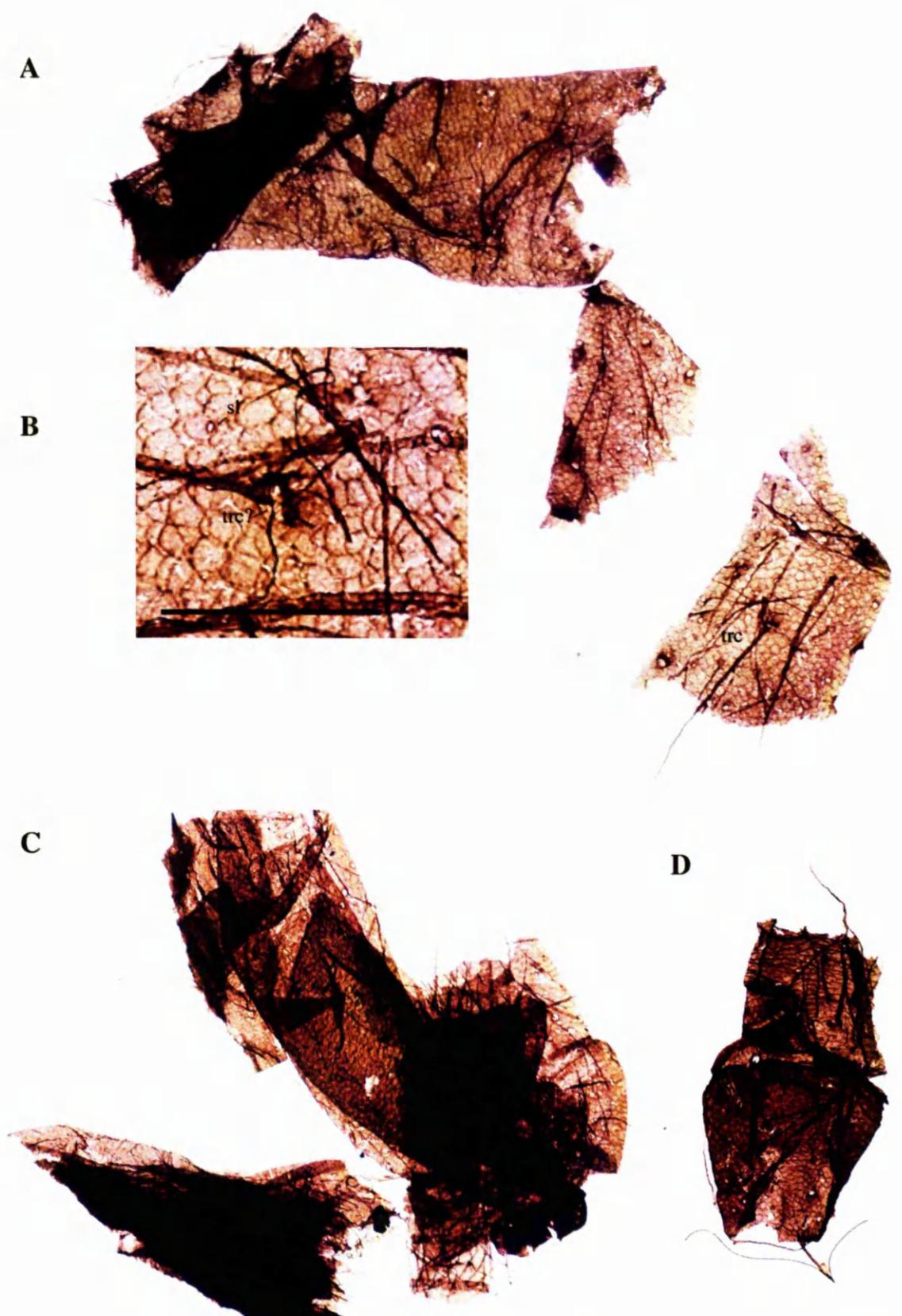
Figure 8.3 Reticulate A cuticle. **A**, two podomeres with ?part of carapace - SM1.120.V2. **B**, high magnification of base of macrosetae from tibia. Small slits in cuticle possibly represent ornamented base of trichobothria. Scale bar reprepsents 0.1mm. **C**, four femora and two patella associated with a flagelliform structure and part of the abdomen (see figure 8.4 for explanation) - SM1.120.V7. **D**, patella and tibia - SM1.11.13. Magnfication x 100.
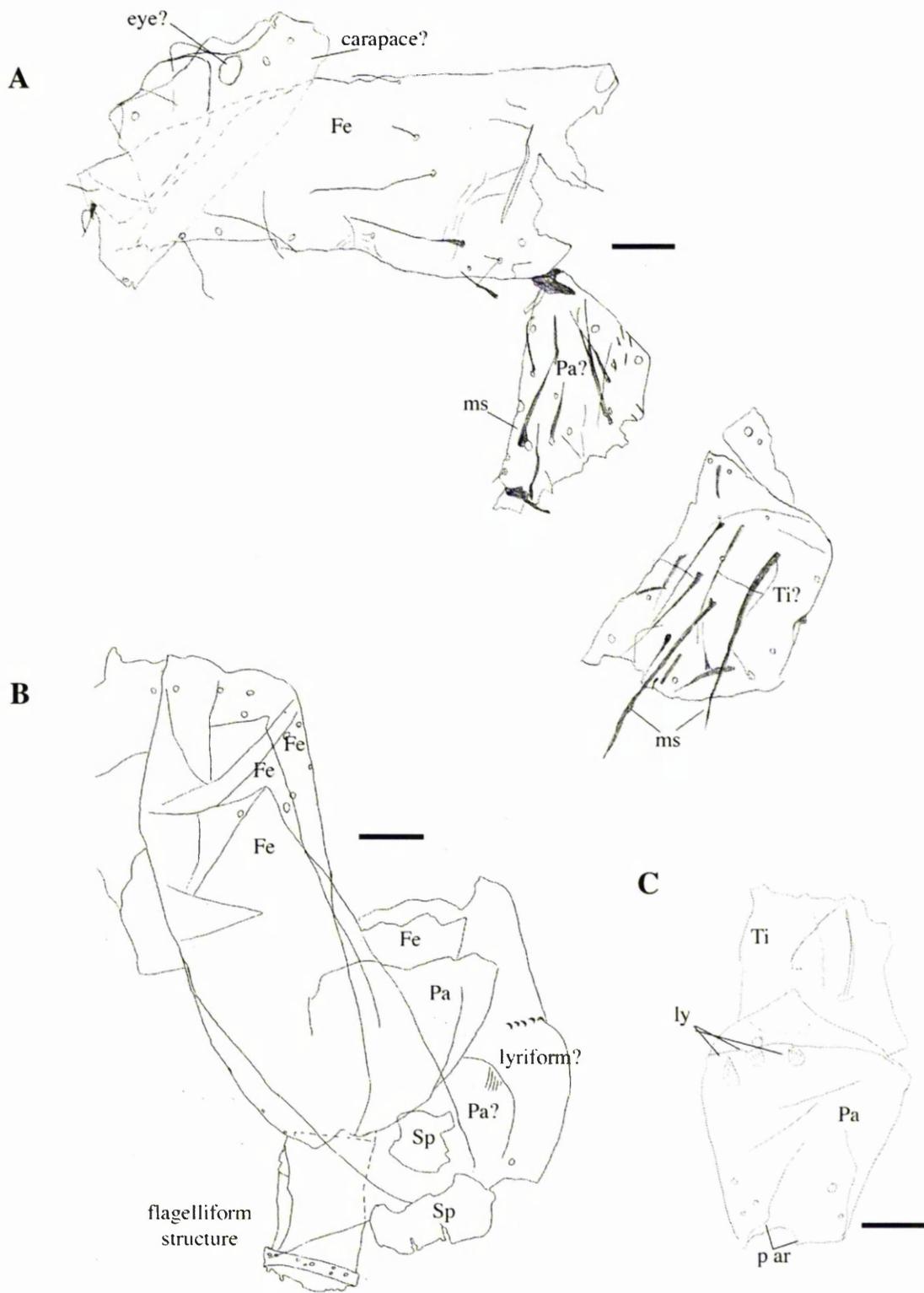
Figure 8.4 Interpretive drawing to accompany figure 8.3. **A**, femur. patella and tibia(?) with macrosetae, associated with part of carapace - SM1.120.V2. **B**, four femora and two patella associated with a flagelliform appendage and ?part of the abdomen - SM1.120.V7. **C**, patella and tibia - SM1.11.13. Scale bars represent 0.1mm.

Figure 8.5 *Heptathela kimurai*, female mesothelid spider, dorsal aspect. Scale bar represents 10mm.

Abdomen:

A cuticle fragment possibly representing part of the abdomen is preserved in specimen SM1.120.V7 (figures 8.3C, 8.4B). The cuticle is only partially visible and much of it is obscured behind a mass of podomeres and setae (see description of femora for same specimen). The visible part of the cuticle is divided into two areas by a thickened row of granules running across the cuticle perpendicular to the long axis. The area towards the top of the image in figure 8.3C (anterior?) has a straight lateral margin, whilst the section below the granules has a curved edge. The cuticle piece tapers towards one end and may represent the posterior end of a pseudosegmented abdomen not unlike those seen in living mesothelid spiders (figure 8.5). The cuticle pattern, podomere morphology and setal structure are all identical to specimens of *A. fimbriunguis*; however, this is the first known example of an abdomen, therefore there are no previously described examples with which to compare.

A flagelliform structure is preserved compressed amongst the cuticle pieces in specimen SM1.120.V7. It is long and narrow (120μm) and consists of a number of overlapping rings of cuticle bearing long fine setae along the distal margins. A similar structure was described by Shear and Selden (1987) found in association with specimens of *A. fimbriunguis* but not necessarily attached to any of the described cuticle fragments. The function and implications of this structure are discussed at the end of this chapter.

Femur:

SM1.120.V1 and SM1.132.13 (figures 8.6 A, B; 8.7 A, B) represent two femora. They are of similar proportions and measure approximately 300μm across the short axis. The length of the long axis is unknown as the proximal margins of both are missing. The cuticle is covered entirely with reticulations, and numerous long, fine setae are concentrated on dorsal and ventral surfaces. Curved rows of three or four slit sensilla occur near the distal joint. The slit sensilla measure 10–15μm long and generally increase in length towards the dorsal surface. Assuming that distal emargination of the femur is greatest retrolaterally, there are three slit sensilla prolaterally and four reterolaterally. This tallies with observations made by Selden *et al.* (1991) on specimens of *A. fimbriunguis* from Blenheim-Gilboa.
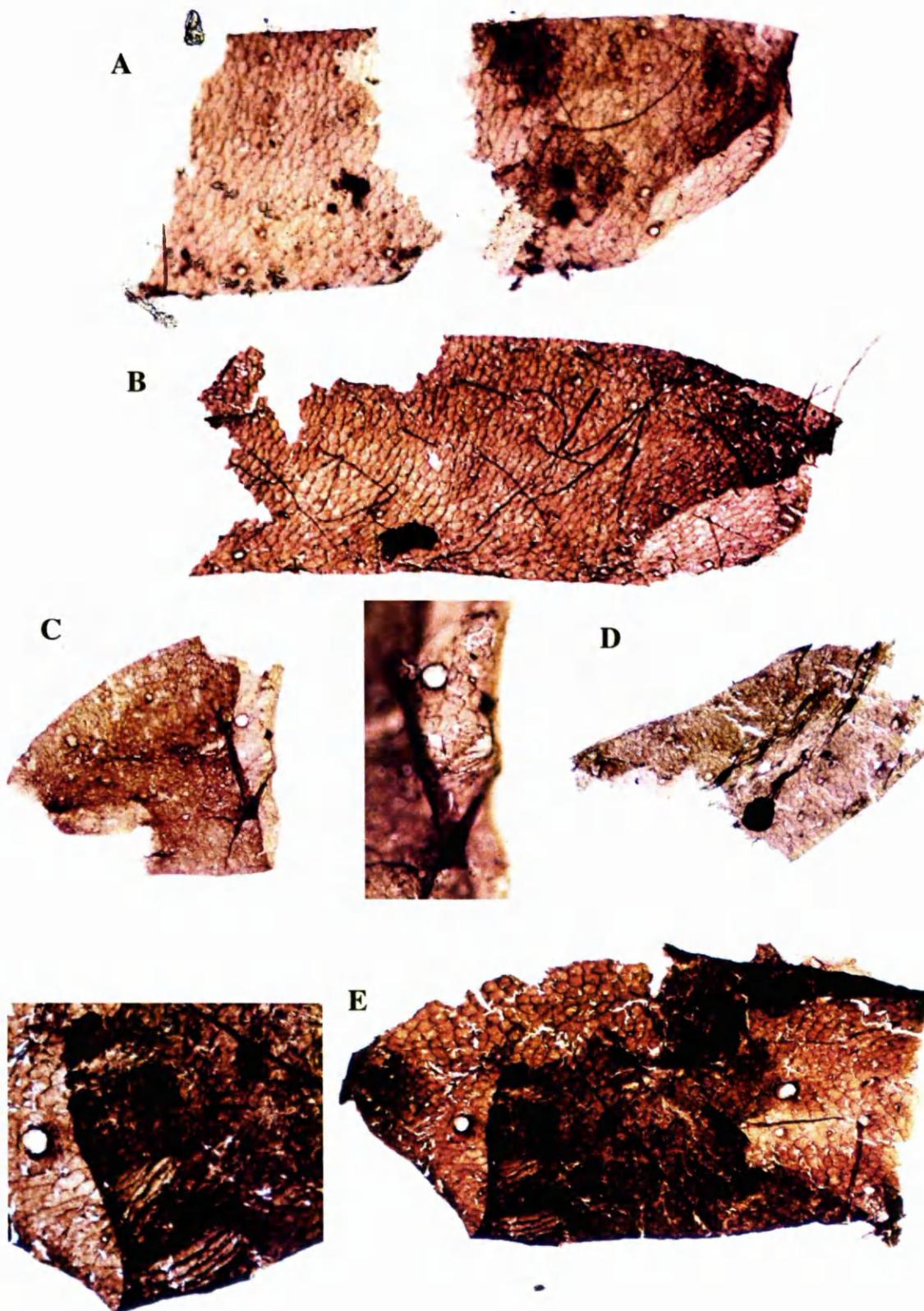
Figure 8.6 *Attercopus fimbriunguis.* **A**, femur, probably from left walking leg. Cuticle fragments separated on slide, but clearly associated. SM1.132.13. **B**, femur of left walking leg, SM1.120.V1. **C**, patella with single lyriform organ, SM1.212.6. **D**, unknown fragment with spines, SM1.115.V6. **E**, patella? with three well developed lyriform organs and distal articulation, SM1.4.7. Magnification x200, except for enlarged detail.
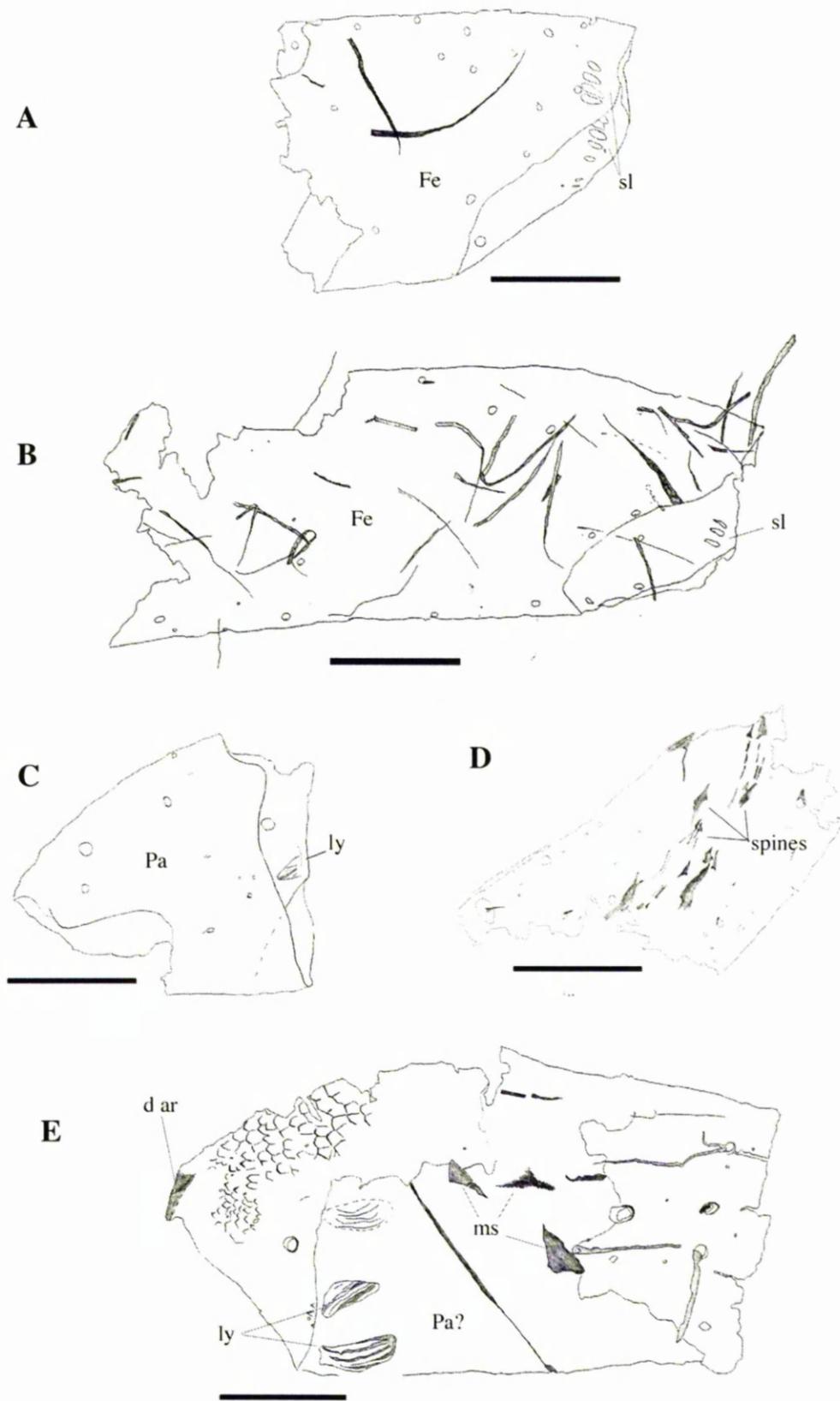
Figure 8.7 Interpretive drawings to accompany figure 8.6. *Attercopus fimbriunguis*. **A**, femur, probably from left walking leg. Cuticle fragments separated on slide, but clearly associated. SM1.132.13. **B**, femur of left walking leg, SM1.120.V1. **C**, patella with single lyriform organ, SM1.212.6. **D**, unidentified fragment with spines, SM1.115.V6. **E**, patella? with three well developed lyriform organs and distal articulation, SM1.4.7. Scale bars represent 0.1mm.

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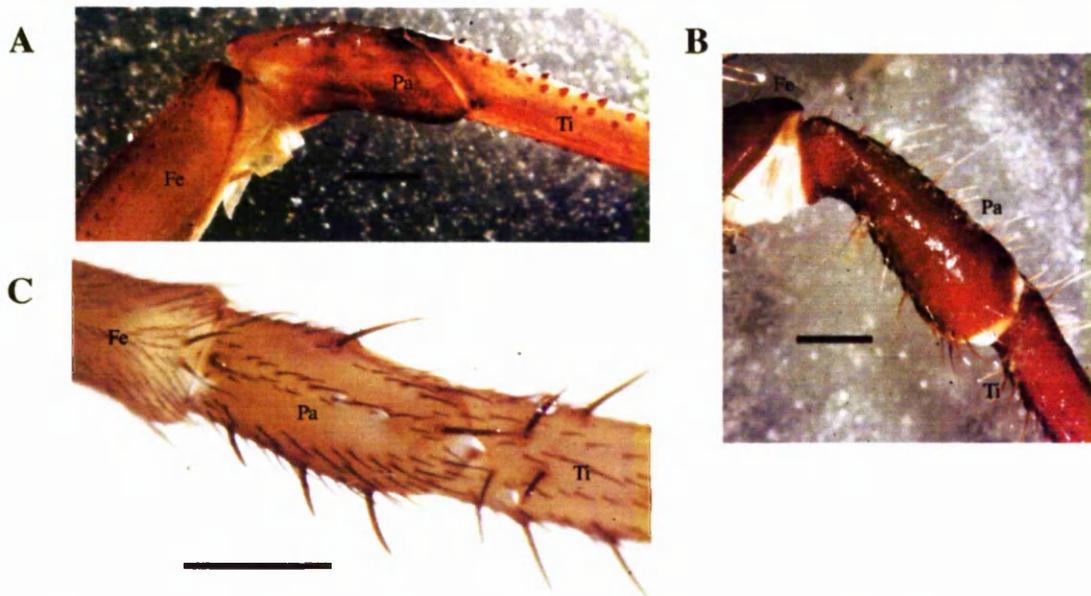
Figure 8.8 Arachnid patellae **A,** *Heterophrynus elaphus* (Amblypygi) showing almost fused articulation of patella and tibia. Retrolateral aspect. **B,** *Mastigoproctus giganteus* (Uropygi). Retrolateral aspect. **C,** *Heptathela kimurai* (Araneae) showing overlap of the dorsal surface of the patella onto the tibia resulting in ventral emargination of the patella at the distal joint. Dorsal aspect. Scale bars represent 1mm.

The specimens described above are indistinguishable from the described femora of the walking leg of *Attercopus fimbriunguis*. Both specimens described here belong to the left walking leg. Variations in emargination mirror those of *Liphistius* femora, in which least emargination occurs in legs 1 and 4 (Selden *et al.*, 1991). The lesser emargination of specimen SM1.132.13 would therefore indicate that it is either the first or last ambulatory leg.

Four femora and at least two patellae are preserved in specimen SM1.120.V7. In contrast to other specimens of femora, only the proximal portions of the femora are visible with overlying cuticle obscuring the distal margins. Although the presence or absence of slit sensilla on the distal margins of these femora cannot be confirmed, all other characteristics (size, shape, and cuticle patern) suggest that these are similar to the described femora of *A. fimbriunguis*.

Patella:

Specimen SM1.212.6 (figures 8.6C, 8.7C) is a short podomere measuring approximately 200μm across the short axis. It has a convex dorsal margin that is approximately twice the length of the ventral margin resulting in a pronounced emargination on the ventral side of the proximal joint. The dorsal surface bears at least two large (8–10μm) setal sockets, and a greater number of smaller (c. 5μm) sockets (see figure 8.11). Two lyriform organs occur near the distal joint, one on both retrolateral and prolateral sides. Superficially, this specimen
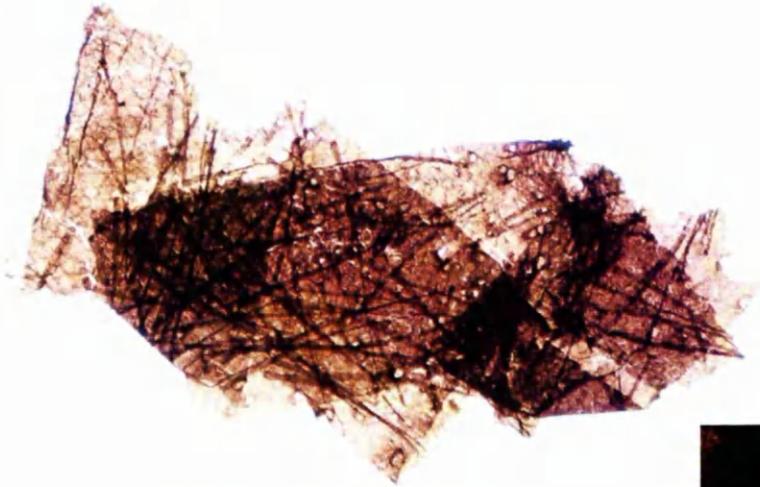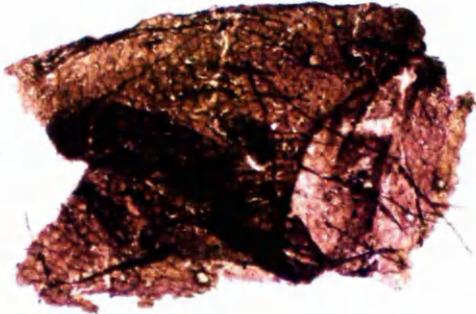
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Figure 8.9 *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). **A**, Metatarsus and detail of metatarsal organ - SM1.120.V5. **B**, SM1.120.V2b. **C**, Metatarsus?, SM1.120.V6. **D**, tarsus with terminal fimbriate claw. Lateral claws missing, SM1.12.2. Magnification x200.
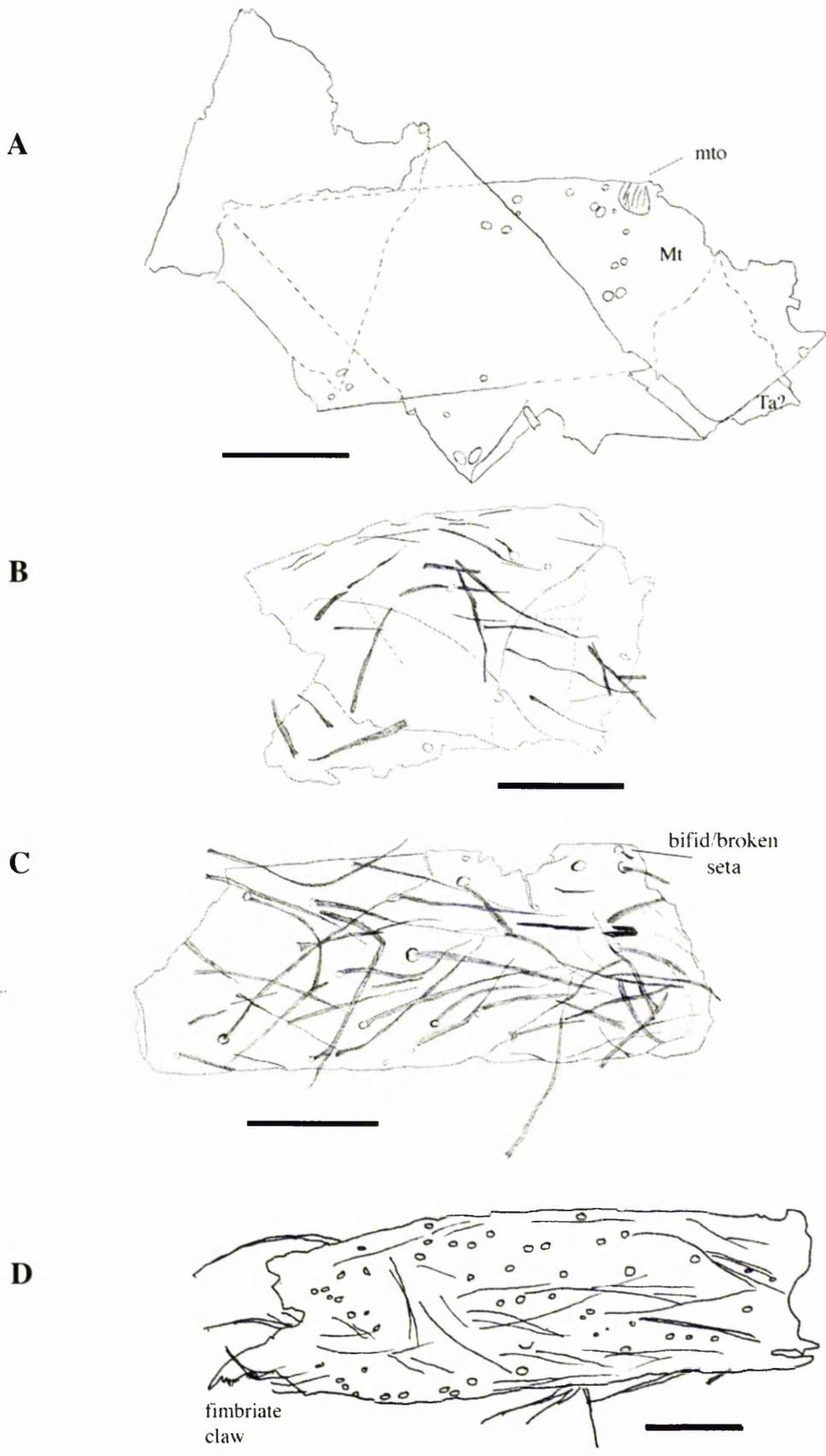
Figure 8.10 Interpretative drawings to accompany figure 8.9. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). **A**, Metatarsus and detail of metatarsal organ - SM1.120.V5. **B**, SM1.120.V2b. **C**, Metatarsus?, SM1.120.V6. **D**, tarsus with terminal fimbriate claw. Lateral claws missing, SM1.12.2. Scale bars represents 0.1mm.

resembles the patella of *A. fimbriunguis*, however there are only two lyriform organs, rather than the five described by Selden *et al.* (1991). Specimen SM1.11.13 (figure 8.3D, 8.4C) shows a ventrally compressed patella and tibia in connection. Three lyriform organs are visible and two macrosetal sockets. Selden *et al.* (1991) commented that the patella of *A. fimbriunguis* has no pronounced emargination of the distal joint, which is typical of Recent spiders, and in that respect it more closely resembles the patellae of the ambulatory legs of uropygids. A comparison of arachnid patellae is illustrated in figure 8.8.

The shortest podomere in specimen SM1.120.V2 (figure 8.3A) is also interpreted as a patella. Although the podomere is incomplete the short length and superior articulations both proximally and distally rule out all other podomeres. It measures approximately 260µm long and a very small fragment of the proximally adjoining podomere (femur) is preserved at the point of articulation.

Specimen SM1.4.7 (figures 8.6E, 8.7E) is a strongly curved podomere bearing three well-developed lyriform organs and a prominent distal articulation. At least three or four spines occur on what is presumed to be the ventral surface, and at least two large setal sockets and several smaller ones are concentrated on the dorsal surface. The strongly curved dorsal surface and presence of thorns on lateral surfaces could indicate that this specimen represents a cheliceral podomere. However, it is quite a large podomere measuring 260µm at its widest point, and with a minimum length of 450µm, and the described chelicerae from *A. fimbriunguis* have well-developed serrations on the prolateral margins and bear only a few slit sensillae adjacent to the fang articulations. The curved dorsal surface, proximal emargination, presence of two dorsal macrosetal sockets and the three distally situated lyriform organs most closely resemble features from the patella of *A. fimbriunguis*. The proportions of the podomere and the presence of ventral thorns, however, do not. The presence of a patch of cuticular spinules on the proximal prolateral side of certain femora associated with *A. fimbriunguis* was argued by Selden *et al.* (1991) to be a modification of the palp. Female species of *Liphistius* also have palps bearing spines (Platnick and Sedgwick, 1984) and a similar argument could be applied to specimen SM1.4.7. Specimen SM1.115.V6 (figure 8.6D, 8.7D) is an unidentified podomere also bearing rows of spines across one surface.

Tibia:

Specimen SM1.120.V6 (figures 8.9C, 8.10C) bears a reticulate cuticle surface and numerous long, fine setae. It is a flattened rectangular shape measuring approximately 500µm along its length and 190µm at its widest point (2–3 times longer than wide) with little emargination at either end. This podomere has a relatively high density of setal sockets, and they have a bimodal size range with large sockets measuring 8–10µm and the smaller

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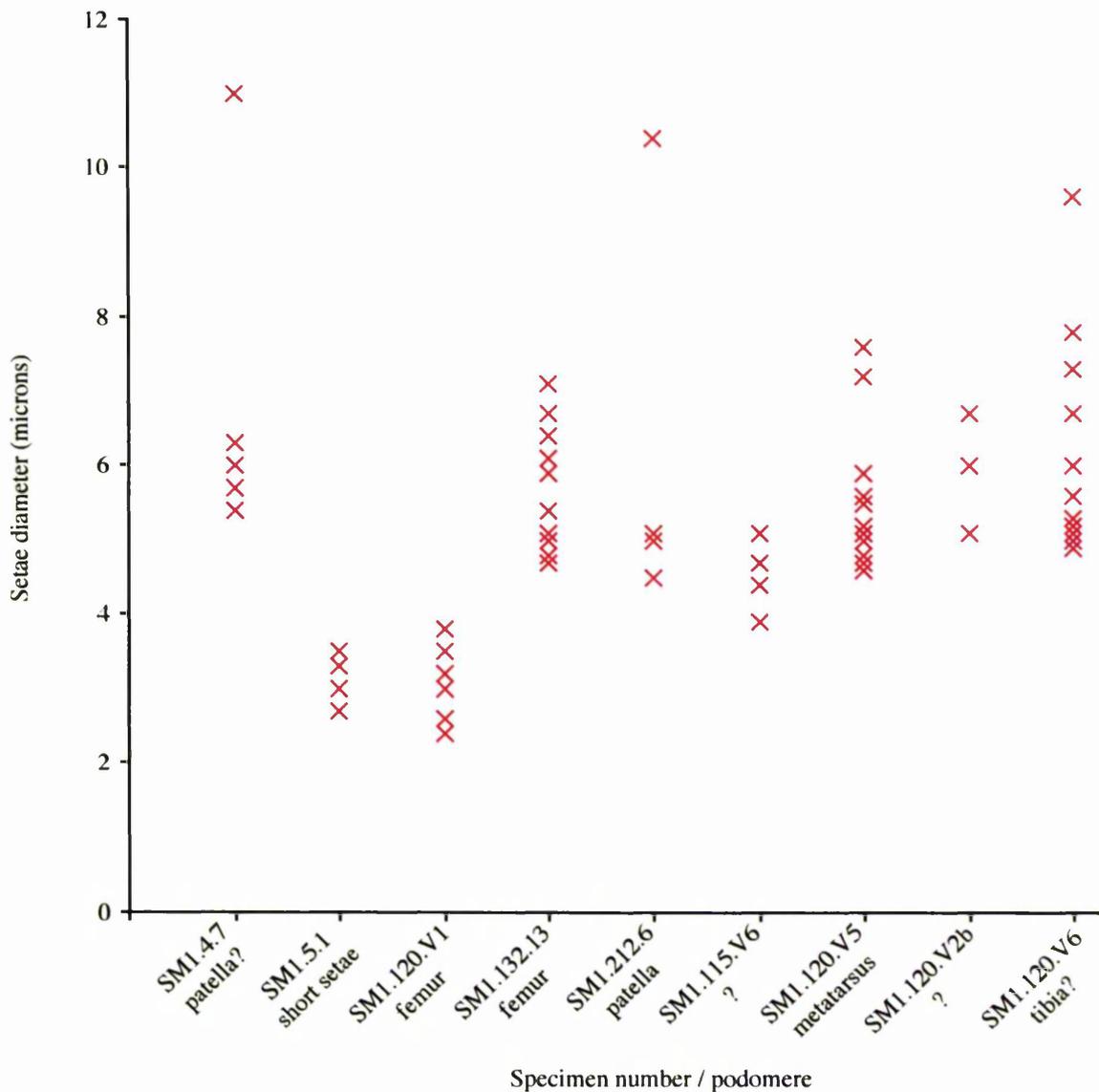
Figure 8.11 Size ranges of setal sockets in podomeres with reticulate A cuticle patterning. Setae on some, but not all, podomeres have an approximately bimodal size range. Patellae consistently show the largest difference in setal socket size.

sockets less than 5μm (see figure 8.11). The tip of one of the proximal corners is missing and there are no slit sensilla visible on the podomere.

The shape and overall proportions of SM1.120.V6 are similar to the described tibia of *A. fimbriunguis*, however there are no slit sensilla visible. There is one small seta with an apparently bifid tip towards the distal margin (orientation of this specimen is by attitude of setae). Bifid setae and reticulate cuticle are diagnostic features of the trigonotarbid *Gelasinotarbus bifidus* (Shear *et al.*, 1987). However, *G. bifidus* also possesses larger setal sockets and trichobothria, both of which are absent from SM1.120.V6. This, combined with the absence of other similar setae, and the prevalence of long fine setae, suggests that the seta has probably been torn into a fortuitous shape and that the resemblance is superficial.

One of the incomplete podomeres in specimen SM1.120.V2 (figure 8.3A, 8.4A) is interpreted as a tibia, and bears two prominent macrosetae. Under very high magnification the setal socket of one of the macrosetae appears to be crossed with tiny striations, possibly representing the ornamented cup of a trichobothria (figure 8.3B). Trichobothria are so far unknown from specimens of *A. fimbriunguis*, a surprising observation given the primarily terrestrial nature of all other known spiders and associated terrestrial elements of the assemblage. Macrosetae were described from the tarsus and metatarsus of *A. fimbriunguis* (Selden *et al.*, 1991), however it seems unlikely that either of these are represented by the podomere bearing macrosetae in specimen SM1.120.V2 given the significantly lower density of setal sockets. If this does represent a trichobothrium then it is the first known example from *A. fimbriunguis* and confirms its terrestrial nature.

Metatarsus:

SM1.120.V5 (figure 8.9A, 8.10A) is a folded podomere, or possibly podomeres, with long, straight, parallel margins. In its 'unfolded' state, it measures approximately 680μm in length and 170μm wide. A lyriform organ orientated parallel to the short axis of the podomere (metatarsal organ) lies at the distal end of the podomere, which identifies it as the metatarsus of a spider. In *A. fimbriunguis* the metatarsus is the longest podomere on the leg, being nearly four times as long as it is wide in its flattened state, and the lyriform organ is situated at the base of a cuticular projection, which bears articulations at either side. In Recent spiders the metatarsal organ is positioned on the dorsal surface behind a cuticular ridge (Barth, 2002). This is not clearly visible in specimen SM1.120.V5 because the distal margin is incomplete. In *A. fimbriunguis* macrosetae are prominent on the metatarsus. Although there are no obvious macrosetae preserved in specimen SM1.120.V5 there are two sizes of setal sockets (see figure 8.11). This is the only example of a metatarsus recovered from South Mountain.

Tarsus:

SM1.12.2 (figure 8.9D, 8.10D) is a parallel margined podomere (tarsus), terminating in a curved claw. As in other podomeres it bears a high density of setae with a bimodal size range. The claw is fimbriate, which is a diagnostic feature of *A. fimbriunguis*. Although this specimen has only one claw, it does not taper distally like the palpal tarsi of *A. fimbriunguis*, suggesting that two of the claws (paired claws) are missing. This is the only example of a tarsus to be recovered from South Mountain.

8.2 Reticulate B cuticle

Large sheets of cuticle with a reticulate pattern differing from that of reticulate A cuticle came largely from one sample (SM1.4.8) from the quarry at South Mountain. The relatively large size of these cuticle pieces is unusual and suggests that they originate from the carapace. Only two podomeres with reticulate B cuticle were recovered (figures 8.12D, E; 8.13B, D) in comparison to the numerous podomeres recovered for other cuticle types. It is possible that the larger cuticle fragments from SM1.4.8 were originally united but fragmented during the maceration process.

8.2.1 Cuticle topography

Type B reticulate cuticle is characterised by a scale-like pattern of polygons with thickened margins on all sides. The pattern is entire over the cuticle surface, although the polygons vary considerably in shape and size from equant to elongated polygons arranged into rows (e.g. SM1.120.2, figure 8.12E). It differs from the reticulate A pattern in the size and shape of the polygons, giving an overall appearance of much denser scales, and it lacks the minute slit sensilla seen scattered across the surface of reticulate A cuticle. The differing size and shape of polygons makes it difficult to match cuticle fragments with this type of surface topography. For example, SM1.4.8 and SM1.4.8a (figure 8.12A, B, C) are covered with very elongated polygons and appear quite different to the rest of the cuticle types; however SM1.120.2 (figure 8.12F) shows both elongated polygons and more equant shaped polygons varying with position on the body that can be matched to both specimens SM1.4.8 and specimens SM1.120a. Therefore, until further examples are found, both variations of this type B reticulate cuticle are dealt with together.

8.2.2 Sensory organs

The most obvious difference between cuticle types reticulate A and reticulate B is the absence of long fine setae in the latter. Very few setae are preserved in any of the recovered specimens, and where they do occur they are short and straight and apparently restricted to podomeres (figure 8.13B, D). Small, circular setal sockets are scattered over the surface of most specimens, and specimens SM1.4.8 and SM1.4.8a bear large conspicuous sockets that are elliptical rather than round, measuring approximately 30μm across their long axes.

Slit sensilla are not apparent in any of the recovered specimens with a reticulate B cuticle pattern. However, there are only a handful of specimens recovered from South Mountain with this cuticle pattern, and only two possible podomeres. Further macerating may well produce more specimens and reveal the presence of slit sensilla. An eye structure consisting of several minor and one major lens is preserved in specimen SM1.120.2a (figure 8.12F) and is discussed below.
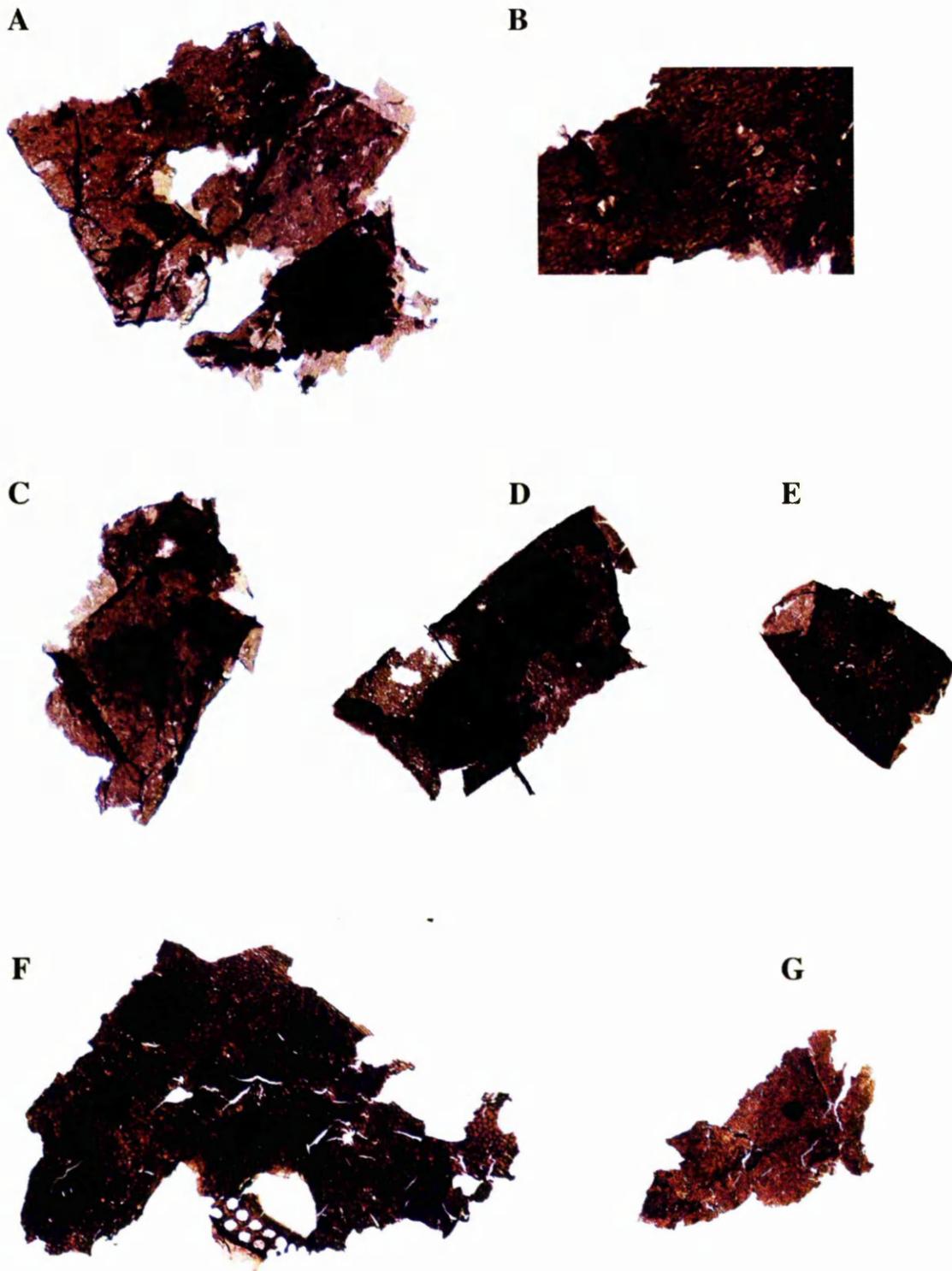
Figure 8.12 Reticulate B cuticle from South Mountain, New York. **A**, possible carapace fragment - SM1.4.8a. **B**, detail of cuticle sculpture - SM1.4.8a. **C**, SM1.4.8. **D**, podomere - SM1.4.8b. **E**, podomere - SM1.120.2. **F**, carapace fragment and eye structure with minor lenses - SM1.120.2a. **G**, SM1.212a. Magnification x100.
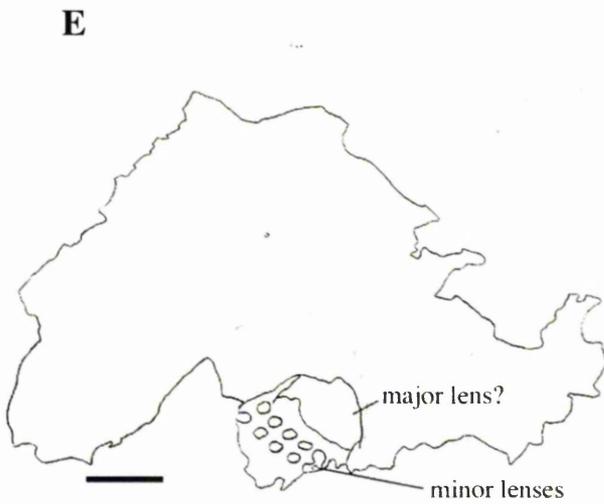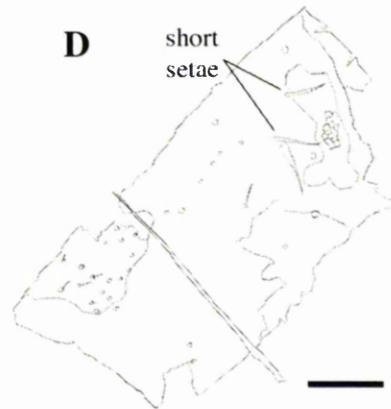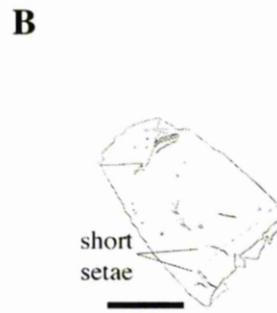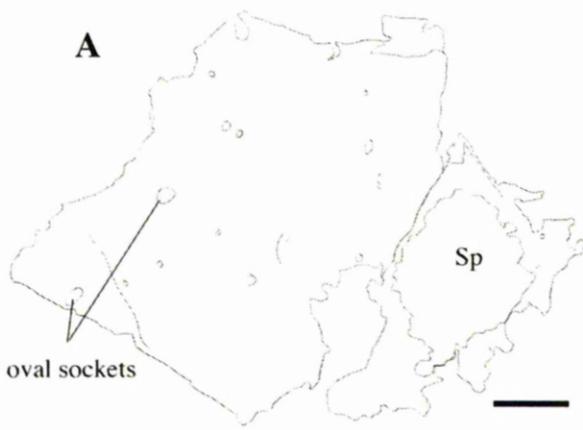
Figure 8.13 Interpretative drawings to accompany figure 8.12. **A**, possible carapace fragment - SM1.4.8a. **B**, SM1.120.2. **C**, podmere - SM1.4.8 **D**, podomere - SM1.4.8b. **E**, carapace fragment and eye structure with minor and ?major lenses - SM1.120.2a. **F**, SM1.212a. Scale bars represent 0.1mm.

Only six examples of cuticle with a reticulate B pattern were recovered and as such any interpretation of this material may prove to be improvident until more material comes to light. A general description of these pieces follows and a discussion and interpretation is made at the end of this chapter.

Carapace:

The largest fragment of cuticle recovered is specimen SM1.120.2a (figure 8.12F). The reticulations vary across the cuticle surface, merging from approximately equant polygons near the centre of the cuticle fragment, to elongated polygons towards the edges of the cuticle. A large hole surrounded on one side by rows of smaller holes is interpreted as an eye structure consisting of one major lens and at least 14 (possibly 16?) minor lenses arranged in two parallel rows, presumably anterior to the major lens. The hole in the cuticle where the major lens would have rested is elliptical and measures about 120µm by 75µm. The holes representing the minor lenses are between 15 and 18µm. A slight darkening of the cuticle surrounding the major lens gives the impression that the eye sat in a convexly domed structure in life.

Podomeres:

Specimens SM1.4.8b and SM1.120.2a (figure 8.12D, E) are both elongated tubes of cuticle and are interpreted as podomeres. SM1.4.8b is a rectangular podomere measuring approximately 470µm long and 250µm wide. Numerous small (5µm) sockets are scattered over the surface and are associated with very short (15µm) setae. Only a couple of larger (8µm) round sockets are visible and were probably associated with longer setae. By analogy with other described podomeres this probably represents a tibia.

SM1.120.2 is a much shorter podomere that tapers gently towards one end from 210µm at its widest point to 120µm at the narrowest. The morphology of the podomere suggests that it had been compressed dorsoventrally and had a longer (290µm) dorsal margin than the ventral margin (220µm). Small setal sockets measure approximately 7µm in diameter and there are possible larger, oval setal sockets on the midline of the specimen. Both lateral margins are gently convex.

SM1.4.8a (figure 8.12A) is a considerably larger and broader specimen, and consists of a double layer of cuticle forming a flattened tube structure probably representing a podomere. Both proximal and distal margins are missing, and it measures 500µm across the short axis. The reticulations are more elongate than in specimens SM1.4.8b (figure 8.12D) and SM1.120.2 (figure 8.12E) and give the appearance of a row-like arrangement across the cuticle. The largest setal sockets have an oval outline with a maximum diameter of 30µm,

which is approximately twice the minimum diameter. Specimen SM1.4.8 has an identical cuticle structure to SM1.4.8a and consists of a folded cuticle layer with setal sockets but no setae.

8.3 *Reticulate C cuticle*

Type C reticulate cuticle is defined as cuticle in which the reticulations are restricted to certain parts or areas of the exoskeleton. Examples of this type of cuticle patterning have previously been observed in trigonotarbids from Rhynie and Gilboa.

8.3.1 *Cuticle topography*

Type C reticulate cuticle (figures 8.14, 8.15) generally has a smooth, unornamented cuticle surface with reticulations restricted to the margins of the carapace and podomeres. Unlike in type B reticulate cuticle, the reticulations are only thickened on one side so that individual polygons merge into one another much like in reticulate A cuticle. Where they occur, setae are long and straight and concentrated on ventral and dorsal surfaces of the podomeres. There are no minute slit sensilla as occur in reticulate A cuticle.

8.3.2 *Cuticle morphology*

Cuticle pieces included within the 'reticulate C' category exhibit quite a range of morphologies and probably did not all originate from the same species of animal. A complete carapace is included together with the posterior part of an abdomen and several podomeres that may or may not be related. The podomeres are included here as they can be excluded from most other groups discussed in previous chapters, and there is a higher probability that they represent part of an animal for which other body parts are known than an entirely new taxon.

Carapace and abdomen:

Specimen SM1. 130.1 represents a large carapace with a reticulate pattern running in a narrow band around the margins (figures 8.14A, 8.15A). The carapace is preserved in ventral aspect and measures 600μm long and approximately 350μm wide. The margins of the carapace are sculpted and towards the anterior are four large circular structures measuring approximately 40μm in diameter. Two of the circular structures are empty holes and two are pale patches of cuticle with smaller holes in them. These are interpreted as two median eyes and at least one pair of lateral eyes, although the distribution of major and minor lenses is unclear. The domed nature of the carapace is indicated by crescental folds in the dorsal cuticle.
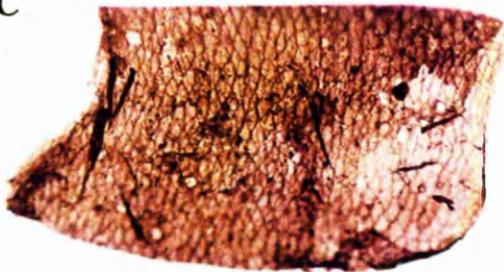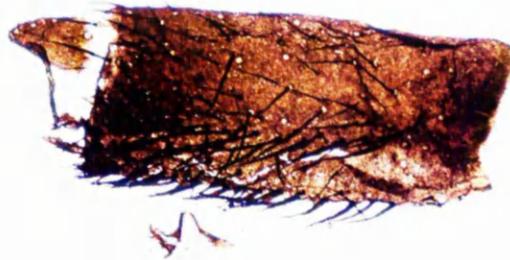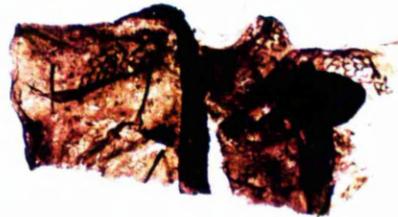
Figure 8.14 Trigonotarbid fragments from South Mountain, New York. **A**, trigonotarbid carapace with reticulate margin and eyes - SM1.130.1, x100. **B**, trigontotarbid abdomen - SM1.118.6, x100. **C**, ?trigonotarbid reticulate podomere with slit sensilla - SM1.5.1, x200. **D**, setose podomere with blunt terminal claw - SM1.8.1, x200. **E**, smooth podomere with row of small spines - SM1.3.12, x200. **E**, trigonotrabid? coxa and trochanters - SM1.5.1b, x200.
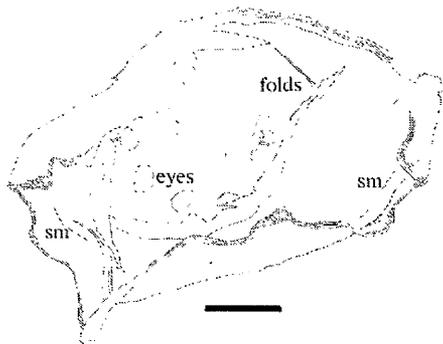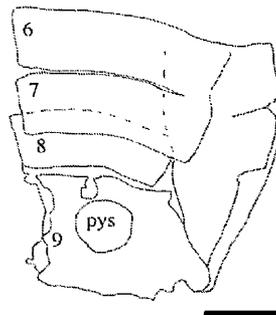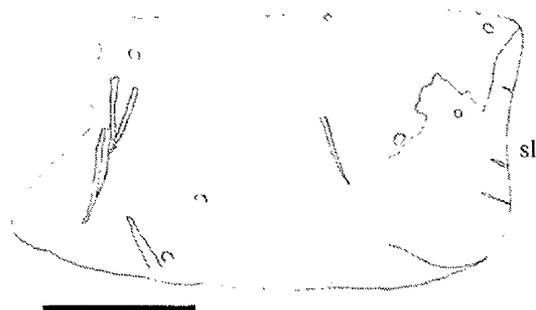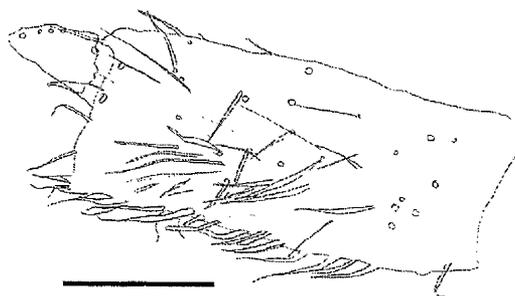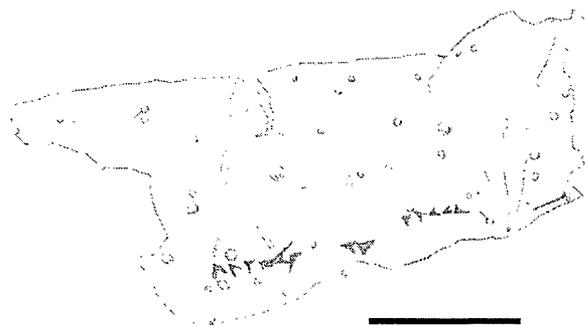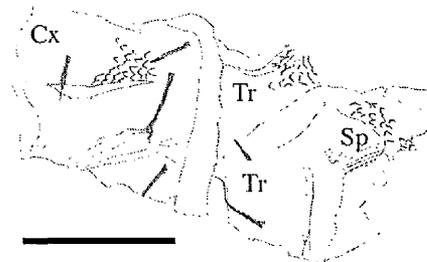
Figure 8.15 Interpretative drawings to accompany figure 8.14. **A**, trigonotarbid carapace with reticulate margin and eyes - SM1.130.1. **B**, four posteriormost segments of a trigontotarbid abdomen - SM1.118.6. **C**, ?trigonotarbid reticulate podomere with slit sensilla - SM1.5.1. **D**, setose podomere with blunt terminal claw - SM1.8.1. **E**, smooth podomere with row of small spines - SM1.3.12. **E**, trigonotrabid? coxa and trochanters - SM1.5.1b. All scale bars represent 0.1mm.

In addressing the problems inherent in selecting characteristics for the higher classification of trigonotarbids, Shear (2000) discussed the difficulties in comparing taphonomically different specimens. Clypeal projection may be significant and an undulate lateral carapace margin appears to be unique to the Palaeocharinidae (Shear *et al.*, 2000). Dorsoventral compression of specimen SM1.130.1 makes determination of clypeal projection difficult. There does not appear to be a clypeal ridge and the specimen most closely resembles a described carapace of *Gelasinotarbus reticulatus* from Blenheim-Gilboa (Shear *et al.*, 1987).

Specimen SM1.118.16 (figure 8.14B, 8.15B) represents the four posteriormost segments and pygidial socket of a trigonotarbid abdomen. The prepygidial unit is fused, which is a character that Shear (2000) considered a good synapomorphy for Palaeocharinidae. Further identification of this specimen is prevented by an absence of diagnostic features, but there are no characters to suggest that it does not represent a species of *Gelasinotarbus*.

The only reticulate cuticle to be recovered from High Knob is specimen HK3.2.3a (figure 8.18C). This fragment has no true margins, and probably represents cuticle from the carapace or abdomen. It is characterised by the presence of setal sockets raised upon tubercles, and small stubby spines. Tuberculate setal sockets and a reticulate cuticle pattern are seen amongst some palaeocharinid trigonotarbids, but as yet there is insufficient material to make a firm identification.

Podomeres:

Three examples of podomeres were recovered, two of which are united by their smooth cuticle and the presence of numerous setae and setal sockets. Specimen SM1.5.1b (figure 8.14F, 8.15F) probably represents the distal part of a coxa and two trochanters. Each podomere bears reticulations on the distal margins and could be assigned to either *Gelasinotarbus* or *Palaeocharinus*.

SM1.8.1 (figure 8.14D, 8.15D) is a smooth cuticled tarsus with a single terminal claw, probably from the pedipalp. The tarsus measures approximately 270µm long and 120µm wide and is rectangular in its flattened state. Ventrally there are two rows of long, dense setae, and other setae occur dorsally. The claw is straight and blunt and bears at least four setae on its dorsal surface. There are no reticulations on the cuticle surface and its association with other fragments is unclear. A second podomere, specimen 1.3.12 (figure 8.14E, 8.15E) has a similarly smooth cuticle with setal sockets, but no setae preserved. It is at least 350µm long and approximately 150µm wide, tapering very gently towards one end. Larger setal sockets measure approximately 5µm in diameter.

The fourth podomere (specimen SM1.5.1; figures 8.14C, 8.15C) is entirely covered with reticulations, resembling reticulate A cuticle but with shorter, thicker setae. It measures about 540μm long and 370μm wide, with gently convex lateral margins. Several slit sensilla are evident on the distal margin.

8.4 *Non-reticulate cuticle*

Cuticle without any reticulations or surface ornamentation, but that can be assigned to the arachnids, is so far limited to those specimens recovered from High Knob quarry. A description of all recovered fragments is set out below.

8.4.1 *Cuticle topography*

One of the most characteristic features of this type of cuticle is the ostensible absence of surface microsculpture. The cuticle surface is almost entirely smooth, but frequently bears thickened 'ribs' of cuticle, which are sometimes adorned with spines (*e.g.* figure 8.19G). Very few setal sockets are found preserved, and even fewer setae. The single possible example of a preserved seta is in specimen HK2001.1a where two extremely fine hairs are seen on cuticle associated with the proximal portion of a coxa (figures 8.19E, 8.20E).

8.4.2 *Cuticle morphology*

Essentially two types of morphologies occur amongst these cuticle pieces. One of the most characteristic pieces is a rosette shaped structure with a dark central plate in which lines can be observed spiralling in towards the centre. These are interpreted as the ventral prosoma (sterna and coxae) of an arachnid and are illustrated in figures 8.16–8.18. The second morphological group, broadly speaking, consists of related podomeres characterised by their box-like construction with thickened margins. These are illustrated in figures 8.19–8.21.

Ventral prosoma:

All of the following specimens were recovered from samples collected from the High Knob quarry (figures 8.16–8.18). These cuticle pieces appear as rosette shaped arrangements of coxae surrounding an approximately hexagonal sternum. Sternum size and coxal length are shown in table 8.

Specimen HK3.2.4b (figures 8.16A, 8.17A) is the most complete example and clearly shows ten coxae arranged tightly together around a darker area of cuticle interpreted as the sternum. The coxae are interpreted as those from the pedipalps and four walking legs of an arachnid, with the chelicerae sitting at the top. There is no cuticle microsculpture as such, neither are there any distinctive setae with which to aid an identification. The most characteristic feature of these pieces is an apparently spiral pattern on the sternum which seems to follow the line of the coxae margins as they converge beneath the sternum.

168
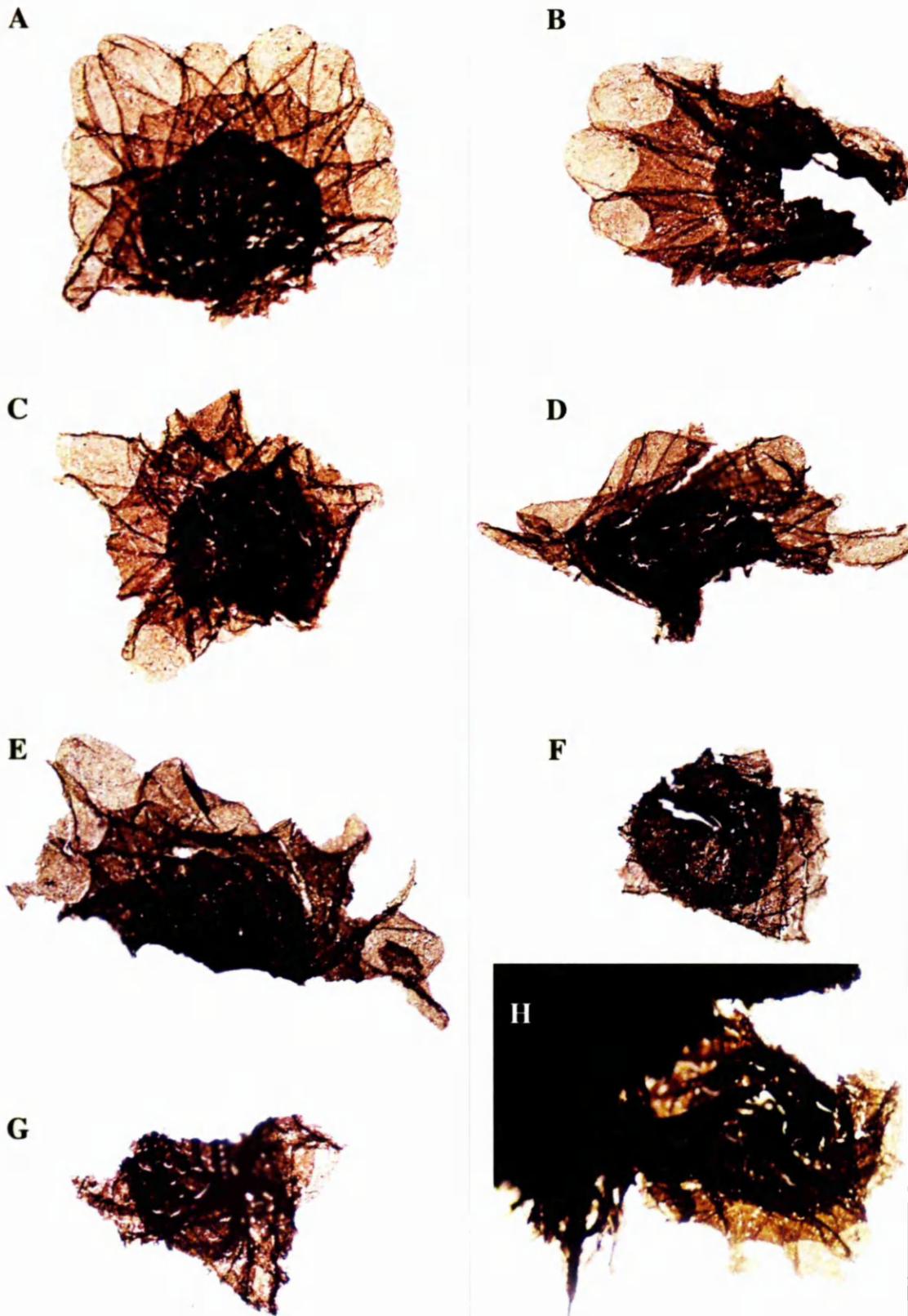
Figure 8.16 Arachnid sterna and coxae from High Knob, New York State. **A**, sternum and complete set of coxae - HK3.2.4b. **B**, half a sternum and three complete coxae - HK3.2.5. **C**, sternum and part of coxae - HK3.2.4. **D**, half a sternum and coxae - HK3.2.4a. **E**, half a sternum and coxae - HK3.2.6. **F**, sternum with attached cuticle - HK3.2.13. **G**, part of sternum - HK3.2.3. **H**, sternum compressed onto mass of plant cuticle - HK3.2.9. Magnification x100.
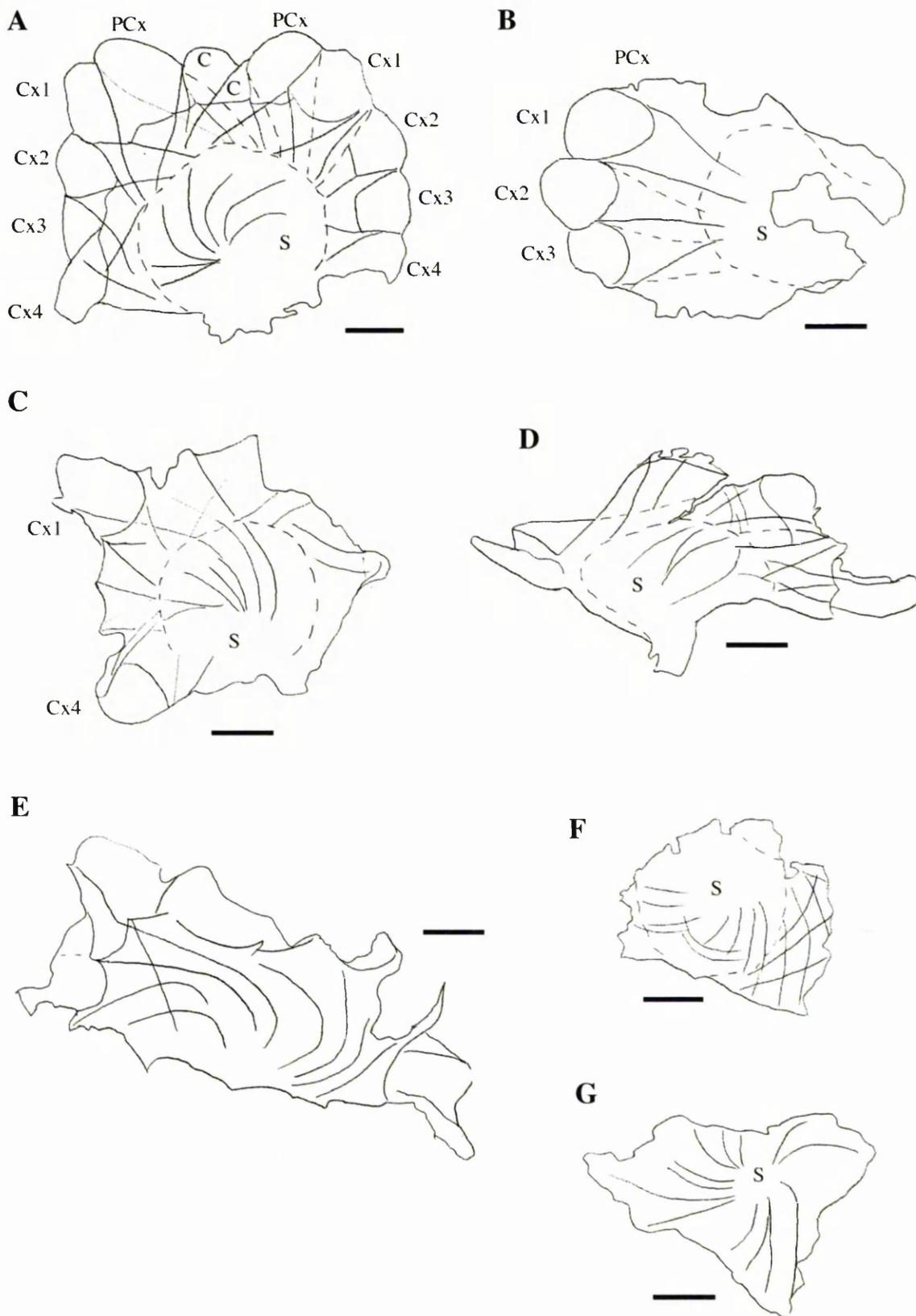
Figure 8.17 Interpretive drawings to accompany figure 8.16. **A**, sternum and complete set of coxae - HK3.2.4b. **B**, half a sternum and three complete coxae - HK3.2.5. **C**, sternum and part of coxae - HK3.2.4. **D**, half a sternum and coxae - HK3.2.4a. **E**, half a sternum and coxae - HK3.2.6. **F**, sternum with attached cuticle - HK3.2.13. **G**, part of sternum - HK3.2.3. **H**, sternum compressed onto mass of plant cuticle - HK3.2.9. Scale bars represent 0.1mm.
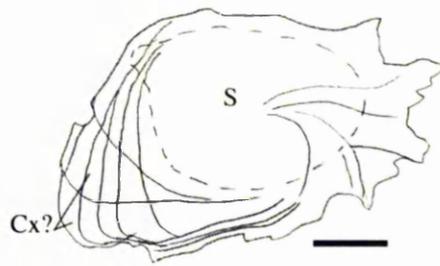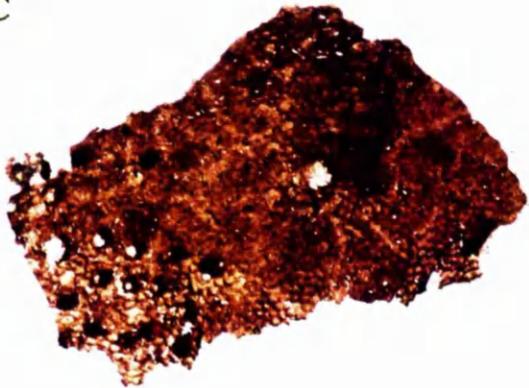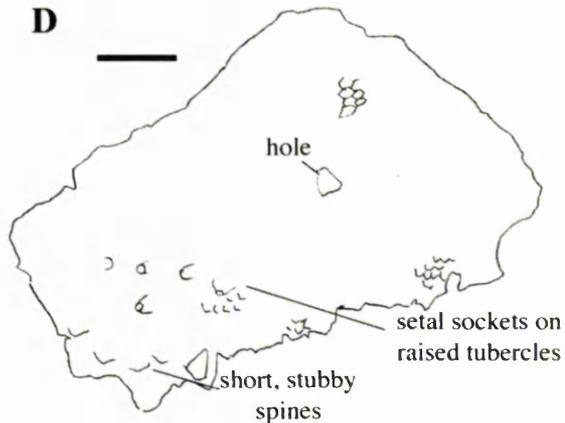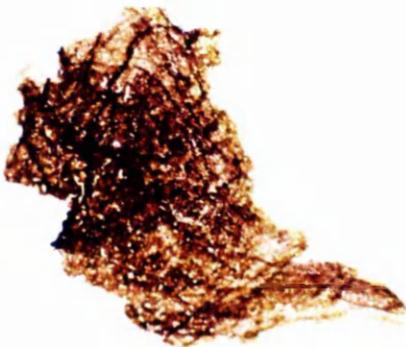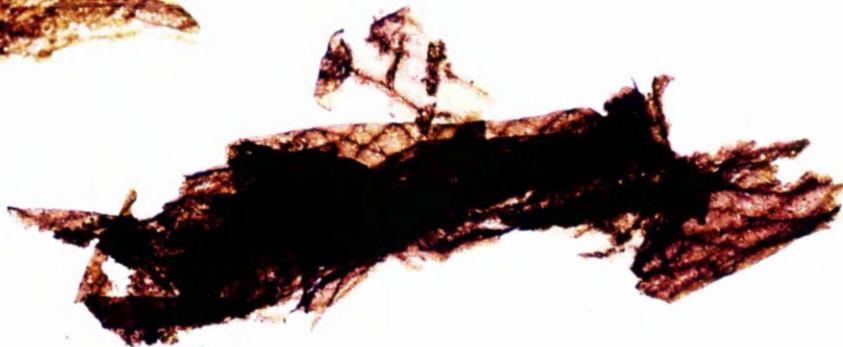
Figure 8.18 ?Trigonotarbida from High Knob quarry, New York State with interpretive drawings. **A**, sternum - HK3.2.14. **B**, interpretive drawing of A - HK3.2.14. **C**, cuticle with setal sockets on raised tubercles and reticulate ornament - HK3.2.3a. **D**, interpretive drawing of C - HK3.2.3a. **E**, cuticle with cross-hatched sculpture - HK3.2.12. **F**, unidentifed cuticle with cross-hatched sculpture - HK3.2.16. Photo magnification x100. Scale bars represent 0.1mm.

Following the margins of the coxae is confusing due to their extreme compression, however there do not appear to be any coxal endites. The shape of the sternum is indicative of a spider or trigonotarbid and the lack of evidence for a labium suggests that they represent the latter. These specimens compare favourably with examples described from Gilboa as trigonotarbids (figures 12, 17 and 31; Shear *et al.*, 1987) and from their small size probably represent juvenile specimens. The main difference, however, is seen in the chelicerae. In specimen HK3.2.4b the coxae are numbered so that they form a symmetrical arrangement around the sternum, resulting in the posterior margin of the coxa of leg 2 and the anterior margin of leg 3 positioned perpendicular to the mid axis of the sternum. The chelicerae are therefore positioned at the top, approximately inline with the mid axis of the sternum, and are represented only by the basal segment. They are more slender than other podomeres, but are smooth and lacking in setae unlike the specimens from Gilboa.

Table 8. Table of measurements from ventral prosomas recovered from High Knob quarry, New York.

Specimen No.	Max. width of sternum (μm)	Average length of podomere from edge of sternum (μm)	
HK3.2.4b	300	Chelicerae	140
		Pedipalp	220
		Coxa1	215
		Coxa2	187
		Coxa3	122
		Coxa4	140
HK3.2.5	265	Coxa1	243
		Coxa2	250
		Coxa3	220
HK3.2.4	250	Coxa1	250
		Coxa4	147
HK3.2.4a	300		
HK3.2.6	380		
HK3.2.13	240		
HK3.2.3	240		
HK3.2.9	300		
HK3.2.14	260		

Cuticle associated with the sternum has a cross-hatched sculpture (specimens HK3.2.13, HK3.2.12 and HK3.2.16; figures 8.16F, 8.17 F, 8,18E, F) formed by thickened ribs of cuticle. This pattern is particularly noticeable on specimen HK3.2.16, which, if it is associated with the other fragments, must be some part of a trigonotarbid.

Coxa:

Podomeres in specimens HK2001a and HK20014d (figure 8.19B, E) are interpreted as coxae. They measure 370–400µm long and are roughly twice as long as wide, which equates well with measurements of the coxae plus half the sternum diameter in specimens of the ventral prosoma. The podomeres are gently curved in the vertical plane and taper proximally. The distal end of the podomere has a rounded, bulbous appearance. In specimen HK2001a (figures 8.19B, 8.20B) there is considerable emargination of the proximal margin, reaching to about halfway along the length of the podomere. This is presumably where the coxa opened dorsally to the haemocoel and is typical of an arachnid construction where the evolution of long legs necessitates greater coxal stability (Manton, 1977). The curvature of the proximal portion of the podomere resembles that observed in specimens of the ventral prosoma, and if it belongs to the same animal would explain the spiralling towards the centre of the sternum as coxae narrow and curve anteriorwards beneath the sternum.

Trochanter:

Podomeres in specimens HK2001.1 and HK2001.1a (figures 8.19A, E, 8.20A. E) are interpreted as trochanters. They are short, boxy podomeres measuring 150µm across and in their flattened state have a hexagonal outline. In specimen HK2001.1 the trochanter is clearly attached to the coxa, and in specimen HK2001.1 there are at least four trochanters preserved, slightly overlapping one another. No spines or setae are seen to be associated with these podomeres.

Femur:

In specimen HK2001.1 (figure 8.19A) there are several longer podomeres associated with the four trochanters. Towards the top of the image are two overlapping elongated podomeres with biconvex margins, measuring 365µm long. The (proximal?) margin is rounded with a slight indent, whilst the distal margin appears to taper into an acute angle, possibly representing emargination of the distal margin. A similar morphology is observed in the podomere towards the bottom of the image, which measures 420µm long and also has biconvex margins converging into an acute angle at one end.
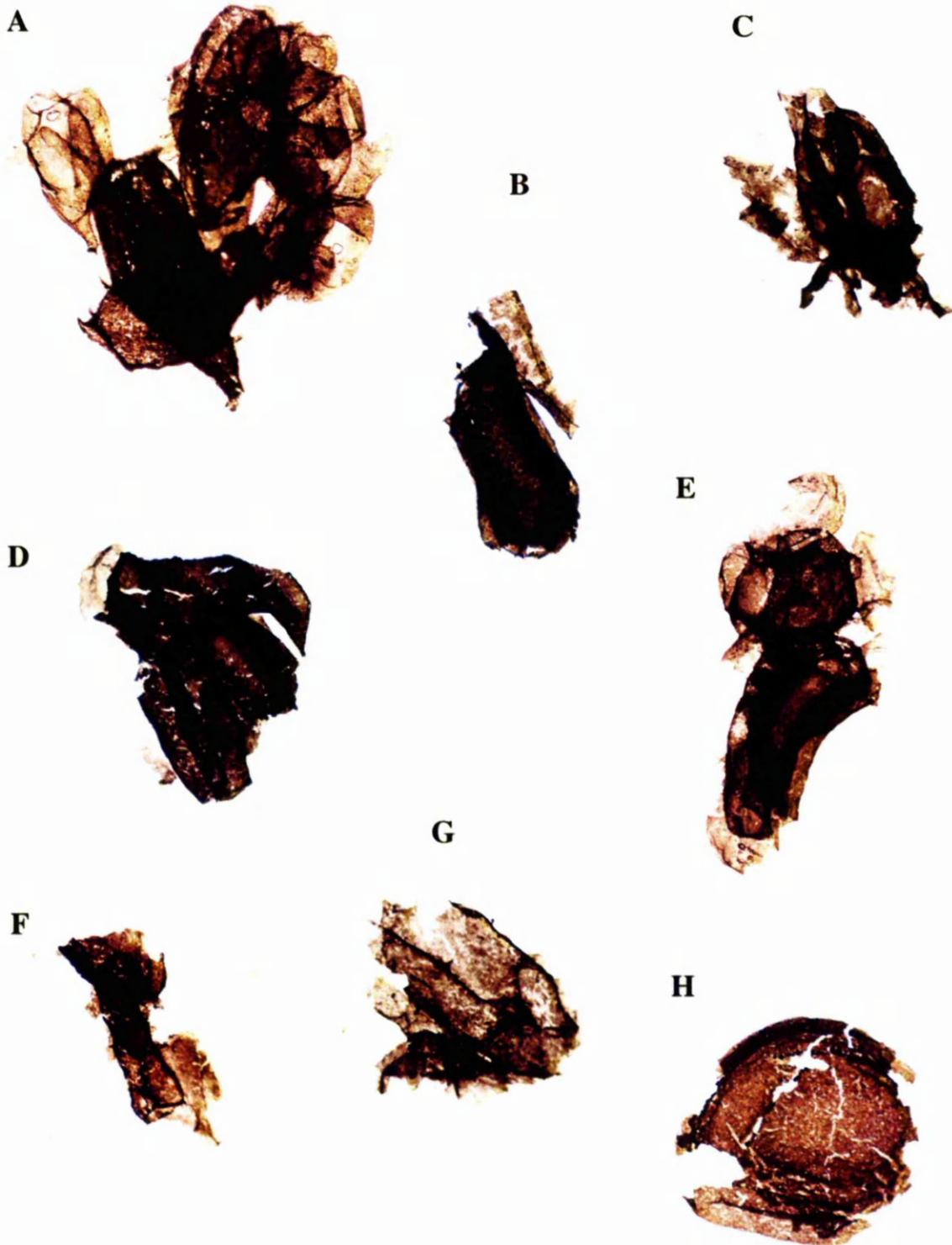
Figure 8.19 Arthropod cuticle from High Knob quarry, New York State, USA. **A**, trochanters and ?femora - HK2001.1. **B**, overlapping femora - HK2001.4d. **C**, boxy cuticle with ribs - HK2001.2. **D**, ?tibia - HK2001.4c. **E**, trochanter and femora - HK2001.1a. **F**, cuticle scrap with thickened ribs - HK3.2.15a. **G**, cuticle fragment (podomere?) with thickened ribs and spines - HK3.2.15. **H**, sternum? - HK3.2.7. Magnification x100.
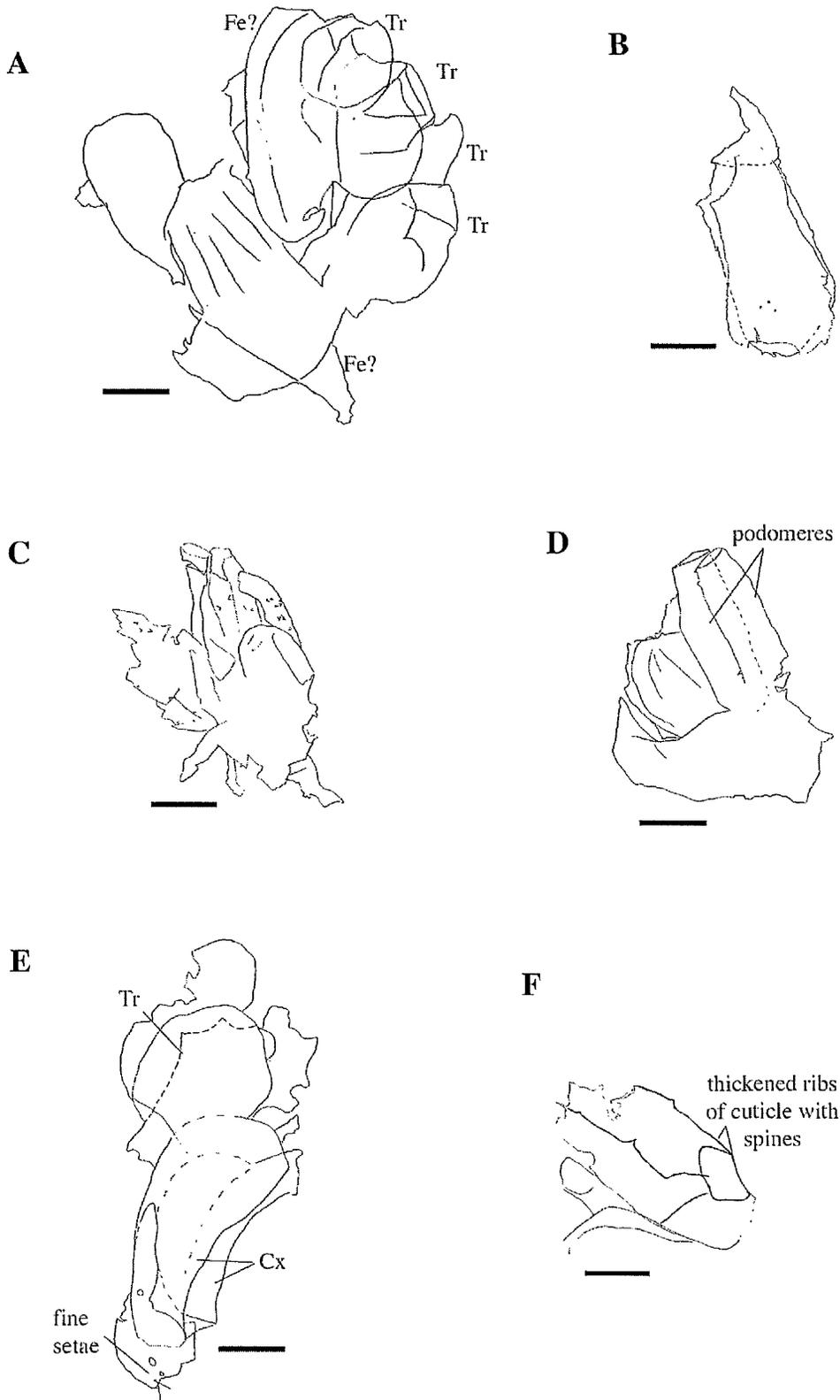
Figure 8.20 Intpreptive drawings to accompany figure 8.19. **A**, trochanters and ?femora - HK2001.1. **B**, overlapping femora - HK2001.4d. **C**, boxy cuticle with ribs - HK2001.2. **D**, ?tibia - HK2001.4c. **E**, trochanter and femora - HK2001.1a. **F**, cuticle fragment (podomere?) with thickened ribs and spines - HK3.2. Scale bars represent 0.1mm.

A cuticle fragment with thickened ribs, sometimes bearing minute spines, is associated with specimen HK2001.1 and also appears as an isolated fragment in specimens HK3.2.15 (figure 8.19G). Like the trochanter, it has a boxy construction, and like the ?femur it tapers asymmetrically to a point at one end. It is possible that these also represent femora, and that the angle of compression causes them to appear slightly differently, or, given their association with the trochanters and femora they could possibly represent patellae. Similar boxy cuticle with ribs is illustrated in figure 8.19C and F.
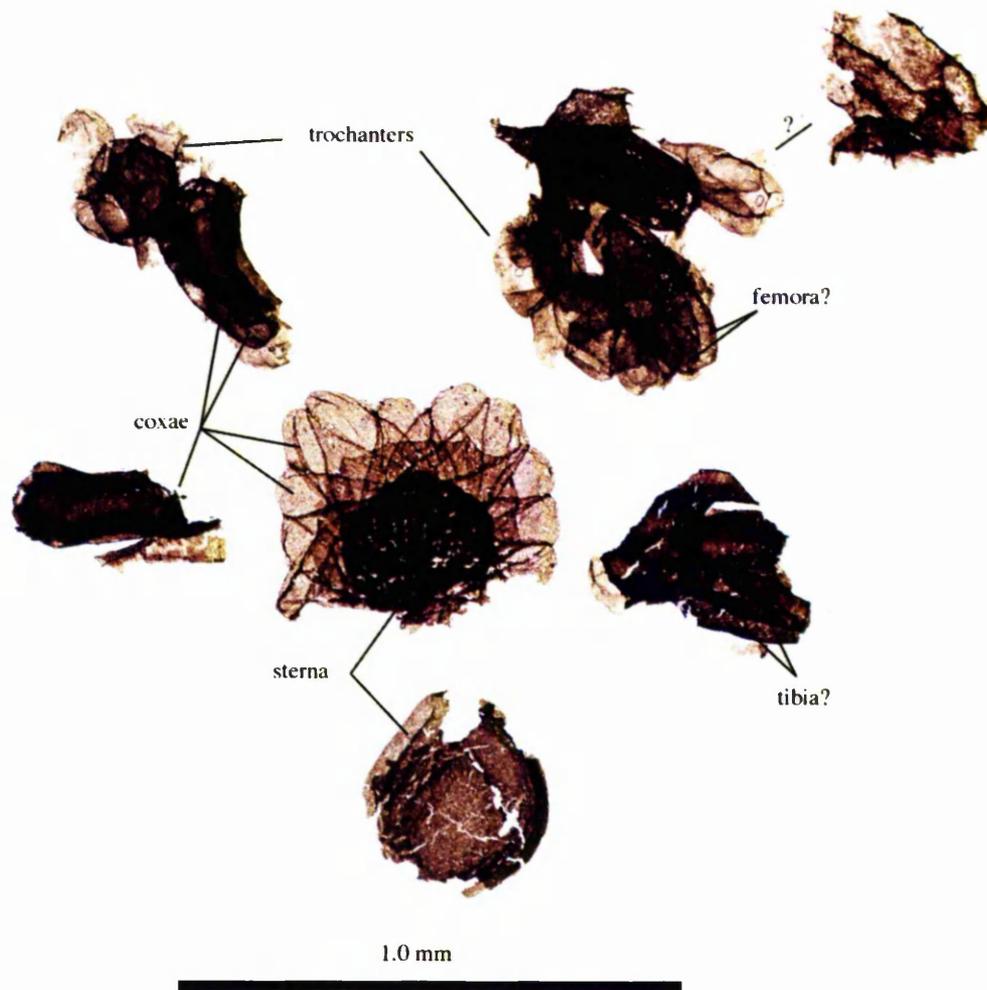
Figure 8.21 Possible association of arthropod sclerites recovered from High Knob quarry, New York state. See text for full description of individual pieces.

Tibia:

Specimen HK2001.4c (figures 8.19D, 8.20D) shows a jumble of cuticle, which includes two cylindrical structures. These measure approximately 270μm long and 80μm wide and are therefore roughly three times as long as they are wide. The associated cuticle fragments are unrecognisable, but by comparison with other arachnid legs these probably represent the tibia.

8.5 Summary

Most of the cuticle described above bears reticulations either over the entire surface of the cuticle or on marginal areas. The majority can be assigned to trigonotarbids, spiders and possibly amblypygids or uropygids, although some groups of cuticle (*e.g.* reticulate A) appear to have sets of characteristics that are not observed in any extant taxa. A comparison of features from three orders of the Pulmonata represented in the fossil record (Araneae, Amblypygi and Trigonotarbida) is given in table 9.

8.5.1 Reticulate A

The presence of slit sensilla and lyriform organs amongst reticulate A cuticle places it emphatically amongst the arachnids. Amongst Recent arachnids, spiders are the only known taxon with lyriform organs on podomeres other than the metatarsus, which suggests that reticulate A cuticle is representative of Araneae. Reticulate A cuticle from Blenheim-Gilboa was described originally as the trigonotarbid *Gelasinotarbus? fimbriunguis* (Shear *et al.*, 1987), but following the discovery of spinnerets with a similar cuticle pattern it was re-described as the spider *Attercopus fimbriunguis* (Selden *et al.*, 1991). Arthropod cuticle bearing lyriform organs was also described from Lower Emsian sediments in Germany (Braun, 1997). Although much of the reticulate A cuticle from South Mountain is almost identical to that of *A. fimbriunguis*, there are notable differences and some features do not conform with a spider identification in the sense of Recent spider morphology.

Aside from minor differences in morphology (*e.g.* number of lyriform organs) which could potentially be explained away by preservational differences, there is the more problematic presence of an annulated structure, which is clearly associated with reticulate A cuticle (figure 8.3B; Selden *et al.*, plate 5, figures 3 and 4). Selden *et al.* (1991) described a flagelliform appendage showing setae and slit sensilla and speculated that it was the caudal flagellum of a uropygid or the flagelliform first leg of an amblypygid. Anderson and Trewin (2003) drew parallels between the flagelliform structure from Gilboa and segmented annular articles described from the Windyfield chert in Aberdeenshire as an unidentified arthropod *Rhyniemonstrum dunlopi* gen. et. sp. nov. They argued that both exhibit a distal ring of sockets and bear similar cuticle sculpture, but finally concluded that the material

Table 9 Comparison of arachnid groups observed in the fossil record with reticulate cuticle microsculpture. Information taken from published data (Weygoldt, 2002; Selden *et al.*, 1991) and personal observations.

	Mesothelae – *Liphistius*	*Attercopus*	Amblypygid	*Ecchosis*	Palaeocharinid trigonotarbids
Cuticle	Scale-like sculpture, minute pores on surface.	Reticulate pattern, scales thickened on one side (distally). Small slit sensilla scattered over surface.	Non-reticulate?	Reticulate pattern, scales thickened on one side but not connecting. Small cuticular pores.	Reticulate pattern varies, may be entire or restricted to proximal parts of podomeres and abdomen.
Setae	Striated macrosetae, raised rims on larger setal sockets.	Long fine setae. Bimodal distribution of setal sockets. Many setae finely serrate, macrosetae bear serrae on their convex surface.	Acicular, leaf-like and rarely clavate.	Striated macrosetae. Very large setae with bifid tip. Larger setal sockets with raised rims.	Various types of setae including efflorescent and bifid.
Carapace	Setae restricted to margins and adjacent to eyes. Eyes situated anteriorly on midline.	Margin is not scalloped and has a narrow doublure. Setal sockets restricted to one end, adjacent to ?eyes.	Eight pairs of eyes, two median eyes sitting on a tubercle close to anterior carapace margin. Lateral eyes form two triads close to the anterior-lateral carapace margin.	Unknown.	Broadly domed with scalloped margins and clypeus produced forward. Four eyes, two on midline. Lateral eyes consisting of two sizes of lenses, smaller generally in a row between larger.
Chelicera	Orthognath, single row of promarginal teeth between promarginal and retromarginal brushes of long, curved setae.	Equant, orthognath. Teeth arranged in single row of 8–11. Fang curves gently with possible subterminal poison gland. Setae are finely serrate and numerous near the teeth. No setae on the fang. Slit sensilla adjacent to fang articulations.	Basal segment stretched anteriorly and with an internal and external row of denticles. Fang directed downwards with one row of denticles.	Unknown.	'Pocket-knife' type. Basal segment with large distal tooth meeting tip of setose fang and three unusual teeth of flattened form. Two teeth proximally.
Femur	Emargination greatest on legs 2 and 3, less on leg 4 and the palp, least emargination on leg 1.	Longitudinal rows of setal sockets on dorsal and ventral surfaces. Curved rows of slit sensillae adjacent to distal joint. Palpal femur with patch of spinules.	Palpal femur armed with spines. Secondary spines added distally.	Two longitudinal rows of three or four larger sockets on ventral side. Small group of slit sensilla adjacent to distal articulation.	Species of *Palaeocharinus* with distinctive thorns near the distal margin of podomeres.
Patella	Pronounced emargination on posterior side of proximal joint.	Short podomere with three lyriform organs situated on distal joint. Lack of pronounced emargination on posterior side of distal joint. Superior surface bears four large setae.	Lack of pronounced emargination on posterior side of distal joint. Reduced to very short podomeres with a nearly immovable patella-tibia articulation designed for autotomy.	Emarginated proximal margin with crescentic articulation points. Four or five setal sockets. Trichobothrium and three small slit sensilla. Two groups of large slit sensilla on inferior side of distal joint.	Short podomere with associated slit sensillae. Patella–tibia joint is a simple bicondylar hinge.
Tarsus	Tarsus bearing three dentate claws, no claw tufts.	Tarsus bearing long, curved fimbriate claws, three on the leg tarsi and one on the palpal tarsus. Tarsal organ present superodistally.	Tibia and tarsus divided into many (over 100 in some species) segments.	Unknown.	Small, smooth median claw situated between larger lateral claws. Single claw on palpal tarsus.

probably represents antennal fragments of a large terrestrial myriapod. On closer inspection of the *Rhyniemonstrum* cuticle, it is unlikely that the two specimens are related. The cuticle sculpture of the Rhynie specimen (Anderson and Trewin, 2003; figure 27C) is reticulate but forms elongated polygons that almost appear to form lines across the cuticle surface, and there are no long, fine setae or minute pores such as those that characterise the cuticle from *A. fimbriunguis*. Similar structures also include the pseudosegemented tarsus of the centipede *Crussolum crusseratum* (Shear *et al.*, 1998) but once again this lacks the reticulate cuticle sculpture and bears major and minor spicules as well as setae. Comparison of the flagelliform appendages of extant uropygids and amblypygids fails to shed much light on this matter and it is likely that the question over the affinity of this piece of arthropod will remain unanswered until more complete and convincing specimens are uncovered. Nonetheless, its consistent association with other arachnid material, in particular that from *Attercopus*, suggests the following possibilities:

1) *Attercopus* had some sort of flagelliform appendage (possibly associated with the legs) and was showing a combination of characters that do not exist amongst modern arachnids.

2) All reticulate A cuticle fragments are not from the same animal and represent at least two different animals (spider and amblpygid/uropygid).
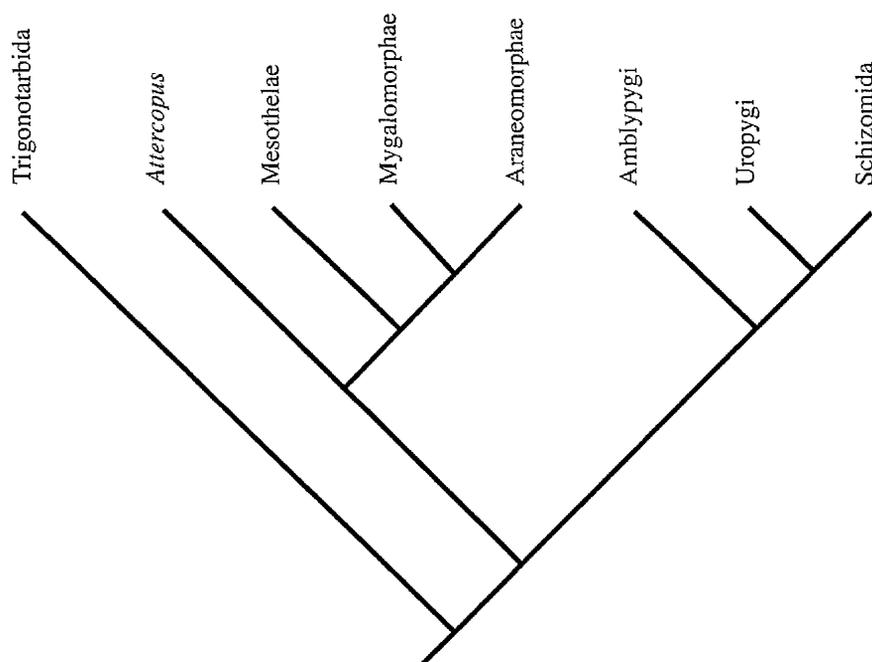
Figure 8.22 Cladogram of relationships between *Attercopus*, infraorders of Araneae, and orders of Pulmonata, as inferred by the cladistic analysis of Selden *et al.*, 1991.

In a comparison of characters from all pulmonate arachnids, Selden *et al.* (1991) determined *Attercopus* to represent a sister group to all living spiders (figure 8.22). As such it is plausible that *Attercopus* displayed a mosaic of features unknown in later examples of spiders, such as the possession of a flagelliform organ and spinnerets. If lyriform organs derived from slit sensillae, then it seems most likely that it was an animal with spinnerets and lyriform organs (spider-like features), and a flagelliform appendage that was subsequently lost. Concerning the second possibility, all reticulate A cuticle is fragmentary, thus it is entirely plausible that the fragments represent more than one animal and highlights the difficulties inherent in reconstructing specimens from dispersed cuticles.

8.5.1   Reticulate B cuticle

Reticulate B cuticle could potentially be divided into two subtypes based upon cuticle sculpture. However, because of the paucity of material with this type of structure they are grouped together for now on the basis that reticulations appear to change shape with position on the body (see specimen SM1.212a; figure 8.12F) and could potentially differ with maturity (the two specimens with very elongate reticulations are considerably larger than other specimens). The cuticle pattern is similar to that described for specimens of *Rhynimonstrum* from Rhynie (Anderson and Trewin, 2003), but only segmented articles have so far been figured. It also bears some resemblance to *Ecchosis pulchribothrium* in the arrangement of reticulations into rows, but with individual polygons thickened on all sides.

The type of eye structure seen in reticulate type B cuticle, consisting of one major lens surrounded by smaller lenses, is a plesiomorphic feature seen only amongst palaeocharinid trigonotarbids, but usually with between three and seven minor lenses. Seven minor lenses occur in *Gelasinotarbus heptops*. The genus is diagnosed by the presence of reticulate cuticle either overall or on carapace margins and proximal ends of podomeres, and the species by the presence of seven minor eye lenses, reticulate cuticle at carapace margins and enlarged setal sockets standing on distinct tubercles on the carapace. Well-preserved specimens of *Palaeocharinus* from the Rhynie chert also exhibit a reticulate cuticle pattern and eyes with multiple minor lenses but were differentiated from *Gelasinotarbus* by the possession of longitudinal clypeal ridges, and distinctive thorns near the distal ends of the podomere (Shear *et al.*, 1987). Since the two associated podomeres with reticulate B cuticle do not possess distal thorns, and given the available features for comparison, specimen SM1.120.2 probably represents a new species of *Gelasinotarbus* diagnosed by the possession of at least 14 minor eye lenses, simple setae and entirely reticulate cuticle.

8.5.2   Reticulate C cuticle

The reticulate C cuticle group contains an assortment of cuticles with varying levels of reticulations and is much less homogenous than the other cuticle categories. Most of

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the material can be assigned to palaeocharinid trigonotarbids, although there is a danger that Trigonotarbida has become somewhat of a dustbin group for otherwise unidentifiable arachnid material from compression fossil assemblages. Selden *et al.* (1991) express their suspicion that *Gelasinotarbus bonamoae*, originally described as a trigonotarbid from an almost complete specimen (Shear *et al.*, 1987), actually represents a uropygid. Similarly, reticulate cuticle from Rhynie, traditionally lumped in with the trigonotarbids, is becoming increasingly problematic, exhibiting features that do not fit with described species (Fayers *pers. comm.*). A complete revision of all reticulate cuticles from Rhynie, Gilboa, South Mountain and High Knob would almost certainly result in the recognition of previously unconfirmed arachnid orders from the Devonian.

8.5.3   *Non-reticulate cuticle*

As discussed in section 8.4.2 these cuticle fragments clearly belong to an arachnid with a rounded sternum and short, stubby podomeres with a box-like construction. All pieces are united in their lack of cuticular ornamentation, and presence of thickened ribs. Since they are all from the same site, and many from the same sample, all are currently assumed to be related, as there is no good reason to believe otherwise. Figure 8.21 illustrates associations between cuticle pieces from High Knob so that even if the interpretations prove to be unfounded at a later stage, the overall morphologies can still be matched.

In an apparent reversal to sites such as Gilboa and South Mountain, most cuticle fragments have been recovered as articulated or multi-layered specimens compressed together, and not isolated sclerites. The cuticle from High Knob is covered with tiny tears suggesting that the cuticle was very thin and fragile, and it is possible that thinner layers of cuticle (*e.g.* cuticle from the carapace and abdomen or isolated podomeres) are fragmented beyond recognition during burial and compression. Currently the evidence points towards a trigonotarbid identification, but more through elimination from other arachnid groups than obvious trigonotarbid features. It is not clear whether the single reticulate specimen recovered from High Knob is associated with the non-reticulate cuticle, but given the total absence of any sort of reticulation in the latter, this seems unlikely. The sediments and associated arthropod cuticle from High Knob are currently in the early stages of investigation and they should prove to be a lucrative source of new arthropod material. Further maceration of sediment samples from High Knob is recommended.

CHAPTER 9   Miscellaneous Cuticle Types

This chapter discusses cuticles recovered from the macerates that either occur in very small numbers, are unidentifiable but probably arthropod, or have a tentative identification but require further examples before they can be described fully. It also addresses the compressed masses of spores and cuticles that are frequently found in the macerates and that, although individual components can be difficult to identify, are an interesting line of evidence for plant–animal interaction.

9.1   Chilopoda

Only two pieces of cuticle identifiable as a centipede were recovered from South Mountain (figure 9.1A,C). Specimen SM1.119.31 represents the modified first leg (forcipules) of a centipede, and specimen SM1.128.4a is interpreted as the apical claw of a forcipule.

Scutigeromorph centipedes are known from the Silurian sediments of Ludford Lane (Jeram et al., 1990), and the Devonian of Gilboa (Shear and Selden, 1988) and Rhynie (Anderson and Trewin, 2003). The majority of the fossil scutigeromorph centipedes from these localities are preserved as individual podomeres with a pentagonal cross-section and serrate margins. At Rhynie, however, the forcipules of Crussolum are preserved and were described by Anderson and Trewin (2003). The anterior margins of the coxosternal podomeres bear stout, socketed setae and the femuroid is thickset, bearing small setal sockets on the outer margin and a single large spine socket on the inner margin.

A second order of centipede from Gilboa is represented by preserved forcipules that have features allying them to the craterostigmomorphs known only from Tasmania and New Zealand (Shear et al., 1984). Shear and Bonamo (1988) placed Devonobius in the order Devonobiomorpha, but Borucki (1996) argued that the similarities with modern craterostigmomorphs did not justify this. The forcipules from Gilboa have a divided coxal plate bearing a distinct toothed process on either side, which is almost identical to specimen SM1.119.31.

A multisegmented piece of cuticle recovered from South Mountain is included here as it may represent the tarsal subsegments of a centipede. It bears a superficial resemblance to the flagelliform appendage described from Reticulate A cuticle, but does not consist of overlapping rings of cuticle and does not bear a reticulate cuticle sculpture. Similar cuticle fragments described as centipede tarsi are figured in Shear et al. (1998) but these exhibit major and minor spicules as well as socketed spines. Specimen SM1.8.2 (figure 9.1D) shows only one size of spine, occurring in pairs, in rows towards the proximal margin of each subsegment.
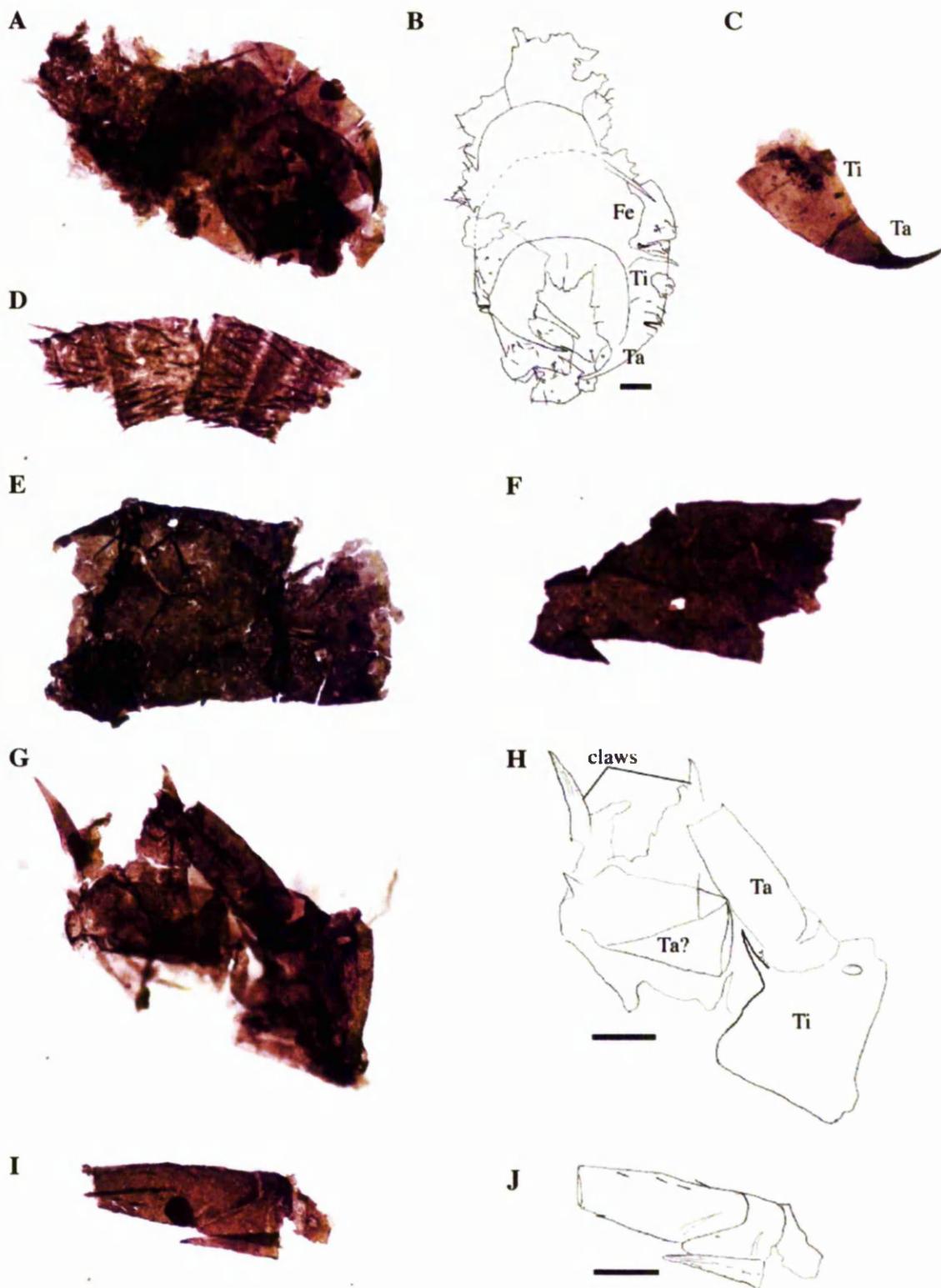
Figure 9.1 Miscellaneous arthropod cuticle from South Mountain, New York. **A**, centipede forcipules - SM1.119.31. **B**, interpretive drawing of A - SM1.119.31. **C**, apical claw from centipede forcipules - SM1.128.4a. **D**, subsegmented appendage, ?centipede tarsus - SM1.8.2. **E**, arachnid podomeres with lyriform organ - SM1.4.8c. **F**, spiny podomere - SM1.120.V10. **G**, spiny posomeres and claws - SM1.115.V49. **H**, interpretive drawing of G - SM1.115.V49. **I**, spiny podomere - SM1.115.V49a. **J**, interpretive drawing of I - SM1.115.V49a. Scale bars represent 0.1mm. A and C, magnification x50; D–I magnification x100.

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9.2   Spiny podomeres

Figure 9.1E–J illustrates a number of podomeres for which a positive identification is uncertain. Specimen SM1.1.4.8c (figure 9.1E) clearly bears a distally located lyriform organ and is therefore identified as an arachnid podomere. It does not bear the same reticulate ornamentation that occurs on specimens of the spider *Attercopus* (see chapter 8) and the setae are shorter. Both podomeres are incomplete and are therefore difficult to identify accurately. If the lyriform-bearing podomere represents a metatarsus then it may be an amblypygid or uropygid. If it represents any other podomere this would suggest that it is a spider. The distal podomere is slightly wider than the proximal podomere, which does not support the interpretation that it is a tarsus. By nentological comparison the evidence suggests that these are the podomeres of a spider, although it is possible (but probably unlikely) that arachnids in the Devonian bore more lyriform organs than they do now. The cuticular ornamentation and setae are entirely different to the only described Devonian spider, *Attercopus*, and this specimen could represent only the second known species of spider from this time.

A spiny podomere is illustrated in figure 9.1F. There is no cuticular ornamentation, but there are very large spines along the margins. Spines such as these are reminiscent of the spiny podomeres of amblypygid pedipalps. A similar spiny podomere is figured in Shear *et al.* (1984; figure 1C) and interpreted as the palpal tarsus of an amblypygid. This podomere also shows no cuticular ornamentation.

Very small podomeres occuring in a jumble of cuticle are illustrated in figure 9.1G and I. These clearly represent the distal portions of legs and bear single terminal claws. SM1.115.V49 and SM1.115.V49a both resemble arthropleurid podomeres with their large spines on the distal margins of podomeres. The podomeres differ from *Eoarthropleura* in the absence of numerous setae and more closely resemble described podomeres of *Microdecemplex* (Wilson and Shear, 2000). *Microdecemplex* was described with a fused claw resulting in the appearance of a very long tarsus. Specimen SM1.115.V49a shows the articulation of a posttarsal claw with the tarsus which would have been essentially immobile, much like the patella-tibia joint of an amblypygid. Unfortunately the tip of the distally tapering podomere is missing so it is unclear whether this represents the tarsus and posttarsus or some other distal leg joint. The claws in SM1.115.V49 are clearly not fused to the tarsi so *Microdecemplex* is discounted as a possible identification for these podomeres.

9.3   'Zig-zag' cuticle—Hexapoda?

Large sheets of cuticle with a distinctive zig-zag pattern of setal sockets arranged in staggered rows were recovered from macerates of sediments from South Mountain. The same cuticle is also known from Gilboa and has tentatively been identified as a primitive

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archaeognath hexapod (Shear *pers. comm.*).

9.3.1   Cuticle topography

'Zig-zag' cuticle fragments are illustrated in figures 9.3 and 9.4. The cuticle surface itself is smooth and unornamented, but the characteristic feature of this cuticle type is the shape and arrangement of sockets. The aperture to the socket is circular and the sockets themselves are slightly raised and oblique to the cuticle surface so that they form a cone shape as they penetrate into the cuticle. In the fossil specimens the cone is usually flattened giving the appearance of triangular sockets forming stepped zigzag lines over the cuticle surface. The sockets are arranged in discontinuous rows that are slightly offset from one another, and occasionally contain long, ribbon-like scales, which extend only as far as the next row of sockets (figure 9.3A, B). These are clearly flat and formed from a single cuticle layer and are therefore scales rather than setae. The oblique insertion and stepped arrangement of scale sockets in the living machilid archaeognath *Trigoniophthalmus alternatus*, is shown in figure 9.2 together with an electron micrograph of the fossil cuticle for comparison.
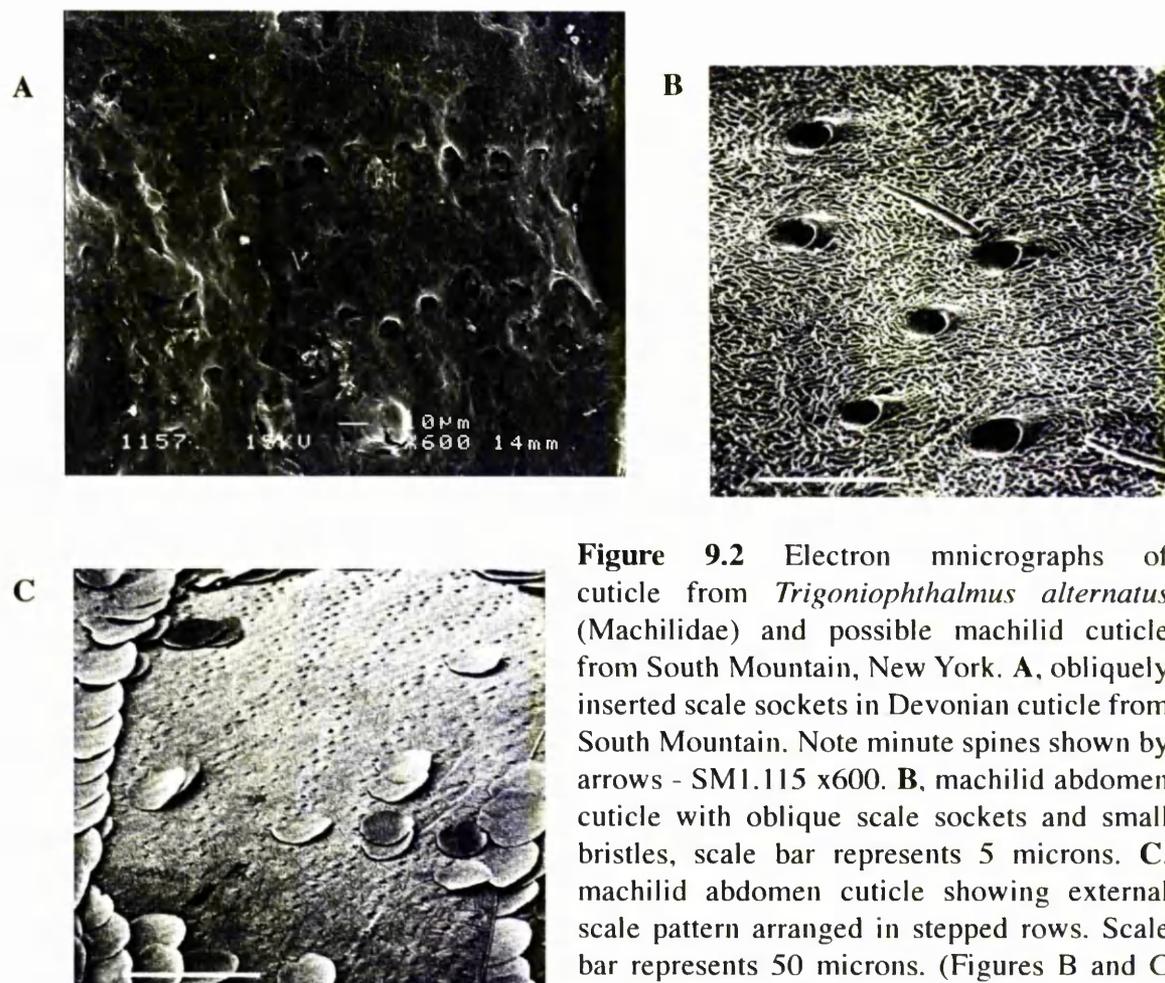
Figure 9.2 Electron mnicrographs of cuticle from *Trigoniophthalmus alternatus* (Machilidae) and possible machilid cuticle from South Mountain, New York. **A**, obliquely inserted scale sockets in Devonian cuticle from South Mountain. Note minute spines shown by arrows - SM1.115 x600. **B**, machilid abdomen cuticle with oblique scale sockets and small bristles, scale bar represents 5 microns. **C**, machilid abdomen cuticle showing external scale pattern arranged in stepped rows. Scale bar represents 50 microns. (Figures B and C modified from Eisenbeis and Wichard, 1987).
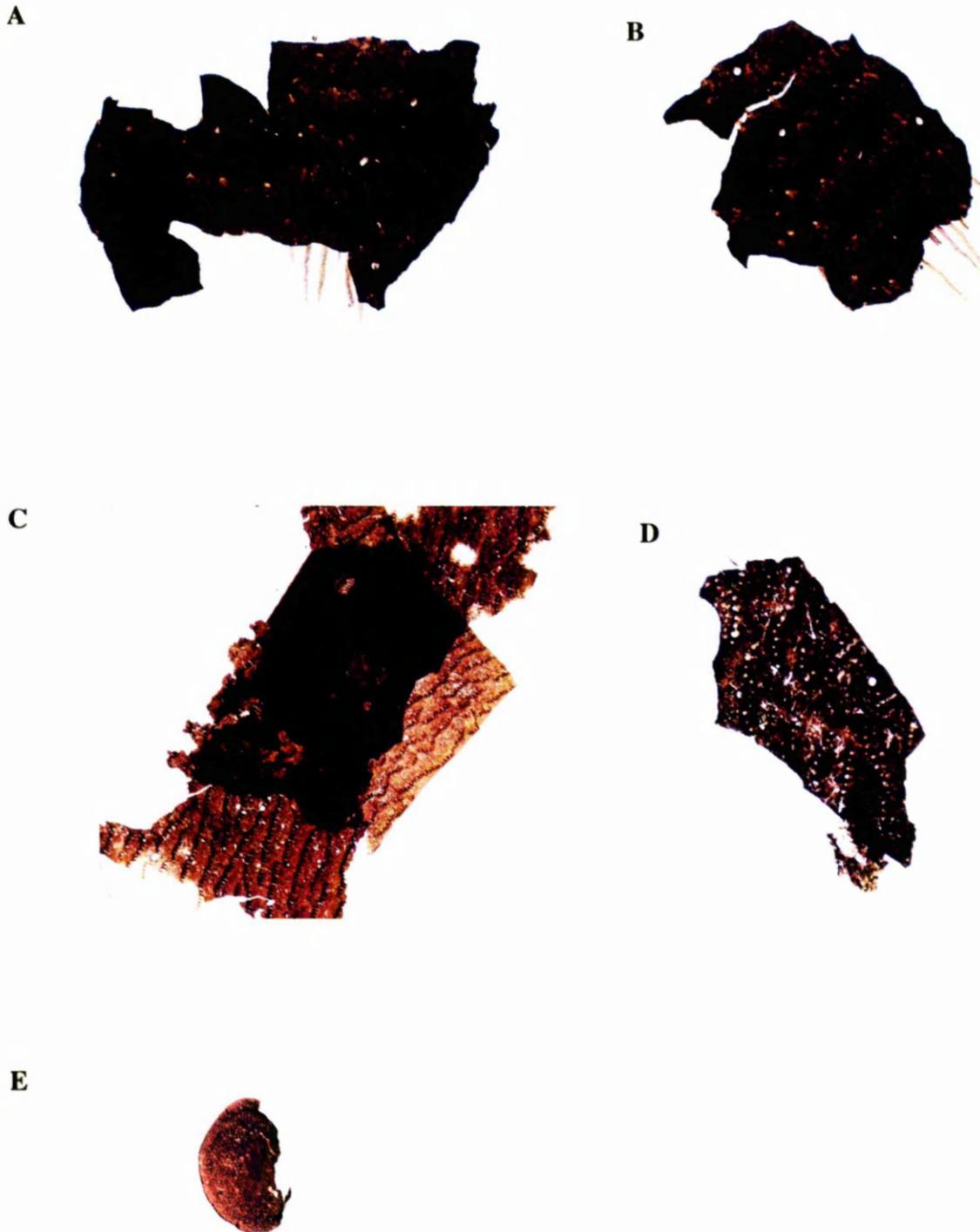
Figure 9.3 Archaeoagnatha? cuticle from South Mountain, New York. **A**, isolated fragment of cuticle with cone shaped setal sockets arranged in rows housing long, ribbon-like setae - SM1.4.9a, x100. **B**, fragment of cuticle from the same sample, and probably associated with A - SM1.4.9, x100. **C**, large cuticle piece with one straight edge and sub-parallel rows of setal sockets. No setae preserved - SM1.120.1, x50. **D**, elongate cuticle piecce with real edges, rows of cone-shaped setal sockets and additional round setal sockets - SM1.212.4, x100. **E**, compound eye with hexagonal lenses - SM1.212, x100.

A

B

round setal
sockets

cone-shaped
scale sockets

long, ribbon-like
scales

C

D

rows of
sockets

E

hexagonal
ommatidia
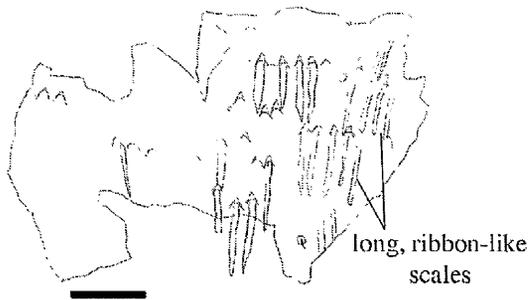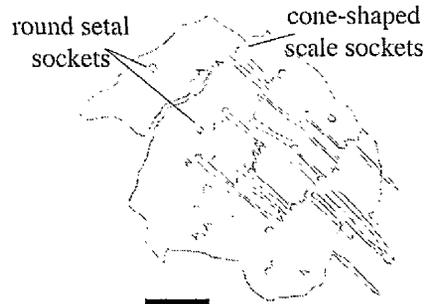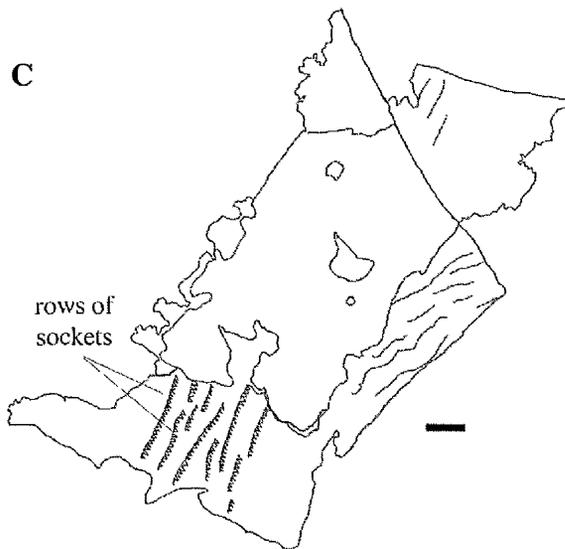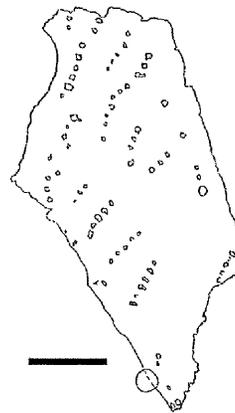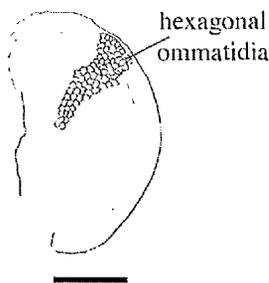
Figure 9.4 Interpretive drawings to accompany figure 9.2. **A**, isolated fragment of cuticle with cone shaped setal sockets arranged in rows housing long, ribbon-like setae - SM1.4.9a. **B**, fragment of cuticle from the same sample, and probably associated with A - SM1.4.9. **C**, large cuticle piece with one straight edge and sub-parallel rows of setal sockets. No setae preserved - SM1.120.1. **D**, elongate cuticle piecce with real edges, rows of cone-shaped setal sockets and additional round setal sockets - SM1.212.4. **E**, compound eye with hexagonal lenses - SM1.212. All scale bars represent 0.1mm.

In addition to the scales and scale sockets, the cuticle also bears a number of larger, circular setal sockets. No setae are seen in association with these sockets using a standard microscope, but under the SEM they are occasionally seen to contain minute spines (figure 9.2A marked with arrow). Small bristles occur between the scale sockets of some Machilidae (figure 9.2B, C) and this was probably also true of the specimens from South Mountain.

9.3.2 Cuticle morphology

Unfortunately the majority of recovered fragments of this type of cuticle are scraps with torn margins and offer very little information concerning the morphology of the animal they belong to. Specimen SM1.120.1 (figure 9.3C) is a large single sheet of cuticle with one long straight edge and may represent cuticle from the dorsal surface of the thorax. SM1.214.4 (figure 9.2D) is the only fragment with at least two real edges. It is asymmetrical and appears to be formed from a single layer of cuticle, but without more complete or articulated cuticle pieces it is impossible to speculate any further.

A structure resembling a compound eye was recovered from South Mountain (specimen SM1.212, figures 9.3E, 9.4E). Unfortunately no cuticle was found adhering to it, and it is not necessarily associated with the cuticle described above. Compound eyes are found particularly in insects and crustaceans and are formed from numerous ommatidia. Fine focusing reveals that the fossil specimen has a convex structure with a flatter ledge around the base of the eye. It measures about $10\mu m$ across its short axis and twice that across the long axis. Each ommatidium measures approximately $4\mu m$ in diameter, and there are several hundred of these on the surface of the eye. The alleged fossil bristletail reported from Québec was described as having prominent bulging compound eyes, and two to three hundred ommatidia, a character diagnostic of modern archaeognathans and winged insects (Labandeira et al., 1988). The only other described insect from this period is the springtail from the Rhynie Chert (Greenslade and Whalley, 1986). Collembolans, however have compound eyes with no more than eight almost circular ommatidia (Eisenbeis and Wichard, 1985).

It seems plausible that this cuticle represents an early archaeognath but without more diagnostic body parts it is unwise to speculate further. Apparently compound eyes are also found in scutigeromorph centipedes, but they are in fact pseudofacetted and the lenses are round. The compound eye would certainly fit with a hexapod identification, and it is unfortunate that it was not associated with any other cuticle fragments. It is hoped that continued maceration will eventually produce more complete and/or diagnostic specimens.

9.3.3 Palaeozoic insects

Pre-Carboniferous insects are extremely rare in the fossil record and evidence

for hexapody comes from only a few sites. The oldest known insects are a collembolan and pterygote insect from Rhynie (Tillyard, 1928; Engel and Grimaldi, 2004), and a bristletail described from the Lower Devonian of Québec (Labandeira et al., 1988). The three dimensional preservation and lack of fragmentation of the bristletail however, raisees questions over its authenticity (Jeram et al., 1990). The electron micrographs show the cuticle surface to be relatively smooth and show none of the undulations caused by individual sediment grains compacting onto the cuticle, which is typical of the material recovered from South Mountain and elsewhere. Collembolans have been described from the Old Red Sandstone at Rhynie (Greenslade and Whalley, 1986) and Shear et al. (1984) indicate the presence of archaeognath cuticle in the Gilboa assemblage.

9.4   Opaque cuticle with spinules—Hexapoda?

Opaque cuticle covered with tiny spinules is illustrated in figure 9.5. Only a few pieces were recovered from the macerates, but it is possible that many more were missed as they bear a strong resemblance to coalified plant fragments. The recovered fragments were discerned as possibly arthropod by their morphology of articulating segments, which is reminiscent of some arthropod podomeres.

The specimens from South Mountain are flattened tubular structures with a thick, sclerotised cuticle covered entirely with small spines. Specimen SM1.115.V35 (figure 9.5A, B) consists of three articulated pieces of cuticle, possibly representing the podomeres of a leg. The middle podomere is greatly inflated and measures 430µm long and 290µm at its widest point. Along the dorsal surface of the podomere the cuticle is pulled out into broad thorns, and towards the centre there appears to be a cluster of circular holes of varying sizes. One of the articulating margins has a deep embayment where it attaches to a rectangular podomere measuring approximately 200µm long and 150µm wide. The third sclerite in this specimen is asymmetrical, measures 320µm long and gradually tapers to a narrow point. At the end of this tip is a circular structure that appears to be part of the same sclerite. This 'podomere' bears a remarkable resemblance to specimen SM1.212.4 (figure 9.3D), which, as discussed above, might represent an archaeognath. Furthermore, Jeram et al. (1990) described a very similar cuticle type from the Silurian of Ludford Lane in Shropshire. They illustrated a cuticle fragment (their figure 1Q) that they considered to represent the 'posterior end of an unknown arthropod with a pair of cerci and ornament of minute spinules'. If this specimen does represent a pair of cerci then this suggests that this cuticle type is also representative of some kind of insect. However, the specimen has not been re-examined and the only information available is small black and white photograph.
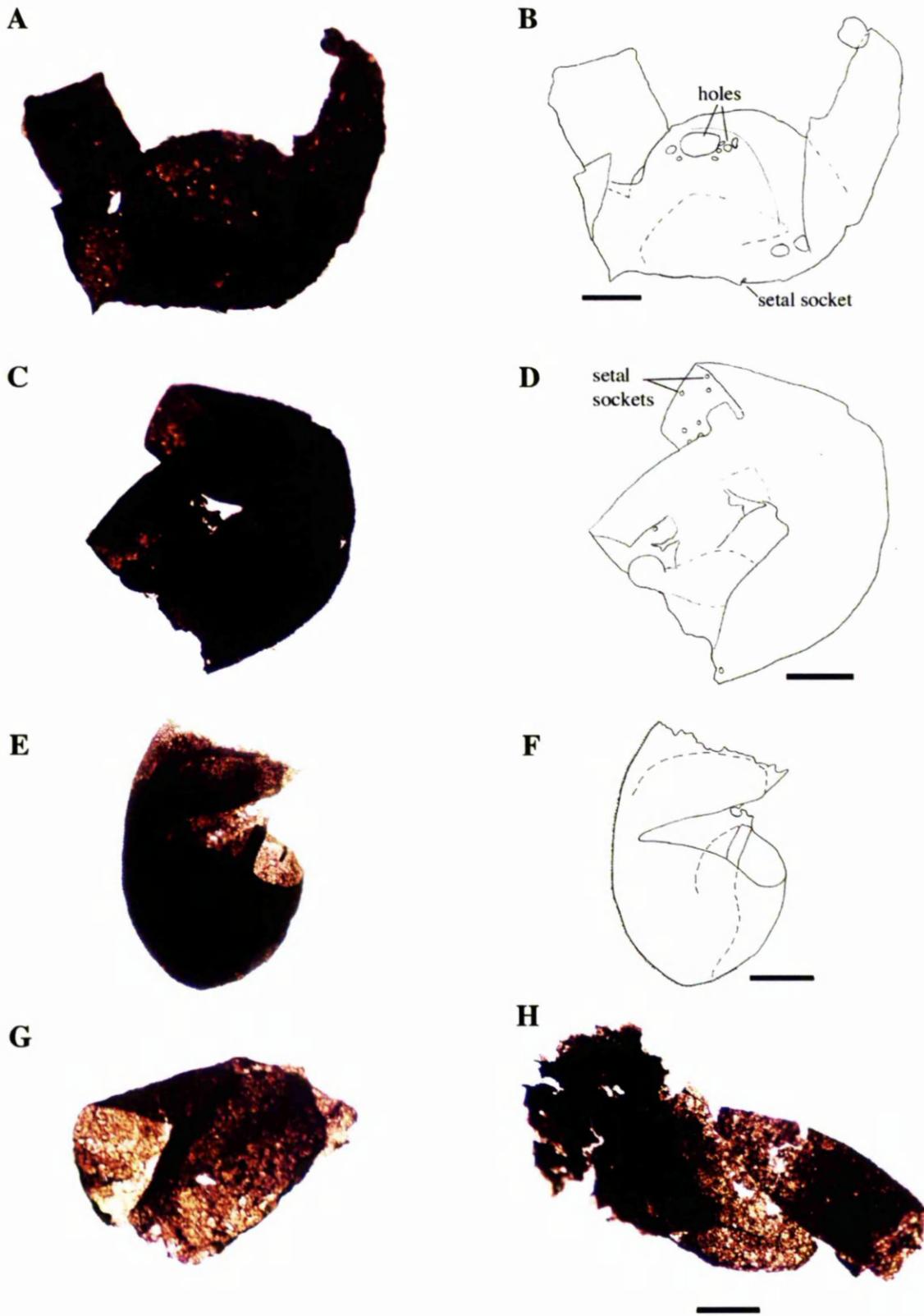
Figure 9.5 Opaque cuticle with spinules from South Mountain, New York. **A**, three associated articles of dark cuticle - SM1.115.V35, x100. **B**, interpretive drawing of SM1.115.V35 showing broad thorns and circular structures in cuticle. **C**, ?three podomeres - SM1.213.11, x100. **D**, interpretive drawing of SM1.213.11 showing position of setal socket. **E**, bowl-shaped structure - SM1.212.1, x100. **F**, interpretive drawing of SM1.212.1. **G**, ?podomere - SM1.213.11c, x100. **H**, unidentified dark cuticle - SM1.213.11b. Scale bars represent 0.1mm.

Specimen 213.11 (figure 9.5C, D) similarly appears to consist of at least two articulated sclerites, probably podomeres. Delimiting the margins of theses podomeres, however, is difficult because the cuticle is so dark and dense. The podomeres appear to have emarginated margins and are similar in overall morphology and proportions to the isolated podomere in figure 9.5G (specimen SM1.213.11c). This podomere measures 240µm long. The lateral margins have splayed during compression, but it probably measured about 140µm wide in life. Irregular holes of varying size and shape occur towards the margin of the podomere, possibly representing a combination of setal sockets and tears in the cuticle. Specimen 212.1 (figure 9.4E, F) measures 420µm along its length and is 300µm wide. It forms a bowl shaped structure open at one end and is comparable to the middle article of specimen SM1.115.V35 (figure 9.5A, B).

The surface pattern of this cuticle type is unlike any other arthropod cuticle reported from amongst terrestrial arthropod cuticle assemblages. The presence of setal sockets and overall morphology suggests that it is arthropod cuticle, and part of one of the specimens bears a strong resemblance to a piece of cuticle identified as an archaeognath. On the other hand, the surface of the cuticle is reminiscent of some spores (in particular, specimen SM1.212.1), and could easily have been dismissed as such had the material not been recovered in its articulated state.

9.5   *Unidentified cuticle from High Knob*

A few examples of cuticle recovered from High Knob do not fit comfortably into any of the previously described groups of cuticle. These are illustrated in figure 9.6. Specimens HK2001.4a and HK2001.1b (figure 9.6A, B. C) both exhibit a similar overall morphology and appear as elongated masses of cuticle, which could possibly be subdivided into articulated segments. HK2001.4a is particularly interesting because, towards one end of the cuticle mass, there appears to be a pair of triangular structures with convex inner margins. These could possibly represent mouthparts (*e.g.* forceps of a centipede), or paired cerci from the posterior end of an arthropod (*e.g.* a predatory japygid diplurid). The general lack of setae and absence of other sclerites from the head region renders paired cerci a more likely interpretation of the triangular projections, and could provide yet another piece of evidence in support of insect life during the Devonian.

Remaining specimens in figure 9.6(D, E, F, G) are either scraps of cuticle that resemble other pieces of arthropod cuticle in colour and texture, or jumbles of possible arthropod cuticle too distorted to identify. There are no diagnostic features with which to identify these specimens, but they are included here for the sake of completeness.

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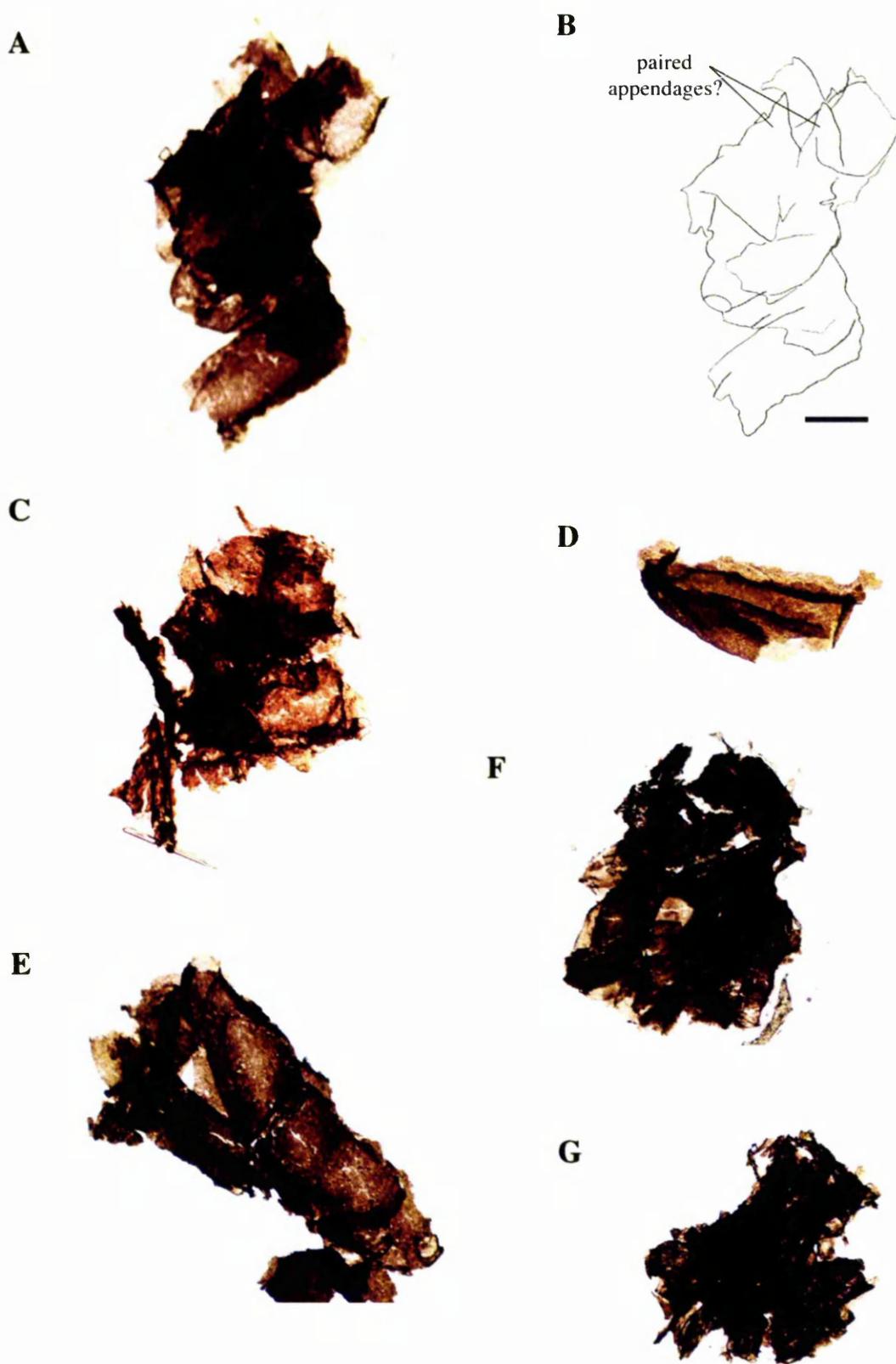
Figure 9.6 ?Arthropod cuticle from High Knob quarry, New York State, USA. **A**, segment specimen, possibly with paired appendages - HK2001.4a. **B**, interpretive line drawing of specemin HK2001.4a. **C**, possible segmented cuticle - HK2001.1b. **D**, unidentified cuticle scrap, possibly arhropod - HK3.2.16. **E**, possible arthropod cuticle - HK2001.6. **F**, distorted mass of ?arhtropod cuticle - HK2001.4b. **G**, distorted mass of ?arthropod cuticle - HK2001.2a. Magnification x100, scale bar represents 0.1mm.

9.6 Organic aggregates—coprolites?

Aggregates of spores and cuticles were recovered from the macerate residues from South Mountain. These are illustrated in figures 9.8 and 9.9. The aggregates consist of complete and fragmented spores, unidentifiable plant material and occasional arthropod cuticle. Very broadly these masses of organic material fall into two morphotypes. Pellets consisting almost entirely of spores are long and slender, measuring approximately 480µm long and 180µm long (figure 9.8). Other pellets have a more irregular outline and are composed of spores and possibly scraps of arthropod cuticle. They are squatter in appearance, measuring 300–400µm along their long axes and 200–250µm along the short axes (figure 9.9). The size ranges of these pellets are plotted in figure 9.7. Within the more regular shaped pellets, spores consistently measure 40–50µm in diameter and exhibit at least two different morphologies. Subtriangular spores bear a trilete mark and are adorned with a fringe of minute projections, giving a finely crenulated appearance to the margins (figure 9.8D). These spores are interpreted as *Aneurospora* sp., although a full palynolygical study would be beneficial. Other, more rounded, spores have a smoother cuticle surface and do not occur as spore tetrads (*e.g.* figure 9.8A). They are frequently cracked. The more irregular pellets are composed of a mixture of spores, plant and arthropod cuticle and other amorphous organic matter. Figure 9.9A and B show an aggregate of spores and cuticles with a stack of single-layered cuticles.
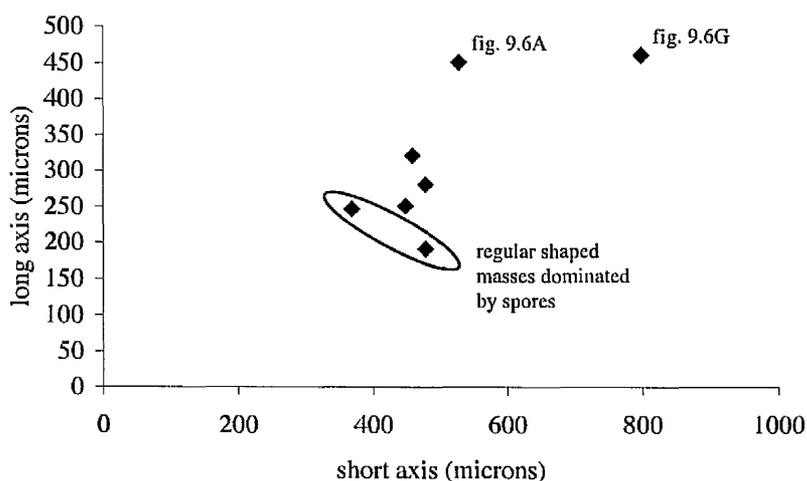
Figure 9.7 Length/width ratios of organic aggregates of spores and cuticles recovered from macerates of shales from South Mountain, New York, USA. All specimens recovered from sample SM1.115.

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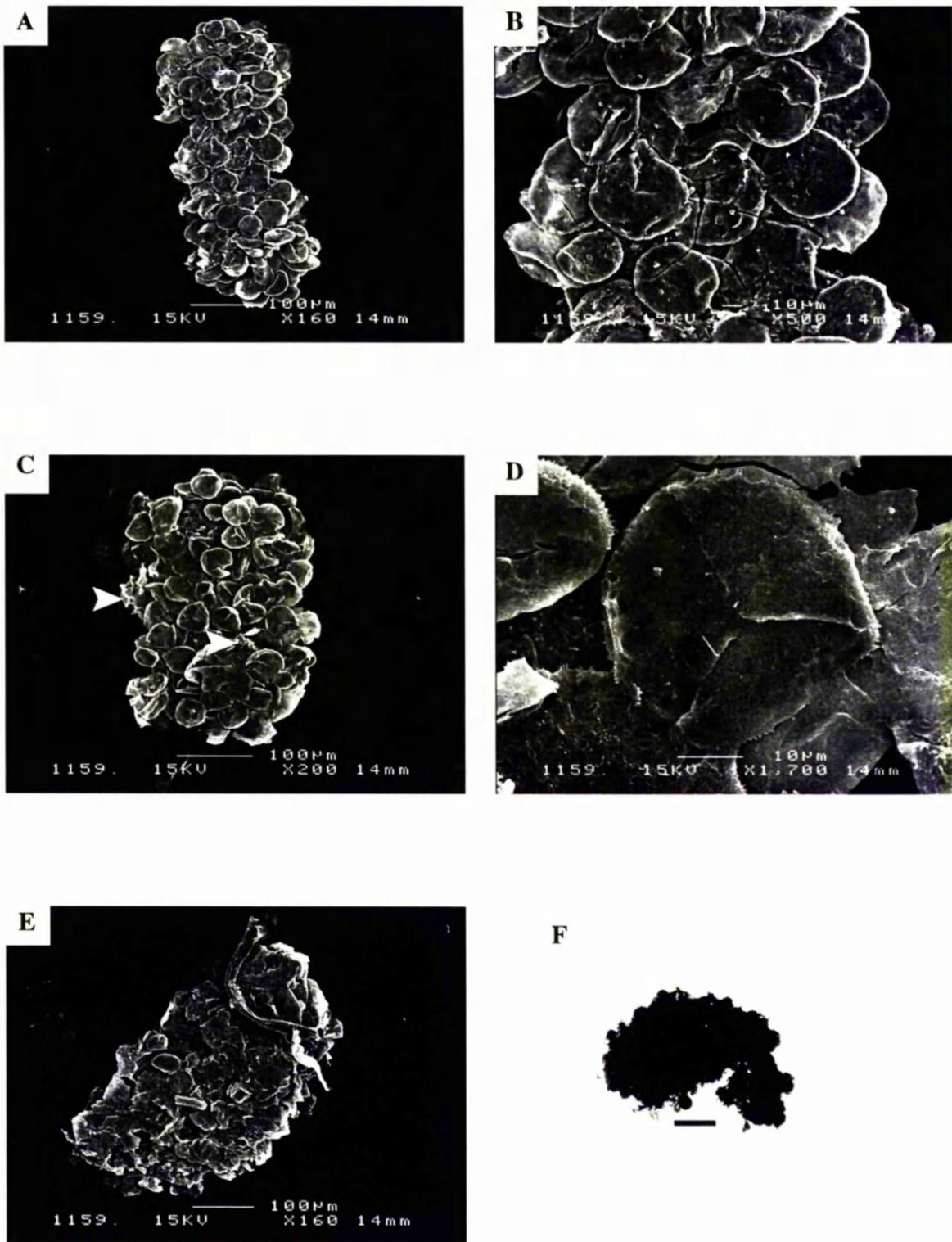
Figure 9.8 Scanning electron micrographs of organic aggregates recovered during acid macerations of shales (sample SM115) from South Mountain, New York State. **A**, elongate pellet composed almost entirely of spores. **B**, detail of spores seen in A. **C**, elongate pellet composed largely of spores. Arrows indicate non-sporous material. **D**, detail of spore seen in C. **E**, pellet of spores and amorphous material. **F**, aggregate of spores viewed under transmitted light, scale bar represents 0.1mm.

194
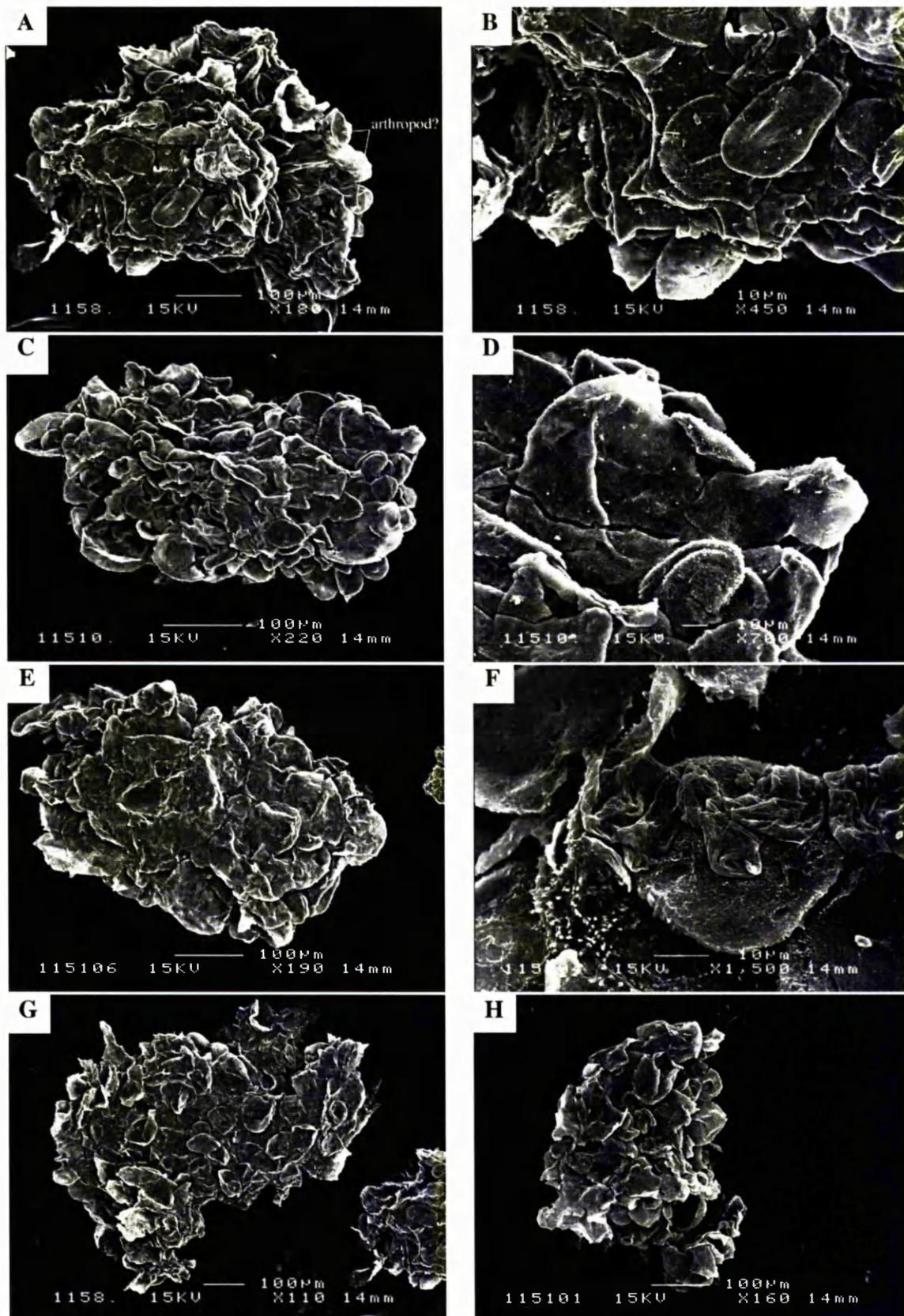
Figure 9.9 Scanning electron micrographs of organic aggregates recovered during acid macerations of shales (sample SM115) from South Mountain, New York State. **A**, mass of spores and possible arthropod cuticle. **B**, detail of spores seen in A. **C**, pellet composed largely of compacted spores and cuticle. **D**, detail of spore seen in C. **E**, pellet of spores and amorphous material. **F**, detail of E. **G**, aggregate of spores and cuticle. **H**, aggregate of spores and cuticle.

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The presence of more than one species of spore and the inclusion of plant, and possibly arthropod, cuticle within these aggregates, rules out the possibility that these represent the preserved contents of a sporangia. The translucent arthropod cuticle can be seen most clearly towards the edges of the aggregates when they are viewed under transmitted light (figure 9.8F). The major drawback of this method is that much of the detail from the centre of the specimen cannot be seen. Using the SEM, however, enables details of the spore structure to be seen most clearly, but is not very useful for spotting the presence of arthropod cuticles. Therefore the best way to study these pellets is to make careful observations first with a light microscope and then transfer the masses to stubs for analysis with the SEM. In practice, however this can be difficult because the pellets are so fragile and are easily broken during transit from the macerate to a slide and from the slide to a stub.

There are two possible explanations for the presence of these organic aggregates. The first is that they are the result of the flocculation of suspended matter in the water column. The majority of suspended particles in estuaries and surrounding coastal waters are formed of flocs of mineral particles and organic matter strongly bound together by mucopolysaccharides produced by bacteria, algae and plants, and mobilized from the suspended matter at low salinity (Eisma, 1986). It is unlikely that this explains the regular-shaped aggregates consisting largely of spores, but it could provide an explanation for some of the more irregular aggregates recovered. However, Eisma (1986) observed that the upper size limit for microflocs was 125μm determined by the binding strength of the organic matter in relation to the total mass of the floc. All of the aggregates illustrated here exceed this size by a factor of two or three. However, Eisma also concluded that macroflocs could occur as accumulations of microflocs, and that these could reach up to 3–4mm. The palaeoenvironment at South Mountain is interpreted as a nearshore, estuarine type and therefore it is likely that at least some of these aggregates resulted from the flocculation of organic particles in the water column.

An alternative explanation for the presence of these aggregates, is that they represent fossilised faecal pellets (coprolites). In support of this, associated cuticles are considered to be representative of terrestrial debris, and it stands to reason that along with the plant and arthropod material there should be also be a component of frass. Faecal pellets from microarthropods make up a major part of humus in modern leaf litter communities. They are documented in the fossil record (see section 1.4.3), possibly from as early as the Ordovician (Retallack and Feakes, 2001) and are significantly more abundant during the Carboniferous—an increase that coincides with a dramatic proliferation in vegetative biomass.

Coprolites are of considerable importance in determining the diet of their producer, and the question then arises as to what produced them. The fossil cuticle assemblage at South Mountain is dominated (in terms of numbers of orders) by predatory arachnids. Arachnids

digest their prey externally and, assuming that they were physiologically similar to modern day equivalents, would produce dry faecal matter consisting largely of guanine and uric acid. If the coprolites represent a truly herbivorous animal, then they would be expected to consist of digested plant material only. However, it has been shown that they consist of at least two types of spores and frequently plant, and possibly arthropod, cuticle. This then rules out an obligate spore feeder and the most plausible candidate becomes a decomposer that fed indiscriminately on the litter ingesting spores, plant material and exuviae alike.

It may be that the collection illustrated in figures 9.8 and 9.9 represents two different animals; one that specifically targeted either sporangia, spore masses in the debris, or even other coprolites (coprophagy) and one that did not discriminate. However, the large proportion of spores that are still intact suggests that spore feeding alone was inefficient and that the relevant gut microflora had not yet developed to enable internal digestion of the spores.

9.6.1 Siluro–Devonian coprolites

Edwards et al. (1995) described aggregates of spores from the Welsh borderland very similar to those from South Mountain. They, too, were composed of a number of different spore species and varying proportions of cuticles, tubes and unrecognisable plant material. These coprolites, however, were considerably larger than those from South Mountain and measured between 530 and 3300µm long. The pellets form compact, regular masses and were even described with anal gland glue preserved as an amorphous slime. Edwards et al. (1995) finally concluded that the most likely producer of the coprolites were myriapods or large collembolans, stating that they were too small to have originated from earthworms and too large for most collembolans, mites and nematodes.

Sherwood-Pike and Gray (1985) also described coprolites from the mid-Silurian. These contained fungal material and were attributed to fungiverous arthropods. From the Devonian there are reports of coprolites from both Gaspé and the Windyfield chert. Pellets described from Gaspé include one large coprolite (3.0x1.5mm) and several smaller pellets preserved within plant stems (Banks and Colthart, 1993). These pellets are dominated by plant tissue (particularly collenchyma) and no mention of any spore element is made. From the Windyfield chert, the myriapod *Leverhulmia mariae* is described with preserved gut contents consisting of broken-up plant tissues and plant and fungal spores and occupying at least two-thirds of the depth of the body cavity. Subcylindrical amorphous objects preserved within the Windyfield chert were also interpreted as representing coprolites, but no size range was given (Anderson and Trewin, 2003).

It is unsurprising that coprolites are a common component of early terrestrial ecosystems, and they are a very useful indicator of plant–arthropod relationships. The

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main difficulty lies in their correct interpretation and ascription, and although their value for determining the origin of herbivory is contentious (see section 1.3.3), they do at least demonstrate the cycling of primary productivity early on in geological history. Those from South Mountain probably represent a combination of true coprolites and mechanically aggregated particles. The large proportion of complete spores in the coprolites suggests that they were largely indigestible to the consumer, and the most likely interpretation is that they were produced by a detritivore feeding indiscriminately on decaying litter. Of the fossil taxa recovered from South Mountain there are two likely producers, *Eoarthropleura* and the possible archaeognath hexapod. Specimens of *Eoarthropleura* from South Mountain probably measured in the region of two to three millimetres across the trunk and could conceivably have produced the size of pellet observed here. There is insufficient information on the size and morphology of the archaeognath, but as modern representatives feed on litter and detritus, it too could have produced the coprolites. The only way to prove the association between the coprolite and its producer is to find a specimen with an intact gut infill such as the myriapod from the Windyfield chert (Anderson and Trewin, 2003). However, given the fragmented nature of the cuticle from South Mountain, this seems unlikely and there is always the possibility that these pellets originated from an as yet unreported organism such as oligochaete worms.

9.7 *Summary*

By the very nature of fragmented cuticle assemblages, there will always be some cuticle that cannot be identified correctly given the available material. Historically, this is shown time and time again as specimens are redescribed and reinterpreted in the light of new material or new trends and concepts. The purpose of this chapter is to illustrate smaller groups of cuticle types and all unidentified fragments in the hope that they can be interpreted at a later date as more complete specimens from New York or elsewhere are described.

Most of the unidentified cuticle hints at a hexapod identification, but falls short of providing absolute proof of their presence. Collembola are known from the Rhynie chert in Aberdeenshire (Greenslade and Whalley, 1986) and another Rhynie specimen has recently been reinterpreted as a pterygote insect with chewing mouthparts (Engel and Grimaldi, 2004). Thus, it is more than likely that wingless hexapods were present at South Mountain during the Devonian.

The presence of coprolites permits some understanding of the plant–animal relationships at South Mountain, but do not support herbivory. Instead they indicate the presence of indiscriminate detritivores, and/or detritivores that targeted spore masses or coprolites in the litter. The break down of spores for nutritional gain appears to have been

inefficient or impossible in the producers. The coprolites represent the only direct evidence for the cycling of primary productivity at South Mountain and are an important addition to the overall picture of this early terrestrial ecosystem.

CHAPTER 10   VERTEBRATE FOSSILS

Vertebrate remains from South Mountain are concentrated in a bone bed, approximately 0.4m thick, exposed in a quarry on the northeast flank (see chapter 5 for stratigraphic details). The bones are concentrated in a turbulent mass of lithoclasts and plant debris, including large branches up to 0.5m long (figure 10.1). The vertebrate material consists largely of fragmented placoderm plates with a tuberculate texture (figure 10.2), and acanthodian scales (figure 5.10) with their characteristic bulging base of acellular bone and crown of layered dentine (Janvier, 1996). Due to the siliceous matrix the specimens are not easy to disaggregate and detailed analysis of the material is beyond the scope of this research. HF acid maceration of sediments from the bone bed did not produce any arthropod specimens and destroyed all vertebrate material.

On the other side of South Mountain, in SM-1 quarry, vertebrate fossils had remained absent until the recent discovery of a single tooth preserved amongst plant and arthropod material in an organic-rich lens of shale on the quarry floor (figure 10.3). The tooth is partially pyritised and vertical striations on the lower third of the tooth represent infolding of the tooth wall—a characteristic feature of labyrinthodont teeth. The upper two thirds of the specimen represents an internal mold of the tooth pulp cavity formed by infilling sediments. At its widest point the tooth measures 6mm across, and an x-ray of the specimen shows the lower portion of the tooth to penetrate only a few millimetres into the host rock, measuring 9mm from crown to base. This isolated specimen represents the first vertebrate discovered at SM-1 and is of particular interest for its labyrinthine structure, which is restricted to the teeth of crossopterygian fish and lower tetrapods. Placoderms had no true teeth as such, but possessed sharp edged plates in their upper and lower jaws, which could be used for puncturing, cutting, and crushing. Acanthodians were similarly devoid of teeth but possessed long gill-rakers to facilitate suspension feeding. Thus the labyrinthodont tooth from South Mountain represents at the very least a new family of fish from the area, and at the most a new record of tetrapod that would predate the previous earliest known example by approximately 10 million years (see section 10.3).

10.1 Labyrinthodont teeth

Labyrinthodont teeth occur amongst crossopterygian fish and basal tetrapods and are characterised by the infolding of the dentine and enamel of the pulp cavity wall into a labyrinthine pattern (Schultze, 1970). The uppermost part of the tooth has a round construction with a concentric layer of dentine, and towards the base of the tooth the folding of dentine becomes increasingly intense (figure 10.4). A thin layer of enamel covers the entire

Figure 10.1 Bone bed on northeast flank of South Mountain (SM-2), New York, USA.
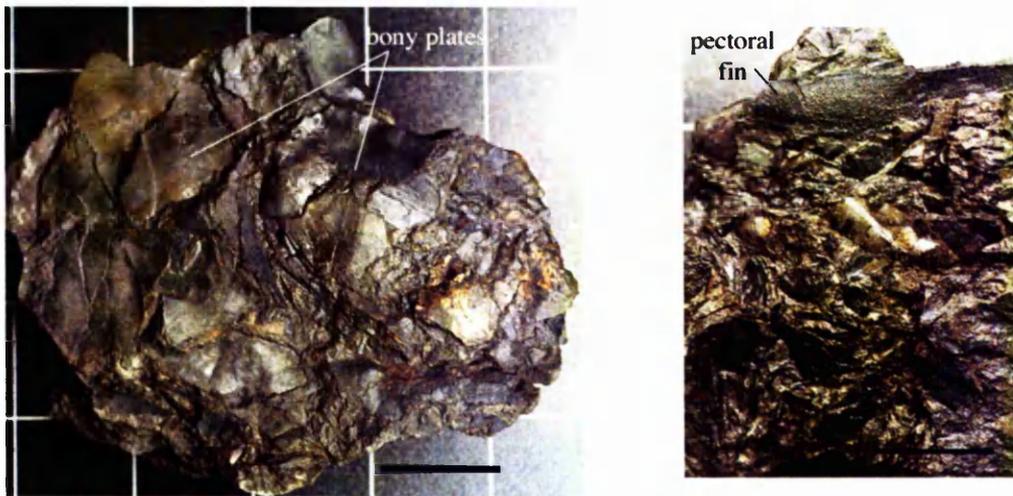
Figure 10.2 Fragmented placodern plates from the bone bed at South Mountain (SM-2), New York, USA. Scale bars represent 30mm.
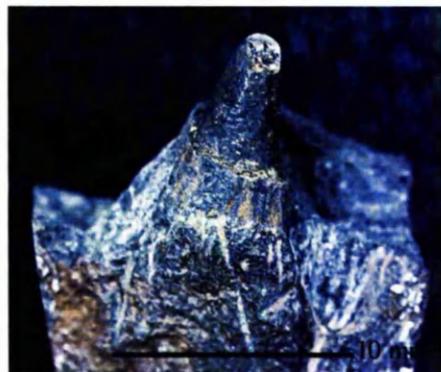
Figure 10.3 Labyrinthodont tooth from South Mountain, New York.

tooth. Preuschoft *et al.* (1991) investigated the function of labyrinthodont teeth in terms of mechanical strain and deduced that internal folds only serve to increase the mechanical strength of the tooth in the immature stages of growth as it erupts alongside already mature teeth. Beyond this, they reasoned that was no discernable benefit from the labyrinthodont structure.

The most comprehensive studies of the internal structures of labyrinthodont teeth are those conducted by Schultze and Brystrow (Bystrow, 1938, 1939; Schultze, 1969, 1970). Schultze (1970) divided the folded tooth patterns of Rhipidistia (sarcopteryians excluding coelacanths and lungfish) into three types—polyplocodont, eusthenodont and dendrodont (figure 10.4). These were differentiated by the shape and intensity of the folds, the presence or absence of osteodentine in the pulp cavity, and the mode of attachment to the jaw *i.e.* the
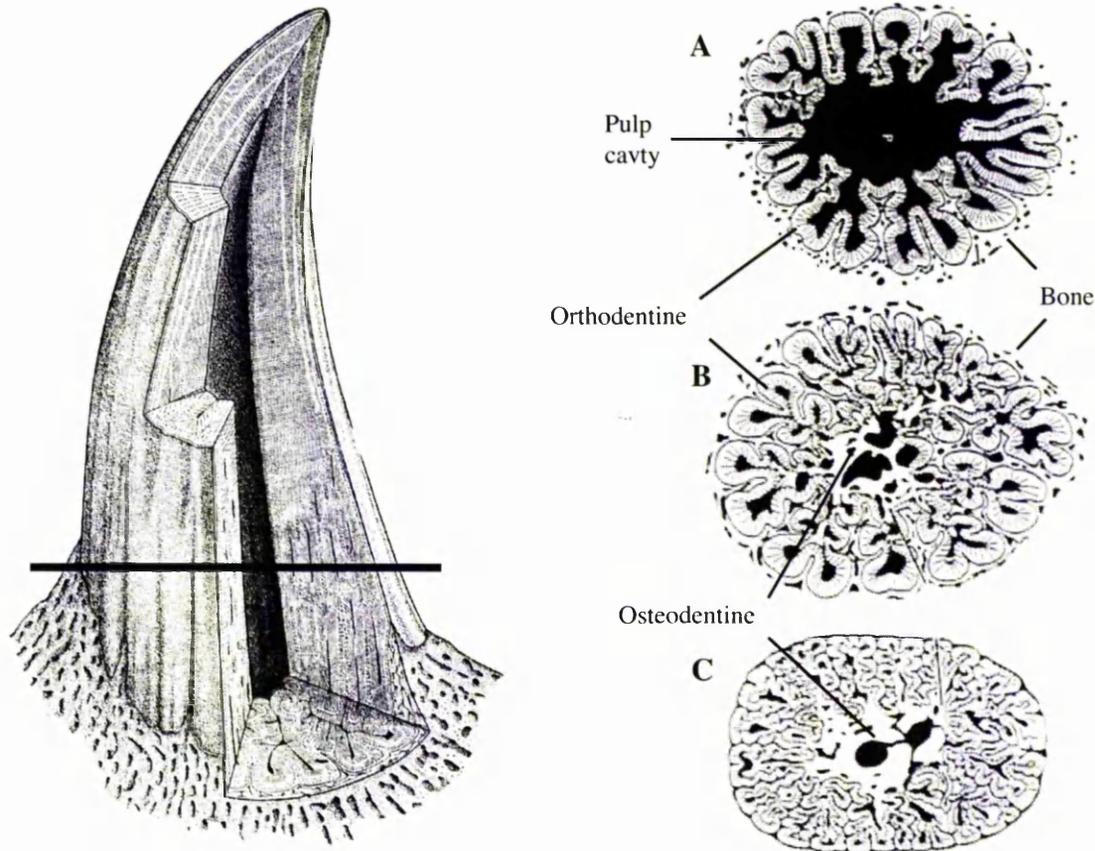
Figure 10.4 Parabasal section through types of labyrinthodont teeth. **A**, polyplocodont (*Eusthenopteron*). Open pulp cavity with bone extending between folds of dentine. **B**, eusthenodont (*Eusthenodon*). Pulp cavity filled with ostedentine, bone extending between folds. **C**, dendrodont (*Hamodus*). Pulp cavity filled with ostedentine, no bone extending beteween folds. Modified from Schultze (1970).

distribution of osseous tissue around the folds at the base of the tooth. The polyplocodont and eusthenodont teeth occur amongst osteolepiform fish. Amongst polyplocodont teeth, small differences in the tooth structure separate Osteolepiformes into two distinct groups. One group, represented by *Eusthenopteron* and *Strepsodus,* possessed polyplocodont teeth in which the folded dentine branched in an irregular pattern and the attachment bone extended to the ends of the folds and branches. In the second group, represented by *Panderichthys,* the dentine was folded into meandering branches and the bone of attachment extended only a short way between the folds. *Panderichthys* probably belongs within a clade representing the sister group to all other tetrapods (Ahlberg *et al.,* 2000), and the tooth pattern is very similar to that of *Ichthyostega* and other Labyrinthodontia (Schultze, 1970). The third type of labyrinthodont teeth (dendrodont) is restricted to Porolepiformes and all known members of this group have dendrodont teeth (Schultze, 1970).

These studies on labyrinthodont teeth traditionally relied on mechanical sectioning techniques that resulted in complete destruction of the original specimens. Since the tooth from South Mountain represents such a rare and interesting specimen, the non-invasive technique of computed tomography was selected to examine the internal structure of the tooth and thus ascertain whether the tooth had fish or tetrapod affinities (see section 2.3.4 for details of the technique).

10.2   South Mountain tooth

In order to facilitate comparison and identification, two labyrinthodont teeth were taken to a high-resolution computed tomography facility for imaging. A tooth preliminarily identified as a tristychopterid fish tooth (Deaschler, *pers. comm.)* from the late Devonian (late Fammenian), Red Hill site was used as a standard with which to compare the unknown labyrinthodont tooth from the Middle Devonian of New York State. A representative selection of digital slices from each tooth is illustrated in figures 10.5–10.9. The complete data set is saved onto a disc at the end of this thesis (appendix D).

In each section electron density is represented in shades of grey with the highest density material (pyrite) appearing white, and the lowest density material (air surrounding the specimen and in cavities) appearing black. High-resolution tomography has been largely unsuccessful in imaging Palaeozoic specimens (Cornell, *pers. commm.*). Older specimens tend to become homogenised through diagenetic alteration, which occludes density contrasts and thus produces a poor quality, low contrast image. It is therefore noteworthy that the imaging of the labyrinthodont teeth from South Mountain and Red Hill has been so successful. Clearly high-resolution tomography is a viable technique for these types of studies, and is a valuable alternative to the destructive methods of serial grinding and sectioning.

LABY001.TIF   LABY005.TIF   LABY010.TIF

LABY015.TIF   LABY020.TIF   LABY024.TIF

LABY025.TIF   LABY030.TIF

10mm.
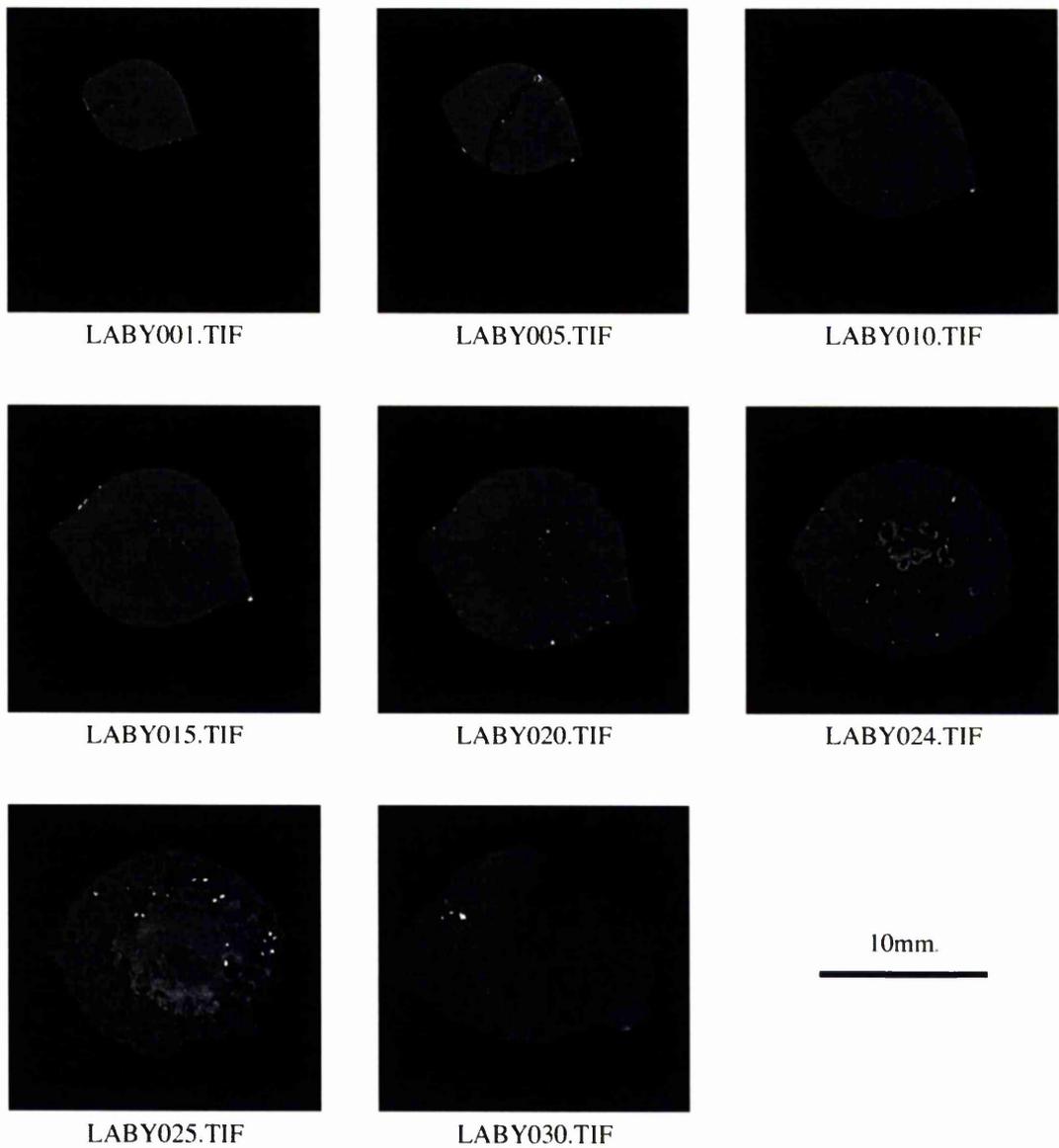
Figure 10.5 Digital images of horizontal slices through a Middle Devonian porolepiform fish tooth from Red Hill, Pennsylvania. Images obtained with a 150-Kv microfocal x-ray source at the high-resolution computed tomography unit, University of Texas, USA. Labels refer to slice number.
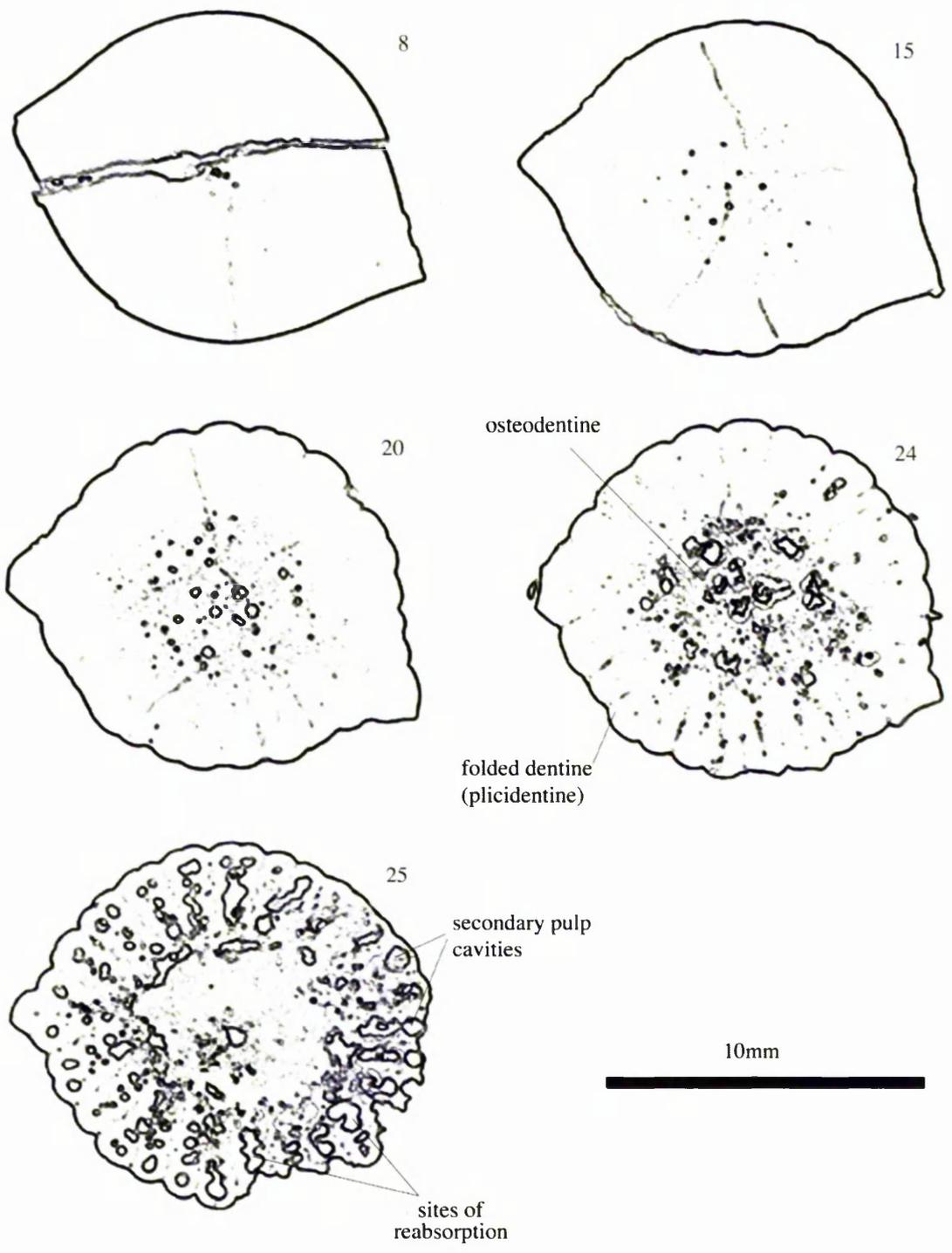
Figure 10.6 Digital line drawings of slices through a porolepiform fish tooth from Red Hill, Pennsylvania to accompany figure 10.5.

10.2.1   Red Hill tooth

The labyrinthodont tooth from Red Hill is the more complete specimen of the two and has produced the best quality images (figures 10.5 and 10.6). The tooth has an oval cross section, with a sharp lateral carina. The tooth wall is folded and branches in a fire-like pattern towards the centre of the tooth, which is filled with osteodentine, leaving a small pulp cavity. The dentine is relatively thick so that numerous secondary pulp cavities have formed, some of which are enlarged and probably represent sites of reabsorption (figure 10.6). There are no gaps extending between the folds for the attachment bone.

All of these features correspond with the dendrodont teeth described by Schultze (1969) and which are unique to porolepiform fish. One of the more common fish from Red Hill is the osteolepiform *Hyneria lindae* (Thomson, 1968), and two juvenile rhizodonts similar to *Sauripterus* have also been described (Davis *et al.*, 2001). However, teeth from both genera are polyplocodont. By comparing the Red Hill tooth to figured sections of other dendrodont teeth it appears most similar to a specimen of *Holoptychus* figured by Schultze, (1970; plate 30/23, figure 3). *Holoptychus* is known from other sites within the Catskill region, but without comparing the tooth to all known Devonian porolepiform teeth it is impossible to make a firm identification.

10.2.2   South Mountain tooth

Although the rather poor state of preservation precludes an accurate identification of the tooth from South Mountain, several important features can be observed in the available data. The most obvious feature of the tooth is its sculpted margin, which is seen most clearly where the tooth is still enclosed in shale, and also in hand specimen where it appears as vertical striations towards the base of the tooth (figures 10.3, 10.7 and 10.8). The marginal dentine is thick and is best preserved on the side still protected within the shale sample. The inside of the tooth has been filled with sediment, and this infill projects above the preserved dentine to form the crown of the tooth. In the Red Hill tooth, the osteodentine contains small cavities with bright rims where mineral replacement has occurred. Small, bright spots in the interior of the tooth from South Mountain give a mottled texture, which could shadow the structure of the original osteodentine. However, this hypothesis seems less likely when the tooth is seen in a traditional thin section and the infilling sediment is consistent with sediments surrounding the tooth (figure 10.10).

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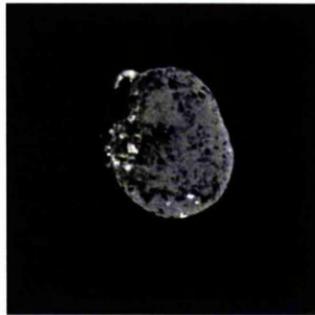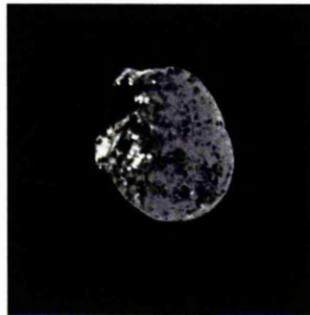
TOOTH020.tif   TOOTH025.tif   TOOTH030.tif
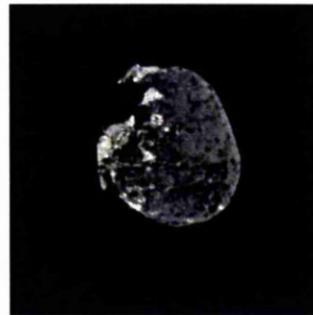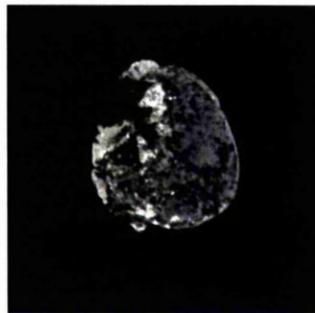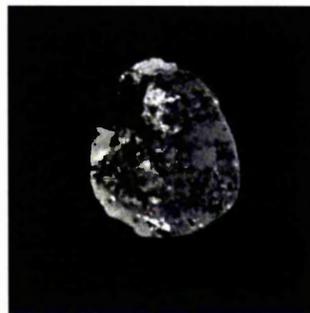
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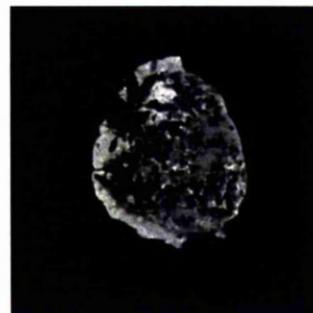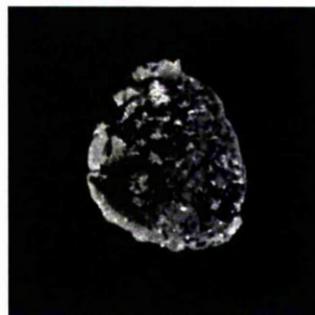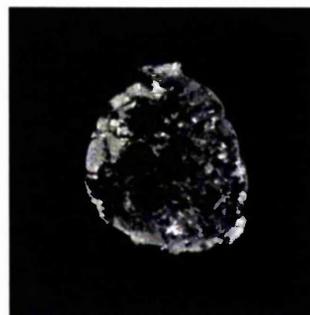
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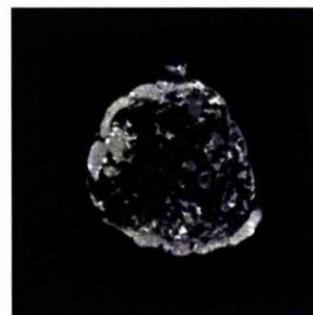
5mm

Figure 10.7 Digital images of horizontal slices through a labyrinthodont tooth from South Mountain, New York. Images obtained with a 150-Kv microfocal x-ray source at the high-resolution computed tomography unit, University of Texas, USA. Labels refer to slice number.
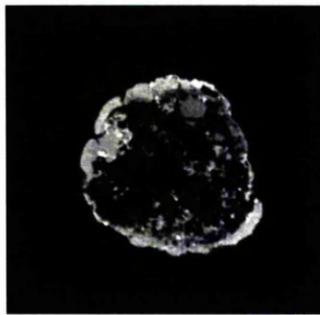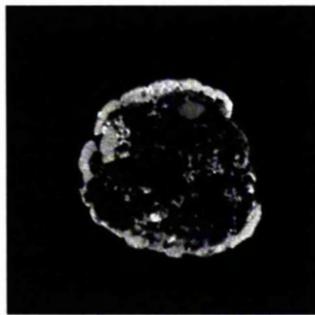
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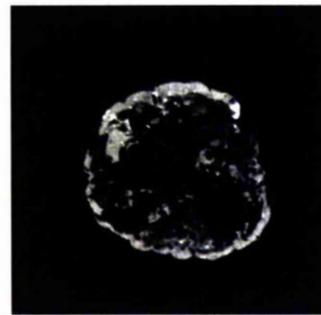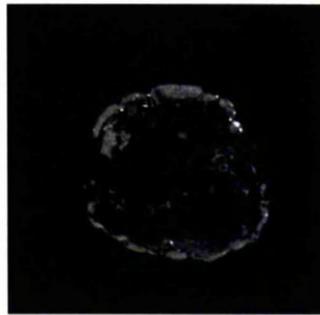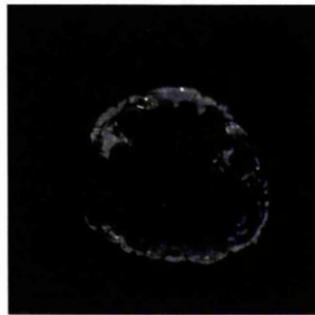
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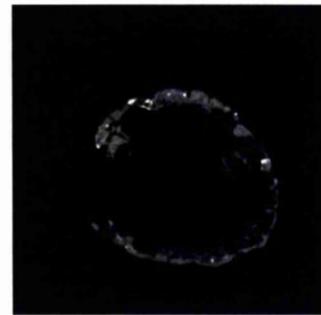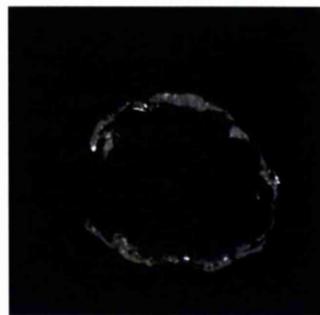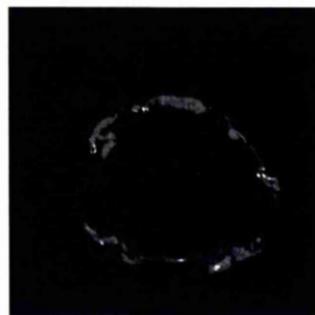
TOOTH095.tif   TOOTH100.tif   TOOTH105.tif

5mm

Figure 10.8 Digital images of horizontal slices through a labyrinthodont tooth from South Mountain, New York. Images obtained with a 150-Kv microfocal x-ray source at the high-resolution computed tomography unit, University of Texas, USA. Labels refer to slice number.
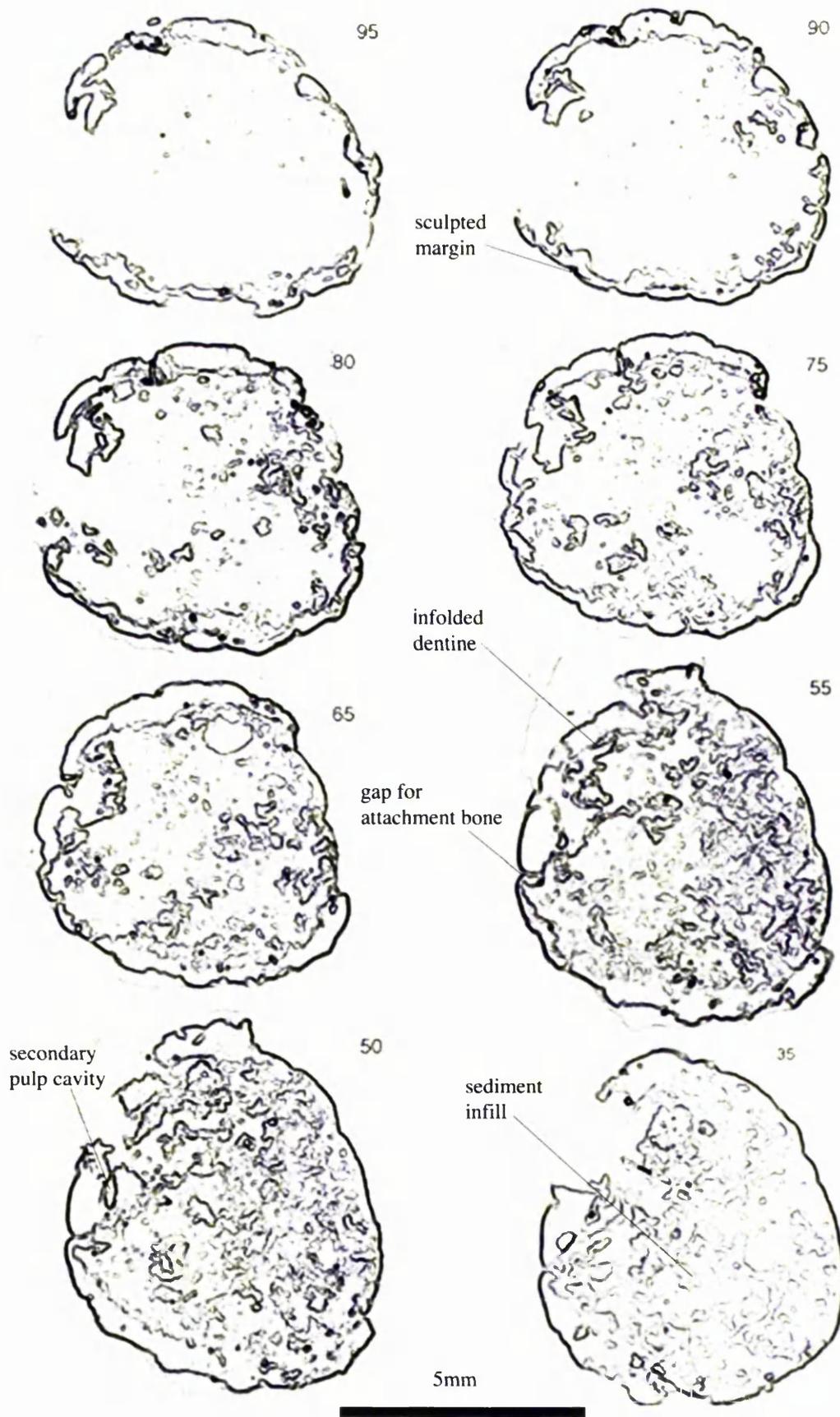
Figure 10.9 Digital line drawings of slices through a labyrinthodonot tooth from South Mountain, New York, USA, to accompany figure 10.7 and 10.8.
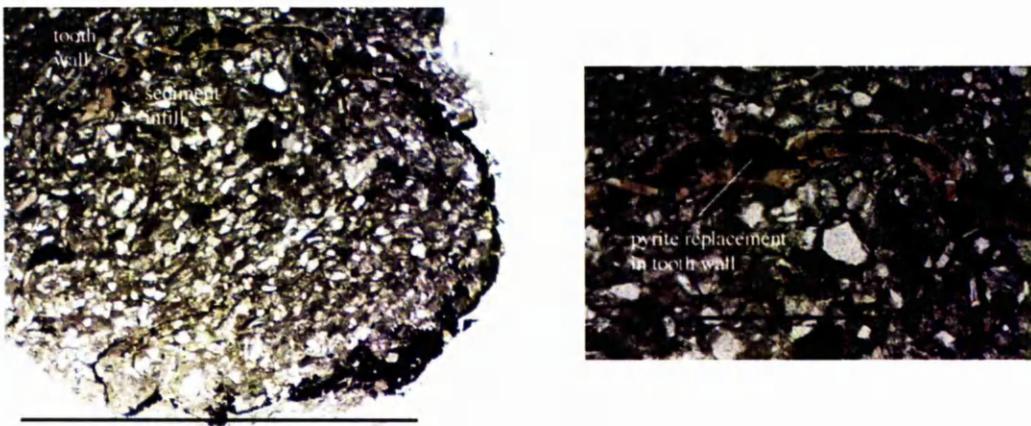
Figure 10.10 Thin section of the basal portion of the labyrinthodont tooth from South Mountain, New York, USA, viewed under plane polarised light. Sculpted margin partially replaced with pyrite. Scale bar on the left represents 4mm, scale bar on the right represents 1mm.
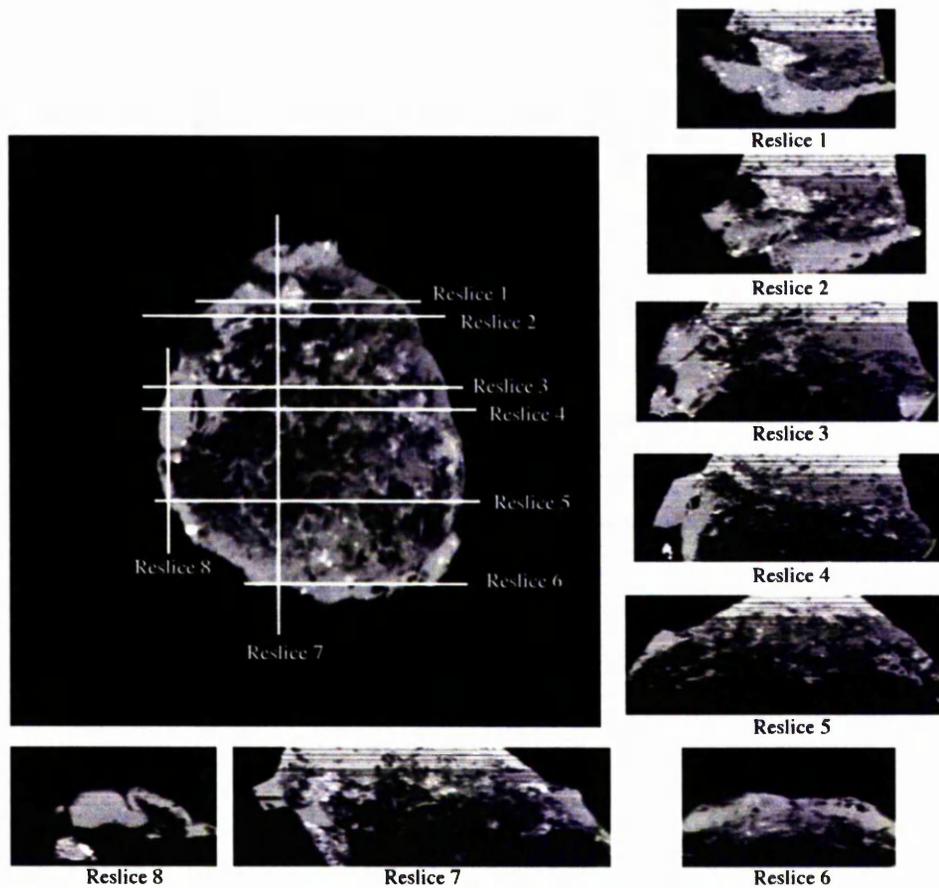
Figure 10.11 Vertical sections through a labyrinthodont tooth from South Mountain, New York. Data resliced using ImageJ freeware.

The dentine in the South Mountain tooth is clearly folded and a small gap on the left hand margin extending for a short distance between the folds of the tooth would have accommodated the bone of attachment (figure 10.9). The most obvious fold in the tooth wall occurs approximately half way through the stack of images where the dentine folds in towards the central pulp cavity of the tooth and doubles back on itself to form a secondary pulp cavity elongated parallel to the margin of the tooth. This same fold also appears in a vertical reslice of this area of the tooth (fig 10.11). A second fold appears towards the top of the digital image, lower down in the tooth (figure 10.7, slices 50 and 55) and also appears to fold parallel to the outer margin.

In a detailed structural study of the dentition of the Triassic temnospondyl *Benthosuchus*, Bystrow (1938) concluded that there were essentially two types of teeth in the jaw. Young teeth had thin walls and thin folds penetrating into a wide pulp cavity giving the appearance of a star-shaped cavity. In older teeth, however, the dentine was much thicker causing the folds to press together and dividing the pulp cavity into a series of secondary sections. In older teeth, Bystrow noted that reabsorption of the tooth began in the central pulp cavity, progressing in an uneven fashion to the secondary pulp cavities where it continued until the sites of reabsorption eventually merged together and the whole inner surface of the tooth was reabsorbed ultimately causing the tooth to come loose from the jaw and fall out. These observations could account for the state of the tooth from South Mountain suggesting that it was an old, aborted tooth with reabsorption having having occurred in the central pulp cavity and causing some of the secondary pulp cavities to merge.

Ichthyostega   *Eusthenopteron*
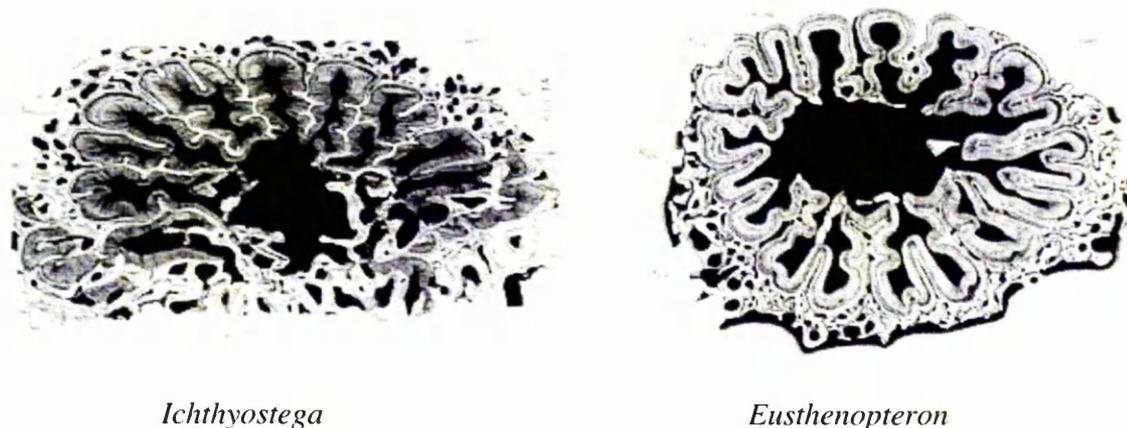
Figure 10.12 Parabasal sections of labyrinthodont teeth from *Ichthyostega* and *Eusthenopteron*. Modified from Schultze (1969).

The small pieces of marginal dentine suggest an open pulp cavity and there is the suggestion of space between the folds of the tooth into which bone would have penetrated to attach the tooth to the jaw. Both of these characters suggest a polyplocodont identification, Schultze (*pers. comm.*). Polyplocodont teeth occur in osteolepiform fish and some amphibians. Amongst the Labyrinthodontia (*i.e.* fossil amphibians) the folds simply meander and the branches of the folds are apparently lost (Schultze, 1970). In *Ichthyostega* and *Panderichthys* bone extends only a short distance between the folds of the tooth wall, whilst in *Eusthenopteron* and *Strepsodus* the bone extends to the ends of the folds and branches (figure 10.12).

10.3 Summary

The labyrinthodont tooth from Red Hill can be identified with some certainty as a porolepiform fish tooth, possibly of *Holoptychus*. Its structure, however, does not assist greatly in the identification of the labyrinthodont tooth from South Mountain. This tooth appears to have a polyplocodont structure, but does not fit convincingly into either of the categories described by Schultze (1970). The gap between the folds of the tooth does not appear to extend very far into the tooth, but at the same time the geometry of the folds suggest that they were fairly complex and did not simply meander towards the centre of the tooth as they do in *Panderichthys* and *Ichthyostega*. Whilst the tooth is certainly primitive, it is not clear whether it originated from a fish or a tetrapod.

If the tooth is from a fish jaw then it represents the first example of an osteolepiform fish from the study area and together with the placoderm and acanthodian fragments adds to the overall picture of the ecosystem at this time. Placoderm fish dominated most near shore and brackish water environments during the Devonian, which fits well with the overall picture at South Mountain of a near shore delta top type environment. It seems likely that terrestrial, or at least amphibious, tetrapods were part of the ecosystem structure and it cannot be ruled out that the tooth is from an amphibian and possibly terrestrial. Furthermore the tooth was uncovered amongst terrestrial debris that is hypothesised to have been eroded from a stream bank and transported downstream. If the tooth is from a tetrapod jaw then it would represent the oldest known example of a tetrapod body fossil in the world. Amongst the lower tetrapods eight are known from the Devonian (Clack, 1997), and currently the oldest known skeletal remains are those of *Obruchevichthys gracilis* from Latvia, and *Elginerpeton pancheni* from Scat Craig in Scotland (Ahlberg, 1991). Both specimens are from the Upper Frasnian. The only tetrapod known from North America is *Hynerpeton bassetti* from the Middle to Upper Famennian (late Devonian 365-363 Ma) of Pennsylvania (Deaschler *et al.*, 1994). The oldest tetrapod trackways, however, are from Genoa River in Australia (Warren and Wakefield, 1972) and have been variously dated as Frasnian and Famennian. Although these represent

the earliest evidence of tetrapods there is no direct evidence for a terrestrial nature and it is possible, if not probable that many Devonian tetrapods were aquatic (Clack, 1997).

Unfortunately the only published images of cross sections of tetrapod teeth for comparison are those of *Ichthyostega* (Schultze, 1969). It would be interesting to borrow and scan tetrapod teeth from known taxa for comparison, especially since so little of the basal tetrapod structure is understood. The use of tomography makes this a viable possibility since it represents a non-destructive alternative to serial grinding or sectioning, and should encourage the loan of specimens for analysis. Either way, the discovery of a labyrinthodont tooth at South Mountain, in association with terrestrial plant and arthropod material, is remarkable and should promote further fieldwork in the region to uncover more of these exciting early vertebrate remains.

Palaeoecological analyses of fossil communities requires consideration of sedimentological and taphonomic details as well as of the fossils themselves. The sedimentology and taphonomy of dispersed cuticle assemblages from New York have already been addressed in chapters 4 and 5. This chapter discusses hypotheses that may be inferred from a population of disarticulated skeletal components using both qualitative and quantitative analyses, and therefore what conclusions can be drawn from the assemblages regarding the palaeocology.

11.1 Palaeoecological analysis

11.1.1   Sedimentological and taphonomic analyses

The environment of deposition has been established for both High Knob and South Mountain as a fluvial floodplain environment, close to the palaeoshoreline. Fossils are concentrated in organic-rich lenses of grey mudstones where they reside amongst concentrations of plant material. It is hypothesized that both plant and animal material were eroded from the riverbank and deposited downstream in abandoned channels or pools on the floodplain. The assemblages represent a sample of litter that formed on land, and contain fossils that have been exposed to degradation, scavenging and dispersal prior to transport and deposition (see chapter 4).

Although these lenses of fossil material are clearly allochthonous deposits, it is assumed that there was a relationship between the fossil elements. Many of the faunal components have modern equivalents that live amongst the litter (*e.g.* millipedes, bristletails) and it is assumed that these early animal pioneers required the protection of a dark, moist habitat to help limit desiccation. It is therefore likely that the fossil animals were living amongst the fossil plants that are preserved with them, and in some cases the plants may have afforded some protection to the exoskeletal elements during transport.

All of the preserved arthropod fossils are very small and typically measure less than 1mm at their widest point. The same is true of the fauna from Gilboa, which Shear *et al.* (1984) speculated were filtered from the water by mats of plant material. In view of the relatively small size and fragmentation of plant material, it seems unlikely that the same process acted at South Mountain. Alternative explanations for the consistently small size of the arthropod cuticles are hydraulic sorting, a skew in the population in favour of juveniles, or an original population of very small arthropods. The latter explanation is probably the least likely since impression fossils of *Eoarthropleura* found at South Mountain were larger

than the equivalent compression fossils, and specimens from other localities are known to be much larger. A skew towards juveniles in a population also seems unlikely. There is no viable mechanism that would permit the selection of juvenile specimens over adults prior to transport, and it would be expected that, even if the population was numerically dominated by juveniles, at least one larger adult would have been preserved amongst them. Hydraulic sorting is therefore the most likely explanation. If this is the case then it should follow that mudstones containing larger, more complete, plant fossils would also preserve larger, more complete arthropod fossils. At South Mountain the plant material associated with the arthropod remains is fragmented and more or less unidentifiable in hand specimen and the arthropod fossils are also small. At High Knob, however, much larger and more complete plant material is associated with the arthropod fossils, which are of a similar size to those at South Mountain. Although this would appear to rule out hydraulic sorting as a mechanism favouring small arthropod pieces, the haphazard arrangement of stems in the fossiliferous sediments at High Knob suggests that they were deposited suddenly, therefore limiting the potential for the sorting of suspended materials.

Hydraulic sorting of sediments and fossils should also result in larger, heavier arthropod fragments being deposited closer to their source in coarser sediments. This would explain the total absence of large specimens since the coarser grains of the host sediment would effectively destroy any large pieces of cuticle by causing them to fragment into numerous tiny pieces. This is supported by the presence of large (100–200mm long) arthropods in sediments from New Brunswick in Canada (Shear *et al.*, 1996), which preserve both impression and compression fossils. A hydraulic study using flow tanks to observe the transport dynamics of moulted cuticle, carcasses and fragmented specimens of arthropods would make an interesting study and should go some way to resolving this issue.

One final taphonomic process that could skew the fossil populations of arthropod cuticles is the composition of the arthropod cuticle itself. Scorpions are known to have a tough, hyaline exocuticle and may therefore be expected to have a better fossil record than some other arthropods. Indeed, upon initial examination of the sediments at South Mountain this was thought to be the case since macerates appeared to be dominated by scorpion cuticle. However, in terms of both absolute numbers and percentages, arthropleurid cuticle outnumbers scorpion cuticle at South Mountain (figure 11.1). Furthermore, Brauckmann (2003) argued that the arthropleurids possessed a very weakly sclerotised cuticle supported by hydrostatic pressure. If this was the case, (although it seems unlikely at least in the case of *Eoarthropleura*) then it would seem that the degree of sclerotisation has a negligible effect on preservation. In other sedimentary settings scorpion cuticle may have an advantage, but at South Mountain and High Knob (where significantly more trigonotarbid than scorpion cuticle is preserved) the preservation of cuticles in fine-grained mudstones does not appear

to be biased towards those arthropods with a more sclerotised exoskeleton.

11.1.2   *Temporal and spatial resolution*

Sedimentation on the Catskill delta was probably fairly continuous, but not sufficiently rapid to dilute organic matter to the point where pyrite formation was inhibited. Although the deposition of the arthropod material may have been fairly instantaneous, the fossils themselves may have been residing in the litter for some time. Accordingly, it is difficult to definitively determine the temporal resolution of these deposits. In chapter 4 the nature of the arthropod cuticle was discussed and it was concluded that the majority of arthropod cuticle would not last very long in the litter layer (due to predation, scavenging *etc.*) and that the fossil accumulations represent episodic burial rather than long-term condensations. Plant remains generally degrade fairly rapidly unless covered with sediment, and undegraded fossil plant parts may represent periods of accumulation of one year or even less prior to burial (Wing, 1988, cited in Behrensmeyer *et al.*, 1992). In geological time, therefore, these lenses of fossil arthropod cuticle probably represent the more or less instantaneous deposition of plants and arthropods that were living at that time.

The spatial relationship of these fossils is harder to ascertain since they have all been transported. As discussed in chapter 5, the vegetation is likely to have been restricted to riverbanks and the immediate vicinity, and given their close associations the arthropods probably were too. It seems unlikely that they were swept into rivers from regions extending very far from the river, but they could potentially have originated from almost any distance upstream. The presence of articulated material suggests that time spent in transport was fairly limited and it could be expected that the fossils were of local rather than regional origin.

11.2   *Quantitative analysis*

In order to quantitatively analyse the cuticle assemblages from South Mountain and High Knob, all cuticle pieces were recorded in a spreadsheet and were identified as far as was possible, or at least assigned to a cuticle type. A breakdown of cuticle types recovered from South Mountain and High Knob is graphically illustrated in figure 11.1. This includes all recovered fragments in varying states of completeness and does not indicate population size, only relative proportions of cuticle types.

The palaeocommunities clearly differ in their faunal compositions, with trigonotarbids dominating the population at High Knob and arthropleurids and scorpions dominating at South Mountain. Prehaps more significant is the absence of particular taxa from one site or another. For example, *Eoarthropleura* is conspicuously absent from High Knob, and the type of trigonotarbid seen at High Knob is absent from South Mountain. Both of these are numerically dominant at their respective sites, and their absence from another

assemblage is therefore notable. Less commonly occurring taxa represented by fewer cuticle fragments may appear to be absent from an assemblage, but this does not necessarily reflect their absence from the original population.

A

B
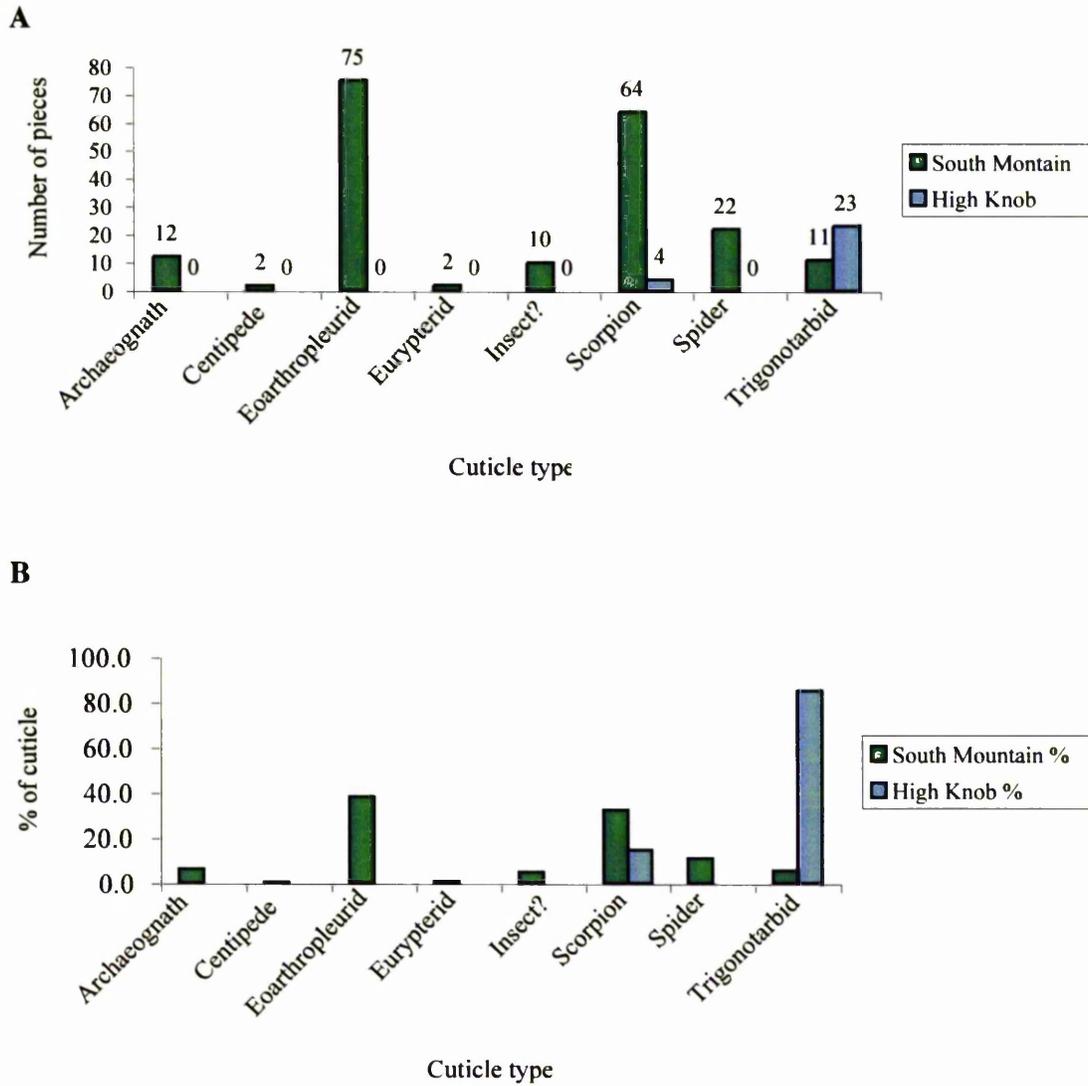
Figure 11.1 Histograms of cuticle types recovered from High Knob and South Mountain, Schoharie County, New York. **A**, Absolute numbers of cuticle fragments. **B**, relative proportions of cuticle types by percentage. All cuticles identified to order level.

Any quantitative analysis on a collection of disarticulated skeletal elements requires certain assumptions. With whole organisms a body count is relatively unproblematic, but with partial organisms that have disarticulated into numerous separate components, the number of variables for analysis are considerably greater. The best method for conducting a quantitative survey of disarticulated fossils is to only count elements of which there are known to be one per organism. Although this would not necessarily account for all members of a population it would at least give a reliable minimum population count. This is acceptable for organisms that only produce one skeleton during their lifetime, but causes problems when dealing with those that produce a number of skeletons during their lives, all of which may become potential fossils *e.g.* arthropods.

By their very nature, arthropods are multi-segmented, multi-legged animals and each individual can potentially disarticulate into tens or hundreds of separate elements. In an assemblage of mixed body parts, the challenge is to work out whether each element has originated from a separate individual, if they all originated from the same individual, or if there is a mix of both. Ignoring moults for the moment and assuming that each element represents a single individual, a total count of body parts would give a maximum population number. For example, at South Mountain there have been a maximum of 75 specimens of *Eoarthropleura* and 64 scorpions recovered (figure 11.1). This is undoubtedly a vast overestimate of population numbers since that number includes numerous cuticle fragments that could not be assigned to a specific body part. For a group such as the scorpions, however, it is also possible to ascertain a minimum population count. Scorpions possess a single pair of pectines, and a count of these gives a minimum population count of four. Therefore somewhere between 4 and 65 scorpions have been recovered from South Mountain. This process can be repeated using different body parts of a known number and dividing them by the total number of elements recovered. For example, each scorpion has two free fingers and six were recovered from South Mountain. Assuming that they are all the same species they may represent a maximum of six individuals or a minimum of three. This process can be repeated for all body parts, so that maximum and minimum population numbers can be calculated. Body parts occurring in lowest numbers will provide the most reliable estimates of population size and reliability will decrease with estimates obtained with body parts of which there are many *e.g.* podomeres. Obviously, if the division results in a fraction it must be rounded up to the nearest whole number. The data for several taxa from High Knob and South Mountain are plotted in figures 11.2 and 11.3 which provides maximum and minimum population estimates for all recovered taxa. Minimum population estimates correspond roughly with total counts of cuticle pieces, but indicate that there are potentially more individuals of scorpions than there are of *Eoarthropleura*. Despite the relatively large
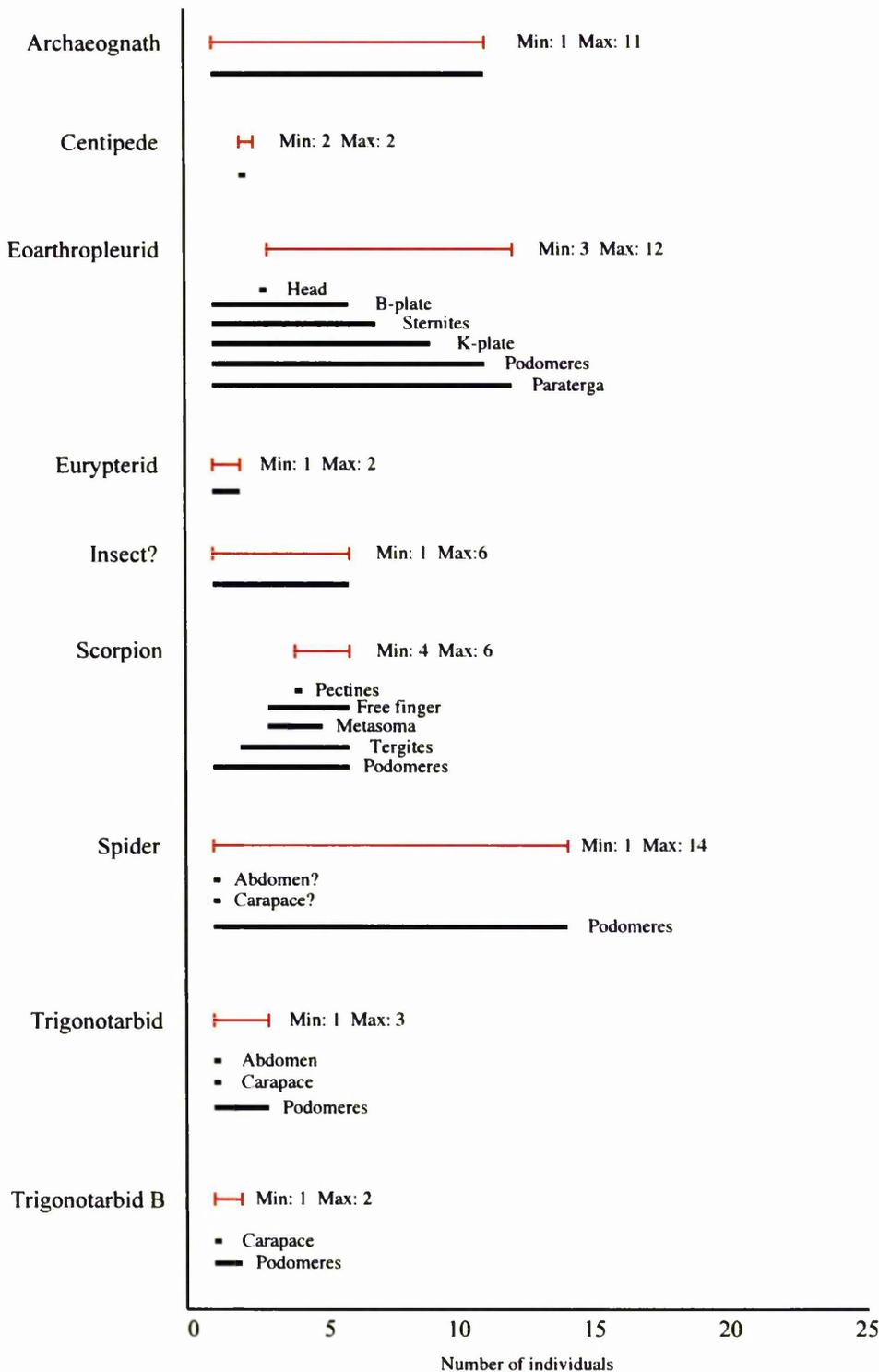
Figure 11.2 Population estimates for dispersed fossil taxa from South Mountain, New York. Estimates based upon numbers of exoskeletal elements and the maximum and minimum number of individuals that they can represent. Exoskeletal elements of which there are only one per individual (*e.g.* heads, pectines) provide the most reliable data, whereas elements that are repeated in the exoskeleton (*e.g.* podomeres and sclerites of *Eoarthropleura*) provide the least reliable estimates.
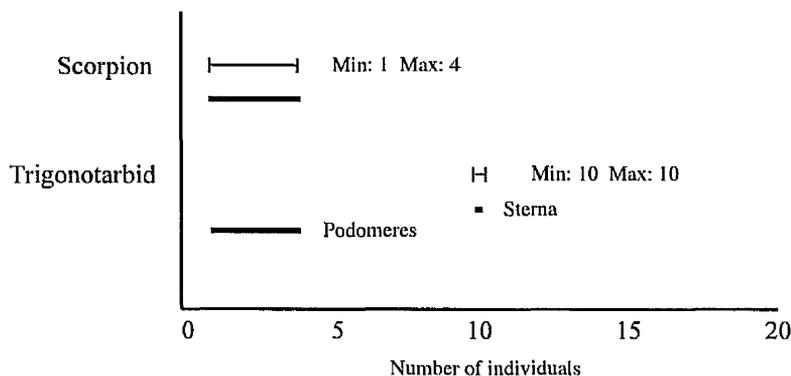
Figure 11.3 Population estimates for dispersed fossil taxa from High Knob, New York. Estimates based upon numbers of exoskeletal elements and the maximum and minimum number of individuals that they can represent. Exoskeletal elements of which there are only one per individual (*e.g.* sterna) provide the most reliable data, whereas elements that are repeated in the exoskeleton (*e.g.* podomeres) provide the least reliable estimates. Scorpion numbers are represented by incomplete cuticle fragments only.

number of cuticle fragments recovered, in this analysis most taxa are represented by less than five individuals, and some by only one.

Although this method provides maximum and minimum limits of individual numbers in the fossil population, there is still considerable spread between the two and it excludes the potential for individuals to be represented by moults as well as carcasses. Size analysis of the skeletal elements could refine the count of individuals, but would probably be most beneficial when applied to a larger data set with more complete specimens. This technique is also more suited to some taxa than others. Analysing populations of arachnids is relatively straightforward since, aside from podomeres, most body parts occur in relatively low numbers. In the case of serially homologous animals such as *Eoarthropleura* the body parts from any one individual are so numerous that in smaller data sets all elements could potentially originate from one individual. The only recovered exoskeletal element of *Eoarthropleura* of which only one occurs per individual, is part of the head region. Only three of these were recovered from South Mountain, although the abundance of other recovered sclerites gives the impression that they were much more prolific.
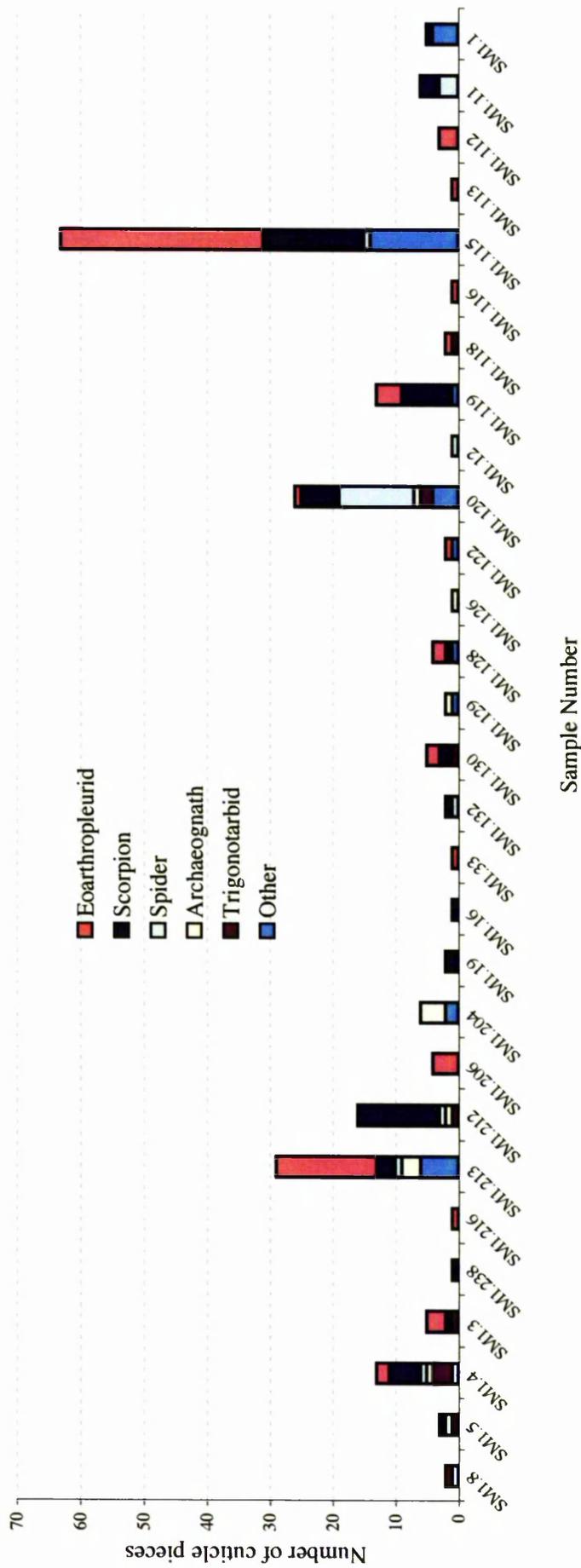
Figure 11.4 Graph showing relative proportions of cuticle types recovered from specific samples from South Mountain, New York. Specimens of the same species from the same sample are more likely to have orginally belonged together than those from separate samples.

A further assessment of population numbers can be made by sample number. The likelihood of similar body parts all belonging to one organism is much higher if the fragments all come from the same raw sample *i.e.* they may have been preserved in association or even connection with each other but defragmented during the maceration process. If the fragments belong to different raw samples, the likelihood of them once belonging together is more remote. Proportions of cuticle type recovered form separate sediment samples from South Mountain are shown in figure 11.4. It can be seen that the majority of *Eoarthropleura* cuticle originated from specimen SM1.115, but was also present in most other samples. The majority of spider cuticle, on the other hand, was limited to only three or four sediment samples, which may suggest an actual population number towards the lower end of the estimated 1–14 individuals.

11.3 Palaeoecology

11.3.1 Habitat

Cuticle assemblages from South Mountain and High Knob are associated with terrestrial elements, but direct evidence for air-breathing amongst the fossil fauna, such as the presence of trichobothria or book-lungs, is lacking. However, most of the taxa have known terrestrial representatives and it is considered that the elements of ecosystems preserved at South Mountain and High Knob are largely terrestrial.

Anatomical features and preservational context, suggests that eoarthropleurids were probably also terrestrial although no respiratory organs have yet been described. Kraus and Braukmann (2003) argued that this suggests that arthropleurids were semi-aquatic, although morphological information from *Microdecemplex* suggests the inclusion of arthropleurids within the Diplopoda, which are now known to have been truly terrestrial by at least Wenlock times (Wilson and Anderson, 2004). The earliest evidence for air-breathing in scorpions comes from a scorpion preserved amongst volcanically derived fluvial sediments of the Emsian Campbellton formation, New Brunswick, Canada. Lamellate structures associated with sternites and abdominal plates clearly represent book-lungs, thus supporting the hypothesis that all of the mesoscorpions, including the largest, were part of the terrestrial fauna (Shear *et al.*, 1996). Trigonotarbids from the Lower Devonian Rhynie chert have similarly been documented with preserved book-lungs and are assumed to be entirely terrestrial (Claridge and Lyon, 1961). Recent spiders and amblypygids are also largely terrestrial and, given their terrestrial associations, the fossil forms are also considered to have been so.

All of the arthropod fauna would probably have lived amongst decaying litter or on the ground surface. By neontological comparison most were either nocturnal or cryptic, both of which are useful strategies for avoiding heat stress, desiccation and UV-light. The

ecological categories of the arthropod fauna from South Mountain and High Knob are given in table 10.

11.3.2   Paleocommunities

South Mountain, High Knob and Gilboa are all isotaphonomic assemblages and exist in spatial and temporal proximity to one another. It is therefore reasonable to directly compare the fossil assemblages since any preservational biases should affect all assemblages equally. All three assemblages appear to be dominated by predatory arachnids, but all are associated with a slightly different flora. At Gilboa, the dominant floral element is the lycopsid *Leclercqia* amongst which the arthropod material is found preserved. Although the *Leclercqia* stems from Gilboa were considered to have been preserved *in situ* (Banks *et al.*, 1985), it is not clear whether the animals were living amongst them or were washed into the stems by a stream. At South Mountain, the dominant floral elements are liverworts, progymnosperms and zosterophylls, and at High Knob large stems attributed to *Archaeopteris* and zosterophylls dominate the flora. The fossil arthropods from Gilboa are dominated by a high diversity of trigonotarbids (six species in three genera), a single species of spider, centipedes, arthropleurids, mites, pseudoscorpions and scorpions. A similar fauna is seen at South Mountain but here there are far fewer trigonotarbids and there is a much higher proportion of scorpion cuticle. At High Knob, there is apparently much lower overall diversity, with a single species of arachnid (trigonotarbid) dominating the fauna and only rare scraps of scorpion cuticle.

High Knob, South Mountain and Gilboa are all part of the Catskill delta, which is composed of interdigitating marine and terrestrial sediments. Local variations in marine influence and floral composition may have affected the local fauna and this is reflected in the differing faunal compositions of the three assemblages.

11.4 Summary

Palaeocological analysis of the cuticle assemblages from South Mountain and High Knob requires consideration of the taphonomy, sedimentology and palaeontology. Both assemblages are allochthonous, cuticles originated locally rather than regionally and were rapidly transported and buried. The small size of the cuticle fragments probably results from sediment sorting rather than a filtering mechanism such as that proposed for the assemblage from Gilboa.

Qualitative analyses of these dispersed cuticle assemblages can calculate realistic estimates of maximum and minimum population numbers for different taxa. The accuracy of these estimates is dependent upon the taxa in question and is influenced by which elements of the exoskeleton are preserved. It does not take into account the potential for individuals

Table 10. Ecological categories for fossil fauna from South Mountain and High Knob. Inferences made from extant relatives in most cases.

	Trigonotarbida	Scorpiones	Araneae	Arthropleuridea	Archaeognatha	Chilopoda	Amblypygid
Food preference	Predator	Predator	Predator	Detritivore	Detritivore	Predator	Predator
Food processing	Preoral	Preoral	Preoral	Gut	Gut	Gut	Preoral
Locomotion	Terrestrial	Terrestrial/aquatic	Terrestrial Ambush predator?	Terrestrial?	Terrestrial?	Terrestrial	Terrestrial
Feeding habitat	Terrestrial Ground surface	Terrestrial Ground surface	Terrestrial Ground surface	Terrestrial Litter layer	Terrestrial Litter layer	Terrestrial Litter layer/ Ground surface	Terrestrial Ground surface
Shelter habitat	Terrestrial Litter layer?	Terrestrial Subterranean	Terrestrial Subterranean	Terrestrial/ ?semi-aquatic Litter layer	Terrestrial Litter layer	Terrestrial Litter layer	Terrestrial
Activity period	Unknown	Nocturnal/ crepuscular	Nocturnal/ crepuscular	Cryptic	Cryptic	Nocturnal	Nocturnal

to be represented several times by moults; but since all of the recovered cuticles are consistently small, and moults should represent incremental growth stages, it seems unlikely that individuals are represented more than once.

The results of the analysis suggest that most taxa are represented by small numbers of individuals, and that the greatest number of individuals (but lowest diversity) is observed at High Knob. The greatest diversity occurs amongst predators, a pattern that was also observed in the assemblage at Gilboa. A comparison of the three isotaphonomic assemblages suggests that local variations in the palaeoenvironment did impact community composition.

The principal aims of this research were to determine the palaeoenvironment and fossil fauna of South Mountain, to identify and analyse potential new fossiliferous sites, and to draw comparisons between contemporaneous, isotaphonomic sites to determine the extent to which the palaeoenvironment influenced palaeocommunities. These aims were met through the collection of sedimentary details, exploration of new quarries for potential fossils, the collection and maceration of fossiliferous material, and the identification and analysis of cuticle types recovered from the macerated sediments. The results of these objectives have been detailed in the previous chapters and the purpose of this chapter is to discuss their relevance to palaeontology, to assess the quality of the data, and to consider the future course that this type of research should take.

Compression cuticle assemblages from South Mountain and High Knob represent two more examples of early terrestrial fossil assemblages from the Devonian. South Mountain alone is important for its preservation of the only known examples of the arthropleurid *Microdecemplex*, well-preserved scorpion cuticle, and is only the second known locality for the spider *Attercopus*. High Knob preserves a new species of arachnid, possibly a trigonotarbid, which is associated with large, well-preserved plant fossils worthy of further investigation. Both fossil faunas lack any direct evidence for a terrestrial mode of life, such as the possession of book-lungs, trachieds or trichobothria, but their terrestrial nature is inferred from contemporaneous fossils and modern representatives of the orders (see section 11.3.1). Both sites can be classed within the same category as cuticle assemblages from Ludford Lane, Alken-an-der-Mosel and Gilboa. They are also comparable with arthropod assemblages from the Rhynie and Windyfield cherts in terms of faunal composition but not in terms of taphonomy. Strictly quantitative data are unavailable for these sites, however published information can be used to compare faunal compositions and palaeoenvironments. This information is summarised in table 11.

Cuticle compression assemblages of early terrestrial faunas are found preserved in freshwater and brackish, deltaic, fluvial, lagoonal, lacustrine, and salt marsh environments. It is suggested that differences in the local palaeoenvironment of cuticle assemblages from New York may have influenced the dominant fauna, but is the same true for other assemblages? Although there may be limitations in the use of presence-absence data (see data quality below) it is reasonable to compare the dominant faunas of well-studied assemblages, as these will be the most thoroughly sampled and therefore least prone to error. The most conspicuous absence of a taxon occurs at Rhynie, where despite over 75 years of research, evidence of scorpions has yet to be uncovered. Scorpions are represented in nearly every other cuticle assemblage from the Siluro-Devonian and terrestrial forms are known from the Lower Devonian onwards. The Rhynie chert represents an ancient thermal spring and is the only assemblage in which terrestrial arthropods are preserved *in situ*. Thus it could

be argued that either scorpions lived away from the aquatic margins, and are therefore only included in allochthonous assemblages, or that the unusual environmental conditions at Rhynie were not attractive to the early scorpions, which possibly preferred more brackish, nearshore environments.

Trigonotarbids are similarly present in nearly every assemblage except for those in Québec and New Brunswick. Québec only preserves a few specimens of *Eoarthropleura* and it is likely that there are elements missing from the ecosystem. However, at New Brunswick both arthropleurids and scorpions have been preserved and the absence of trigonotarbids may have resulted from unfavourable environmental conditions (freshwater fluvial) or an absence of suitable prey. Given the unpredictable nature of recovering early terrestrial arthropod fossils any speculation on a relationship between faunal composition and the palaeoenvironment, particularly in a small data set, should be treated with caution.

12.1 Ecosystem structure

An apparently concurrent theme amongst early terrestrial arthropod assemblages is the dominance of predators. Both assemblages from South Mountain and High Knob are dominated by a greater diversity of predatory arachnids than of detritivores and herbivores. At South Mountain the detritivores are represented principally by Arthropleurida and ?Archaeognatha. Numerically, the number of *Eoarthropleura* cuticle pieces recovered greatly exceeds those for scorpions, trigonotarbids, centipedes, and spiders separately. However, in terms of total numbers of predator cuticles, these easily outnumber the detritivores. A high diversity of predators appears to characterise many of the early terrestrial arthropod faunas, as does an apparent absence of herbivores. Although this seems to be a pervasive pattern amongst early terrestrial arthropod assemblages, it is not clear whether this truly represents the original community structure or is a taphonomic bias in the population.

With increasing study and new discoveries the trend towards predator-dominated communities appears to be reversing. For example, in the Rhynie and Windyfield cherts, predators are represented by only two recognised orders (trigonotarbids and centipedes), whereas detritivores are represented by four (mites, collembolans, insects(?) and myriapods). This *in situ* fauna gives a better representation of true population composition than do some other allochthonous deposits, and although the predatory trigonotarbids may dominate numerically, the diversity of recovered detritivores/herbivores has increased two-fold since 2003. As discussed in chapter 1 there are a variety of explanations for the apparent absence of detritivores and herbivores. Predatory arthropods such as spiders and scorpions tend to live on the ground surface rather than deep within the litter layer and may therefore have been more susceptible to transport and deposition by streams. Soft-bodied soil fauna such as nematodes, tardigrades, and annelids may also have been present within these early terrestrial ecosystems but are unlikely to be preserved as fossils.

In assessing the structure of these early terrestrial ecosystems, floral and faunal elements have traditionally been observed in strictly terrestrial or aquatic terms. Modern-

day examples, however, demonstrate that separation of the two ecosystems is not as clear-cut as this, and that, particularly in early successions, allochthonous input from outside of the ecosystems plays an important role. The apparent absence of primary consumers in the terrestrial ecosystem could therefore be explained by their presence in an aquatic food web. The extension of the aquatic food web into the terrestrial realm would have provided a source of both primary productivity and potential prey in the form of scavengers and algivores that would not be preserved amongst the terrestrial detritus of assemblages such as those from South Mountain and High Knob, but are preserved in the autochthonous Rhynie chert.

An interesting analogue to these early terrestrial ecosystems is the newly formed Midriff islands in the Gulf of California. The arid Midriff islands have low primary terrestrial productivity (typically less than 10% plant cover) yet support high numbers of spiders, scorpions, and centipedes. Spider densities were observed to be negatively correlated with island size, and the primary source of prey for these consumers was allochthonous marine input. Polis and Hurd (1995) determined that energy flowed from the marine environment to the terrestrial environment via marine detritus and large colonies of marine birds. In the supralittoral zone, detritivores and algivorous insects made up >99% of the diet of the terrestrial consumers (spiders, scorpions, and lizards), thus demonstrating that marine and terrestrial ecosystems are operationally connected on small islands. Similar high densities of spiders were observed on newly exposed substrates behind retreating glaciers, and highly correlated with allochthonous inputs of prey items (Hodkinson et al., 2001). Similar observations have been made on the importance of predators and allochthonous prey inputs during early succession on volcanic substrates elsewhere, although in these instances it is often carabid beetles or bugs that predominate rather than spiders (Hodkinson et al., 2001). Finally, in a study of the non-flying terrestrial arthropod fauna of Henderson Island in the Pacific Ocean, Benton and Lehtinen (1995) reported a rich mite fauna, 26 species of spider, and nine species of isopod. Henderson Island is a remote, raised coral island on the southeast edge of the Indo-Pacific plate that only became elevated above the sea level about 0.5Ma. These examples demonstrate that predator-dominated ecosystems are not confined to early palaeocommunites but are also a feature of newly colonised terrains in the present day. Predators dominate the food web, obtaining their energy from allochthonous prey inputs, and this may also have been the case in early terrestrial ecosystems, many of which are preserved close to the palaeoshoreline.

12.2 Data quality

One of the difficulties in studying minute arthropod fossils is that they are not usually visible in hand specimen and therefore their spatial distribution and relationships within the sediment are unknown. Furthermore, cuticles are unevenly distributed within the sediment and the successful recovery of the fossils must therefore be by trial and error. Consequently there is considerable scope for non-representation of taxa and the under representation of population numbers, making it difficult to judge the extent to which the recovered fossils

reflect the original community structure. Presence-absence data may be flawed, as the absence of a particular taxon amongst recovered cuticles could indicate that it has yet to be uncovered rather than that it is actually absent from the assemblage. For example, although *Microdecemplex* has previously been described from South Mountain, further specimens have failed to be recovered despite years of macerating. Obviously the more samples that are macerated, the higher the chances are that all representatives will be accounted for and this must be a major factor to be accounted for when assessing these types of cuticle compression assemblages. For example, evidence for hexapods and insects is present, but insufficient at South Mountain. Scraps of cuticle preserving ribbon-like scales closely resemble that of extant bristletails, but as yet no definitive specimens (such as mouthparts) have been recovered. Insects and hexapods are both present at Rhynie (collembolans and a pterygote insect) and therefore, by analogy, should also be present in the later sediments from New York. However, material from Rhynie has been studied over a much greater length of time than material from South Mountain and it is likely that this is reflected in the observed faunal diversity at each site.

Aside from comparing isotaphonomic sites to predict what elements of the ecosystem should be present, molecular data can also provide clues as to which terrestrial animals were living during the Siluro-Devonian. Using nucleotide and amino acid data sets, Gaunt and Miles (2002) calibrated an insect molecular clock (using sequence data from the orders Blatteria or Odonata) to determine the origin of the insects and its accordance with early biogeographical and palaeontological landmarks. Their results supported previous phylogenetic analyses that showed Malacostraca and Branchiopoda (including Anostraca) to form a sister group to Insecta, and placed the emergence of the Insecta-Anostraca ancestor at 421–434Ma. Gaunt and Miles (2002) argued further that this date corresponds with the earliest vascular plant megafossils and that the correlation is compatible with the hypothesis that true insects evolved from an aquatic arthropod ancestor that formed an association with a particular group of terrestrial plants and coevolved with that plant group (Tillyard, 1928). The date obtained for the origin of Neoptera (Blattaria, Othoptera and Hemiptera), and hence the latest date for the evolution of insect flight, was 373–382.9Ma for amino acid data and 350.1Ma for nucleotide data. These results, however, do not match the fossil evidence. The earliest example of a pterygote insect is from the Rhynie Chert (Engel and Grimaldi, 2004), 20–30 million years earlier than the date indicated by molecular data. The combined evidence predicts that both flying and non-flying insects were around during the deposition of sediments at South Mountain and High Knob.

Table 11. Comparison of flora, fauna and palaeoenvironment for known cuticle assemblages from the Siluro-Devonian. Data collated from published work referenced in the text.

Locality	Age	Fauna	Flora	Taphonomy/ Palaeoenvironment

Ludford Lane, England	Silurian Pridoli	TERRESTRIAL
		Predators:
		Chilopoda
		  Scutigeromorpha
		    Crussolum
		Scorpiones
		Trigonotarbida
		  Palaeotarbus
		Detritivores:
		  Arthropleurida
		    Eoarthropleura
		AQUATIC
		  Myriapoda
		    Kampecarida
		  Eurypterida
		  Crustacea
		    Ostracoda
		  Annelida
		    Scolecodonts
		  Bivalvia
		  Brachiopoda
		    Lingula
			Cooksonia
			Nematothallus
			Sterile rhyniophytoid axes with stomata
				Compressed cuticle fossils. Terrestrial animals probably inhabited a Rhyniophytoid / cryptospore plant saltmarsh environment and were later mixed with a shallow marine fauna after storms washed components of the ecosystem into the estuarine environment.

Rhynie and Windyfield Cherts, Scotland	Devonian Pragian	TERRESTRIAL
		Predators:
		Chilopoda
		  Scutigeropmorpha
		    Crussolum
		Trigonotarbida
		  Palaeocharinus
		Detritivores:
		  Acari
		    Protacarusi
		    Protospeleorchestes
		    Pseudoprotacarus
		    Palaeotydeus
		    Paraprotocarus
		  Hexapoda
		    Collembola
		      Rhyniella
		  Insecta
		    Pterygota?
		      Rhyniognatha
		  Myriapoda
		    Leverhulmia
		AQUATIC
		  Crustacea
		    Lepidocaris
		    Castracollis
		  Euthycarcinida
		    Heterocrania
			Rhyniopsids
			  Rhynia
			  Asteroxylon
			Algae
			Zosterophylls
				Three-dimensional preservation of *in situ* fossils in a terrestial thermal spring. Periodic eruption caused siliceous waters to flow onto and silicify surrounding vegetation.

Table 11. cont.

Locality	Age	Fauna	Flora	Taphonomy/ Palaeoenvironment
Alken-an-der-Mosel, Germany	Devonian Emsian	TERRESTRIAL Predators: Scorpionides Waeringoscorpionidae Trigonotarbida Palaeocharinidae *Alkenia* *Archaeomartus* Araneae? AQUATIC Crustacea Eurypterida Xiphosurans Mollusca Vertebrate	Algae Lycopsids Rhyniopsids	Impression fossils preserved in sediments deposited in temporary brackish lagoons on tidal sand-flats and bordered by a mangrove type vegetation.
Gaspé, Québec	Devonian Emsian	TERRESTRIAL Detritivores: Diplopoda	Trimerophytes Zosterophylls Lycopsids	Impression fossils in fine-grained, grey to grey-green sandstone/ siltstone, which may have been part of a sandy alluvial plain.
New Brunswick, Canada	Devonian Emsian	TERRESTRIAL Predators: Scorpiones Detritivores: Arthropleurida *Eoarthropleura*	Trimerophytes Zosterophylls Lycopsids	Impression and compression fossils preserved in volcanic-derived fluvial sediments. Scorpion undoubtedly terrestrial with preserved book-lungs.
South Mountain, New York	Devonian Givetian-Frasnian	TERRESTRIAL Predators: Araneae *Attercopus* Chilopoda Devonobiomorpha *Devonobius* Scorpiones Trigonotarbida *Gelasinotarbus* Detritivores: Arthropleurida *Eoarthropleura* *Microdecemplex* Hexapoda *Archaeognatha* AQUATIC Mollusca *Archanadon*	Progymnosperms *Eospermatopteris* *Archaeopteris* Lycopoda	Allocthonous deposit of plants and animals in a dark, fine-grained shale at the base of sandy foresets. Deltaic, floodplain.
High Knob, New York	Devonian Givetian-Frasnian	TERRESTRIAL Predators: Trigonotarbida AQUATIC Conchostraca *Euestheria*	Progymnosperms *Archaeopteris* Zosterophylls Trimerophytes Lycopoda	Large, pyrite permineralised stems and branches preserving (probably transported) arthropod material. Coastal floodplain.

Table 11. cont.

Locality	Age	Fauna	Flora	Taphonomy/ Palaeoenvironment

Gilboa,
New York
	Devonian
	Givetian
		TERRESTRIAL
		Predators:
		  Araneae
		    Attercopus
		  Chilopoda
		    Scutigeromorpha
		      Crussolum
		    Devonobiomorpha
		      Devonobius
		  Pseudoscorpiones
		    Drachochela
		  Scorpiones?
		  Trigonotarbida
		    Gelasinotarbus
		    Gilboarachne
		    Aculeatarbus
		Detritivores:
		  Acari
		    Oribatida
		  Arthropleurida
		    Eoarthropleurida
		  Hexapoda
		    Archaoegnatha
		AQUATIC
		  Eurypterida
			Lycopoda
			Leclercqia
				In situ preservation of
				plant stems, possibly
				along the levees of
				streams, preserving
				transported arthropod
				fossils. Deltaic
				mudstone.

Using nuclear and mitochondrial genes, Pisani *et al.*, (2004) inferred that four major colonisation events took place leading to the chilopods and diplopods, insects, arachnids and isopod crustaceans. Their estimates for a divergent split between millipedes and centipedes ranged from 537–357Ma and averaged at 442±50Ma. Xiphosura and Arachnida were estimated to have diverged at 475±53Ma, Myriapoda and Crustacea at 642±63Ma, Insecta and Crustacea 666±58Ma and for Pancrustacea (Chelicerata and Myriapoa) 725±46Ma. Based upon the assumption that the ancestral arthropod was marine and that terrestrialisation is derived within arthropods, Pisani *et al.* (2004) concluded that myriapods colonised the land after the origin of the myriapod lineage (642Ma) and before the millipede-centipede divergence (442Ma) or the earliest fossils (420Ma). These data again coincide relatively well with the observed data from cuticle compression assemblages and suggest that terrestrialisation was relatively well advanced by the Devonian. It should be expected therefore that most primitive terrestrial arthropods should be represented at least within Devonian assemblages, and the irregularity with which new animals are discovered and correctly identified suggests that the full picture of these early terrestrial ecosystems is still far from complete.

12.3 Future directions

As discussed in chapter 11, although seemingly large numbers of cuticle fragments can be recovered from macerated sediments, it is probable that these actually only represent a fairly small number of individuals. The physical processing of sediment samples to obtain the fossils is a tedious and time consuming process, and is one of the main obstacles to this type of research. Ideally the processing should be increased by at least an order of magnitude so that much larger volumes of cuticles could be examined and analysed to produce more meaningful qualitative data. There are two approaches to this problem, both of which would ideally be utilised. The first would be to automate the entire maceration process so that recovered cuticles could simply be collected, sorted, and analysed. The second would be to create an international database of cuticle types that could be accessed and built upon by anyone wishing to do so.

Bulk hydrofluoric acid maceration is a hazardous and protracted method that requires consistent monitoring and produces a great deal of useless waste acid. Currently only very small amounts (approximately inch-sized pieces) of sediment can be macerated. The most time-consuming aspects of the process include waiting for macerates to filter (although this can be improved with the use of a vacuum pump), changing spent acid when samples are no longer breaking down, and neutralising waste acid. The automation of this procedure would have the dual benefits of creating more time for the examination of cuticles, as well as creating a safer working environment for the user. It would also permit the processing of much larger volumes of sediment and hence cuticles. In an ideal world, a mechanised maceration procedure would permit the user to enter a large quantity of sediment samples into the system, which would then be bathed in acid and the resulting residue filtered off and rinsed ready for collection. Regular, automated changes of the acid would expedite the process, and the continual running of the system would permit residues to be treated much more gently, thus improving the chances for the recovery of articulated arthropod material. Ideally, spent acid would be drained away, filtered and recycled within the system so that the waste products were kept to a minimum. Obviously, this is a purely hypothetical scenario and one that would undoubtedly be limited by cost.

One of the other major problems with studying dispersed and fragmented arthropod cuticles is that there is a high probability that specimens are being recovered by other researchers and going unrecognised. Bulk acid maceration of sediments is a technique usually confined to palaeobotanists and palynologists who are not necessarily interested in arthropod cuticle. The creation of an online database would permit users to digitally add any unidentified cuticle types into the database, and to search through cuticle types for their own benefit. It could be used for enigmatic plant as well as arthropod cuticles, and could act as a reciprocal repository for both fossil plant and fossil arthropod workers. The major benefit of this system would be to make cuticle types immediately accessible to the scientific community and to allow the uploading of fossils that may otherwise be dismissed. The creation of such a database would dramatically amplify the volume of cuticles available

for comparison and analysis, thereby contributing to a more comprehensive fossil record for these early terrestrial fossils, and permitting more accurate qualitative analysis of the ecosystem elements.

CHAPTER 13   CONCLUSIONS

South Mountain and High Knob both preserve assemblages of early terrestrial arthropods from the late Middle Devonian. The two assemblages are approximately contemporaneous and are isotaphonomic, thus permitting direct comparisons of faunal composition. Futhermore, these assemblages can be compared with other cuticle compression fossil assemblages from the Devonian and earlier to help identify differences in community structure during the early stages of terrestrialisation.

13.1   Taphonomy and palaeoenvironment

Arthropod fossils in organic-rich mudstones from New York State are preserved as carbonaceous cuticles representing moulted exoskeletons, carcasses and rejectamenta of predators. Decay and burial in anoxic rather than oxic, and terrestrial as opposed to marine conditions, appear to enhance preservation, whilst the long-term preservation relies on diagenetic alteration to an aliphatic composition.

The arthropod material has an uneven distribution within the sediment and occurs as localised concentrations, frequently of a single cuticle type. Cuticles are only rarely recovered as articulated fragments but the consistent clumping of cuticle types suggests a degree of original association and maybe even articulation within the host rock. The assemblages are allochthonous and the source of the arthropod material was probably plant and arthropod detritus (litter) deposited adjacent to stream banks that was periodically washed into the current and deposited further downstream. The range in preservational quality of the cuticles varies slightly, and probably reflects differences in residence time within the litter prior to transport and deposition. The consistently small size of the cuticles is best accounted for by hydraulic sorting of suspended matter.

Sediments in south-central New York were deposited in tropical latitudes by low-gradient, high-sinuosity rivers in close proximity to the palaeoshoreline. Red, root-churned sediments represent well-drained floodplain deposits that supported an autochthonous community of trees (*Eoaspermatopteris* and *Archaeopteris*) and herbaceous plants (zosterophylls and trimerophytes), growing as dense gallery forests. The presence of clams and ostracods suggests a brackish water environment.

13.2   Palaeontology

The simplest method for taxonomic grouping of dispersed arthropod cuticles, is to assume that all fragments belong to one species unless there is sufficient reason to believe otherwise. There is a relatively high diversity of taxa preserved at South Mountain, whereas

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the fauna from High Knob is dominated by a single species.

Cuticle attributed to *Eoarthropleura* forms the largest fraction of cuticle at South Mountain, and is distinguished by its characteristic W-shaped ornamentation consisting of a double spine surrounding a single setal socket. At least two morphotypes of *Eoarthropleura* are recognised from amongst the cuticles from South Mountain. These are interpreted as sexual dimorphs of the previously described *Eoarthropleura huebieri*, but if more examples come to light, they could prove to represent separate species. In the light of the morphological diversity of arthropleurid material from South Mountain, the diagnoses for *E. ludfordensis* and *E. huebieri* should be amended.

Scorpion cuticle forms the second largest fraction of cuticle from South Mountain and also occurs at High Knob but in much smaller quantities. Scorpion cuticle is characterised by a granular ornamentation and characteristic morphologies such as pectines and metasomal segments. It is unclear whether all of the scorpion cuticle from South Mountain is representative of a single species, although currently there is no compelling reason to suppose otherwise. Recovered sclerites exhibit a combination of plesiomorphic and derived characters that are unknown from any other Palaeozoic scorpions. If the scorpion material is representative of a single species, then it might be expected that the animal had long, slender pedipalps and a strong, powerful cauda not dissimilar to some genera of the modern day Buthidae.

Cuticle bearing reticulations can be divided into three sub-types and occurs at both South Mountain and High Knob. Reticulate A cuticle is characterised by the possession of distally thickened reticulations, minute slit sensilla, and lyriform organs on podomeres. This is interpreted as cuticle from the spider *Attercopus fimbriunguis*. A flagelliform structure associated with reticulate A cuticle is problematic in that it is not consistent with Recent spider morphology and suggests that either *Attercopus* exhibited a mosaic of characteristics unknown amongst extant arachnids, or that reticulate A cuticle represents more than one animal (possibly spiders and amblypygids or uropygids). Reticulate B cuticle is exclusive to South Mountain and is attributed to a palaeocharinid trigonotarbid, possibly of the genus *Gelasinotarbus*. The cuticle is characterised by reticulations, which are thickened on all sides and arranged into curved rows. One piece of this cuticle exhibits an eye with at least 14 minor lenses.

Cuticles from South Mountain with a partially reticulate cuticle are also attributed to palaeocharinid trigonotarbids. Fragments include several podomeres and a single carapace, but the general paucity of material prohibits further identification. Reticulate cuticle from Rhynie has traditionally been classed as from trigonotarbids, but there is a danger that this is becoming a dustbin category for any unidentifiable reticulate cuticle. A complete revision of all reticulate cuticles from Rhynie, Gilboa, South Mountain, and High Knob would almost

certainly result in the creation of new arachnid orders from the Devonian.

Possible trigonotarbids were also recovered from High Knob, but with a very different morphology to those from South Mountain. Much of the material consists of the ventral prosoma with a rounded sternum and short, stubby podomeres with a box-like construction. All pieces are united in their lack of cuticular ornamentation, and the presence of thickened ribs. These form the dominant fauna at High Knob.

Other cuticle pieces from South Mountain hint at a hexapod identification, but fall short of providing absolute proof of their presence. Collembola are known from the Rhynie chert in Aberdeenshire (Greenslade and Whalley, 1986) and another Rhynie specimen has recently been reinterpreted as a pterygote insect with chewing mouthparts (Engel and Grimaldi, 2004). Thus, it is more than likely that wingless hexapods were present at South Mountain during the Devonian.

Small aggregates of spores recovered from South Mountain are interpreted as coprolites from a detritivorous arthropod. These indicate the presence of indiscriminate detritivores, and/or detritivores that targeted spore masses or coprolites in the litter. The breakdown of spores for nutritional gain appears to have been inefficient or impossible in the producers. The coprolites represent the only direct evidence for the cycling of primary productivity at South Mountain and are an important addition to the overall picture of this early terrestrial ecosystem.

Vertebrate remains from South Mountain include placoderm fish plates, acanthodian fish scales, and a labyrinthodont tooth. The fish material is preserved in a poorly sorted layer of bones, plant material, and lithic clasts at the base of a sandstone channel. The labyrinthodont tooth is identified as a primitive polyplocodont tooth, which either represents the first example of an osteolepiform fish from the study area or the oldest known example of a tetrapod body fossil in the world.

13.3 Palaeoecology

Quantitative analysis to obtain population estimates of the dispersed cuticle assemblages from South Mountain and High Knob, suggests that the majority of taxa are represented by less than five individuals, and some by just one. A comparison of three isotaphonomic assemblages suggests that local variations in the palaeoenvironment did impact community composition and that the greatest diversity occurs amongst predators. Predators frequently dominate in other terrestrial cuticle assemblages and are also dominant in early tetrapod communities. In the present day, predators dominate on newly exposed terrains with low primary productivity, where the main energy input is derived from allochthonous material and this may also be applicable to Siluro-Devonian terrestrial arthropods.

Recent discoveries, such as terrestrial millipedes from the Silurian and winged insects from the early Devonian, suggest that terrestrialisation occurred sometime during the Ordovician. This is supported by molecular data and suggests that a full compliment of terrestrial arthropods should exist in Devonian terrestrial assemblages. The sporadic nature of these fossils, however, means that recovery of specimens is inconsistent and new discoveries can quickly change current ideas and hypotheses on terrestrialisation. There is a positive relationship between faunal diversity and the length of time over which a site has been studied, which highlights the need for the continued study of these early terrestrial ecosystems.

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Safety (MSDS) data for hydrofluoric acid

Note: this chemical is extremely hazardous. Do not use without taking professional advice

General

Synonyms: HF, hydrogen fluoride solution
Molecular formula: HF (aq.)
CAS No: 7664-39-3
EINECS No: 231-634-8

Physical data
Appearance: colourless liquid
Melting point: -35 C
Boiling point: 108 C
Vapour density:
Vapour pressure:
Density (g cm-3): 1.16
Flash point:
Explosion limits:
Autoignition temperature:

Stability
Stable. Do not store in glass containers. Light sensitive. Incompatible with strong bases, metals, glass, leather, water, alkalies, concrete, silica, sulphides, cyanides, carbonates.

Toxicology
Extremely toxic. May be fatal if inhaled or ingested. Readily absorbed through the skin - skin contact may be fatal. Acts as a systemic poison. Causes severe burns. Possible mutagen. Reaction may be delayed. Any contact with this material, even minor, requires immediate medical attention.

Toxicity data
(The meaning of any abbreviations which appear in this section is given here.)
IHL-HMN LCLO 50 ppm/30m.

Risk phrases

(The meaning of any risk phrases which appear in this section is given here.)
R26 R27 R28 R35.

Transport information
(The meaning of any UN hazard codes which appear in this section is given here.)
UN Major hazard class: 8.0. Packing group: II

Personal protection
Rubber gloves, face mask or safety glasses, apron, good ventilation. **Do not work without calcium gluconate gel available to treat burns. Do not assume that gloves provide an impenetrable barrier to the acid. DO NOT WORK ALONE! Ensure that those working in the same laboratory are aware of how to treat hydrofluoric acid burns in an emergency.**

Safety phrases
(The meaning of any safety phrases which appear in this section is given here.)
S7 S9 S26 S36 S37 S39 S45.

[Return to Physical & Theoretical Chemistry Lab. Safety home page.]

This information was last updated on September 3, 2003. We have tried to make it as accurate and useful as possible, but can take no responsibility for its use, misuse, or accuracy. We have not verified this information, and cannot guarantee that it is up-to-date.

Source: http://physchem.ox.ac.uk/MSDS/HY/hydrofluoric_acid.html

Microprobe raw data:

Quantitative Analyses (x2) for SM204

point n:1 x=-6037 y= -21953.0 z=126

Elt.	Line	Xtal	Spec.	Std.	Posi.			Beam (nA)	Accn voltage (kV)
								10	10
C	Ka	LPC2	Sp5	c	47645				
O	Ka	PC1	Sp4	qtz	40180				
Si	Ka	TAP	Sp2	qtz	27737				
								20	20
S	Ka	LPET	Sp3	py	61433				

Elt.	Peak (Cps)	Prec. (%)	Bkgd (Cps)	P/B	Ix/ Istd	Sig/k (%)	Detection Limit(%)	Beam (nA)	Accn voltage (kV)
								10	10
C	14970.4	0.1	175.2	85.46	0.5865	0.2	0.0444		
O	195.2	1.3	16.1	12.1	0.0812	15.8	0.3013		
Si	45.3	2.7	5.4	8.45	0.0082	31.6	0.0341		
								20	20
S	1385.5	0.5	18.7	74.04	0.0666	5.9	0.0076		

Elt.	k-ratio	Correc.
C	0.5865	1.4251
O	0.0276	3.5167
Si	0.0035	1.1478
S	0.0315	1.117

Iteration: 4   ration : 4

Analysis no.1 within trig (SM204)

Elt.	Conc. (wt%)	1sigma (wt%)	Norm Conc. (wt%)	Norm Conc. (at%)
C	83.5772	0.171397	85.9991	90.5108
O	9.6887	0.144311	9.9695	7.8766
Si	0.4	0.0137	0.4116	0.1853
S	3.5179	0.018203	3.6198	1.4273
total:	97.1838		100	100

point n: 2 x= -6166.0 y= -21968.0 z=126

Elt.	Line	Xtal	Spec	Std	Posi.
C	Ka	LPC2	Sp5	c	47645
O	Ka	PC1	Sp4	qtz	40180
Si	Ka	TAP	Sp2	qtz	27737
S	Ka	LPET	Sp3	py	61433

Elt.	Peak (Cps)	Prec (%)	Bkgd (Cps)	P/B	Ix/ Istd	Sig/k (%)	Detection limit (%)
C	15855	0.1	191.4	82.83	0.6209	0.2	0.0435
O	172.7	1.4	15.9	10.88	0.0711	1.4	0.3038
Si	10.9	5.5	6.2	1.77	0.01	5.5	0.0363
S	850.9	0.6	15.1	56.28	0.0407	0.6	0.0069

Elt.	k-ratio	Correc.
C	0.6209	1.3367
O	0.0241	3.5732
Si	0.0004	1.1511
S	0.0193	1.1147

iteration: 4

Analysis no.2 within trig

Elt.	Conc. (wt%)	1sigma (wt%)	Norm Conc. (wt%)	Norm Conc. (at%)
C	82.9946	0.167629	88.4741	91.9216
O	8.6178	0.138379	9.1868	7.1651
Si	0.0477	0.008846	0.0508	0.0226
S	2.1464	0.014084	2.2884	0.8907
total:	93.8065		100.0001	100

Appendix C

Operating details for scans of labyrinthodont teeth at UT-CT:

tooth: Scans of a upper middle Devonian vertebrate tooth (possibly labyrinthodont) from South Mountain, about 12 km east of Gilboa, Catskill Mtns, New York, Panther Mountain Formation. Scanned for Vicky MacEwan of Manchester University, UK. Scanned by Matthew Colbert on 13 March 2002.

> **16bit:** 1024X1024 16-bit TIFF images. II, 150 kV, 0.2 mA, no filter, air wedge, no offset, slice thickness = 3 lines (= 0.0316 mm), S.O.D. 31 mm, 1200 views, 2 samples per view, interslice spacing = 3 lines (=0.0316 mm), field of reconstruction 7.5 mm (maximum field of view 10.09 mm), reconstruction offset 2000, reconstruction scale 300. Acquired with 9 slices per rotation. Reconstructed off center: x = -0.6, y = -0.7. Total slices = 108.

labyrint: Scans of a labyrinthodont fish tooth from the Catskill Formation, Duncannon Member, Late Devonian, late Famennian; Clinton Co., Red Hill roadcut, Highway 120, 1.5 km west of Hyner, Pennsylvania. Specimen from the Academy of Natural Sciences in Philadelphia. Scanned for Vicky MacEwan of Manchester University, UK. Scanned by Matthew Colbert on 13 March 2002.

> **16bit:** 1024X1024 16-bit TIFF images. II, 150 kV, 0.2 mA, no filter, air wedge, no offset, slice thickness = 2 lines (= 0.0337 mm), S.O.D. 49 mm, 1200 views, 2 samples per view, interslice spacing = 3 lines (=0.0337 mm), field of reconstruction 15.8 mm (maximum field of view 15.887575 mm), reconstruction offset 3000, reconstruction scale 500. Acquired with 3 slices per rotation at 10 evenly spaced increments. Reconstructed off center: Total slices = 30.