Reports

Land Animals in the Silurian: Arachnids and Myriapods from Shropshire, England

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A new assemblage of arthropod cuticles from Upper Silurian rocks in Shropshire, England, includes at least two centipedes and a trigonotarbid arachnid. This unequivocal terrestrial fauna from the Silurian constitutes the earliest direct record of land animals. The presence of predatory arthropods suggests that complex terrestrial ecosystems were in place by the late Silurian (414 × 10^6 years before present) and that the animal invasion of the land occurred earlier than was previously thought.

THE COLONIZATION OF TERRESTRIAL environments by plants and animals during the Paleozoic Era represents a major benchmark in the evolution of the biosphere. Evidence of land animals is sparse in pre-Pennsylvanian strata (*1, 2*), but the discovery of a diverse assemblage of arthropod cuticles in Middle Devonian age mudstones from Gilboa, New York (*3*), demonstrated that dispersed arthropod fragments can shed light on early terrestrial arthropods and ecosystems, just as plant microfossils have improved our knowledge of pre-Devonian land plants (*4*). We report the discovery of terrestrial arthropod cuticles from Upper Silurian rocks of England. This substantially predates the three well-founded Devonian terrestrial faunas (Table 1).

The fossils come from just above the famous Ludlow Bone Bed at its type locality at Ludford Lane, Ludlow, Shropshire, England (National Grid Reference SO 5116 7413) (*5*). This horizon marks the base of the Přídolí Series of the Silurian System (*5*). The Ludlow Bone Bed Member (LBBM) is the basal member of the Downton Castle Sandstone Formation (DCSF), and is overlain by the Platyschisma Shale Member (PSM). At the locality, the LBBM consists of 0.21 m of ripple-laminated, lenticular-bedded siltstones with the Ludlow Bone Bed (*sensu stricto*) at the base, another bone bed 0.09 m above the base, and a series of three bone beds at the top of the member (*5*). The bone beds consist principally of agnathan denticles and acanthodian scales in a sandy matrix. The material described here comes from a single, up to 3 mm thick, muddy siltstone horizon rich in carbonaceous fragments. The siltstone is discontinuous, occupying shallow ripple troughs and is immediately underlain by a 1- to 2-mm-thick bone bed. The horizon occurs within the LBBM, 0.15- to 0.20 m above the Ludlow Bone Bed.

Associated with the fish remains and terrestrial arthropods are abundant fragments of eurypterids, aquatic scorpions, kampecarid myriapods, and land plants; and rarer ostracodes, scolecodonts, bivalves, and lingulid brachiopods. The land plants include the only record of *Cooksonia* at Ludford Lane, and sterile rhyniophytoid axes with stomata (Fig. 1, E and R), this being the first demonstration of stomata in the Silurian. The lower part of the LBBM, and underlying Upper Whitcliffe Formation, contain fully marine faunas (*5*); the bone beds represent lag deposits of drifted debris formed in a very shallow subtidal to low intertidal environment, possibly deposited in storms (*6*). The restricted fauna of the upper part of the LBBM and PSM, suggests that the biota was deposited in an environment of reduced salinity. A possible source for the terrestrial component is the "Tilestones delta" which lay to the southwest (*7*).

Cuticles were isolated by bulk maceration of the sediment in hydrofluoric acid, mounted on glass slides, and studied using a combination of transmitted and incident light microscopy. Opaque specimens examined by scanning electron microscopy (SEM) revealed little useful information because of the disrupted cuticle surface and fragility of the specimens.

The terrestrial arthropod remains, and those of eurypterids, scorpions, and kampecarids, are preserved as thin organic cuticle similar to the Gilboa material (*3, 8*). The quality of preservation varies between taxa, probably reflecting original variations in the structure and composition of the cuticles. In particular, the terrestrial arthropod cuticles are much darker in color than those of aquatic arthropods; thick cuticles from large individuals are opaque. Because the matrix is silty, flattening is less extreme than in the specimens from the Gilboa mudstones. Some of the Ludford Lane specimens retain much of their original relief and can be examined in incident light, but all bear the marks of silt grains impressed during sediment compaction, making the study of this material difficult. Most specimens are highly fragmentary, consisting of portions of sclerites, although complete podomeres, nearly complete legs, and some articulated body material have been recovered. Examination of cuticles in situ on bedding planes suggests that most of the fragmentation is preburial, perhaps caused by comminution during transport. However, larger specimens are commonly traversed by cracks (almost certainly diagenetic) which can cause disintegration during maceration.

The possibility that the arthropods represent modern contaminants is ruled out on the following grounds: (i) the specimens show alteration consistent with the diagenetic history of the matrix and associated flora; (ii) extinct or extopic taxa (or both) are present; (iii) the results are repeatable (*9*); and (iv) specimens can be seen in situ before maceration.

The most spectacular specimen is a trigonotarbid arachnid, 1.3 mm long, flattened, and opaque except in a few places where the cuticle is translucent and reddish brown in color (Fig. 1, A to D). The body is clearly divided into prosoma and opisthosoma. The carapace is triangular in outline, bearing a prominent anterior median keel which is produced into a pointed snout. The posteromedian area was apparently raised in life because it is now flanked by a pair of crescentic folds. The ventral surface of the prosoma is difficult to interpret: the chelicerae and at least the two most anterior pairs of coxae are missing, revealing the inner surface of the carapace with its narrow doublure. Outlines of the fourth leg coxae are clear, but the positions of the anterior two or three pairs, and that of the sternum, cannot be determined with confidence. The remains of a poorly preserved walking leg are pressed against the ventral surface of the opisthosoma; all other appendages are absent. At least seven segments are discernible on the dorsal surface of the opisthosoma; the anteriormost is the longest and probably represents the fused second and third opisthosomal tergites. Complex cuticular

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Table 1. Stratigraphic chart showing terrestrial biotas of Late Silurian to Early Devonian age; B.P., before present.

Period (10^6 years B.P.)	Stage	Silurian and Devonian localities with reported terrestrial biota
Devonian		
374		
	Givetian	Gilboa, New York: lycopsids, progymnospermopsids; arachnids, myriapods, eurypterids; deltaic mudstone
380		
	Eifelian	
387		
	Emsian	Alken-an-der-Mosel, Germany: algae, lycopsids, rhyniopsids; eurypterids, xiphosurans, crustaceans, mollusks, fish, arachnids; brackish lagoon
394		
	Pragian	Gaspé, Québec: trimerophytes, zosterophylls, lycopsids; supposed archeognathan; fluvial swamp Rhynie, Scotland: algae, zosterophyll, rhyniopsids, *Asteroxylon*; probable collembolans, arachnids, myriapods, crustaceans; terrestrial hot-spring
401		
	Lochkovian	
408		
Silurian		
	Přídolí	
414		Ludford Lane, England: rhyniophytoids, *Cooksonia Nematothallus*; arachnid, myriapods, eurypterids, restricted marine fauna; sub- and intertidal lag deposit

folds run along both lateral margins of the opisthosoma where the lateral margins of the ventral sternites are folded over and on top of the dorsal tergites. These folds are characteristic of compressed trigonotarbids, such as those from Gilboa (*8*), and result from the collapse of the three-dimensional opisthosoma, in which the ventral surface is considerably more convex and wider circumferentially than the flatter dorsal surface. On the left side of the opisthosoma, traces of the lateral sutures in some tergites are present, which on the right side are obscured by the overfolded ventral cuticle. At least ten sternites are identifiable on the ventral surface of the opisthosoma. The first is represented by a narrow strip posterior to the last coxa on the left side of the specimen; the second projects anteriorly along the midline between the last pair of coxae and on the right side obscures sternite 1. The pygidium (opisthosomal somites 10 and 11) is obscure. This specimen cannot be assigned with confidence to a lower taxon within the Trigonotarbida because it lacks diagnostic detail such as eyes and cuticle ornament. A number of additional fragments with a characteristic cuticle ornament may also be attributable to trigonotarbids.

Podomeres in the cuticle assemblage have been assigned to two categories on the basis of their ornament and density of setation. Most common are podomeres with prominent carinae bearing long, distally directed, fixed spines, and sparse setae. These are referred to as "sawblade" podomeres on account of their similarity to podomeres with the same characteristic ornament and designation known from Gilboa (*3, 8, 10*). Several of these podomeres have been found in connection, allowing us to reconstruct a typical leg (Fig. 1, H and I and L to P). Isolated podomeres can be assigned to a podomere type by their jointing characteristics and distribution of carinae. The range of variation in length to width ratio of the podomeres suggests that they come from an animal with more than four pairs of walking legs.

The second podomere type is densely setose, and is rarer than the sawblade type. One specimen consists of connected prefemur, femur, tibia, tarsus, and single terminal claw (Fig. 1, J and K). The prefemur and femur are short and extremely hirsute. The prefemur and tibia bear four large distal spines; the femur, at least two. The apparent division in the tarsus could be a cuticular fold.

Numerous fragments of tergites and poorly preserved portions of trunk can be matched with both of these groups of podomeres on the basis of their cuticle characteristics. Several annulated specimens, including an opaque specimen consisting of 15 segments (Fig. 1G), belong to antennae or flagella.

We interpret these legs, tergites, trunk and antenniform fragments as parts of at least two types of centipede. This interpretation is based on comparison with extant and fossil centipede material, and with other arthropods. We cannot demonstrate the identity of these specimens conclusively until more diagnostic material is found, but have eliminated all other known arthropod groups, and there is nothing in the assemblage which is inconsistent with this identity (*11*).

Approximately 70% of the cuticle assemblage consists of featureless fragments of very thin cuticle belonging to kampecarid myriapods. Partial specimens with up to seven articulated segments were recognized on bedding planes before maceration of the sediment (Fig. 1, E and F). These bear a strong resemblance to *Kampecaris dinmorensis* Clarke, from the Pragian of Herefordshire (*12*). The preservation of trunk segments is good, and detailed study will allow reconstruction of the ventral surface which is currently unknown in kampecarids (*13*).

The cuticle assemblage also contains some rare, but distinctive, cuticle types which are as yet unidentified. The most characteristic of these has a reticulate surface ornament with small spines at the reticulum nodes. One such specimen appears to represent the posterior end of an unknown animal with a pair of cerci (Fig. 1Q).

Numerous lines of evidence point to the trigonotarbid and centipede fossils being terrestrial animals. First, known centipedes and trigonotarbids are terrestrial. The trigonotarbids from Rhynie (*Palaeocharinus*) and Gilboa (*Gilboarachne*, *Gelasinotarbus*) bear book-lungs for air-breathing (*8*); modern centipedes are entirely terrestrial, and there is evidence that the Gilboa centipedes were too (*10*). Second, the functional morphology of the centipede limbs described here is ideally suited to rapid terrestrial locomotion, but not to walking in water (*14*). The distal podomers are long and thin, and the femur-tibia joint provides for a wide angle of flexion extension, ideally suited for the large stride lengths necessary in running. The flexible, spinose tarsi would have presented a large surface area for plantigrade locomotion: such footprints are not used by primarily aquatic arthropods in which digitigrade tarsi occur, and the plantigrade stance implies leg-rocking, a device developed for terrestrial locomotion (*14*). Third, the biota preserved with the centipedes and trigonotarbid includes land plants (Fig. 1R).

The Rhynie, Alken, and Gilboa biotas contain many specimens and numerous species of undoubted land animals together with one or more aquatic forms (Table 1), a pattern followed by the Ludford Lane biota, which exhibits many specimens of at least three terrestrial forms, together with predominantly nonmarine aquatic forms. Other, usually solitary, occurrences of supposedly terrestrial animals have been reported from mid-Paleozoic rocks (*1*). A number of Silurian and Devonian myriapods have been described, some of which have since been reinterpreted as fossils of other, nonterrestrial groups (*13, 15*). The remainder, mainly kampecarids from the freshwater Přídolí of Scotland, are considered to have been aquatic (*13*). The record of a single hexapod fossil from the Emsian of the Gaspé Peninsula, Québec (*16*), is less clear. The Gilboa, Alken, Rhynie, and Ludford Lane terrestrial faunas each fulfill all four criteria of authenticity cited above, *Gaspea* does not appear to fulfill them (*17*). Other demonstrably authentic specimens from the deposit are needed before we will consider *Gaspea* as a genuine fossil hexapod.

The basal Přídolí arthropods described here now constitute the earliest known terrestrial fauna. Moreover, like the Devonian faunas, this assemblage is dominated by predators, suggesting that the arthropod occupiers of lower trophic levels remain to be discovered. Paleobotanical studies have indicated that terrestrial floras became established between late Ordovician and mid-Silurian times (*2, 4*). The presence of predatory arthropods on land in the late Silurian supports the idea that the main components of terrestrial ecosystems were in place substantially earlier than this, and that the ar-

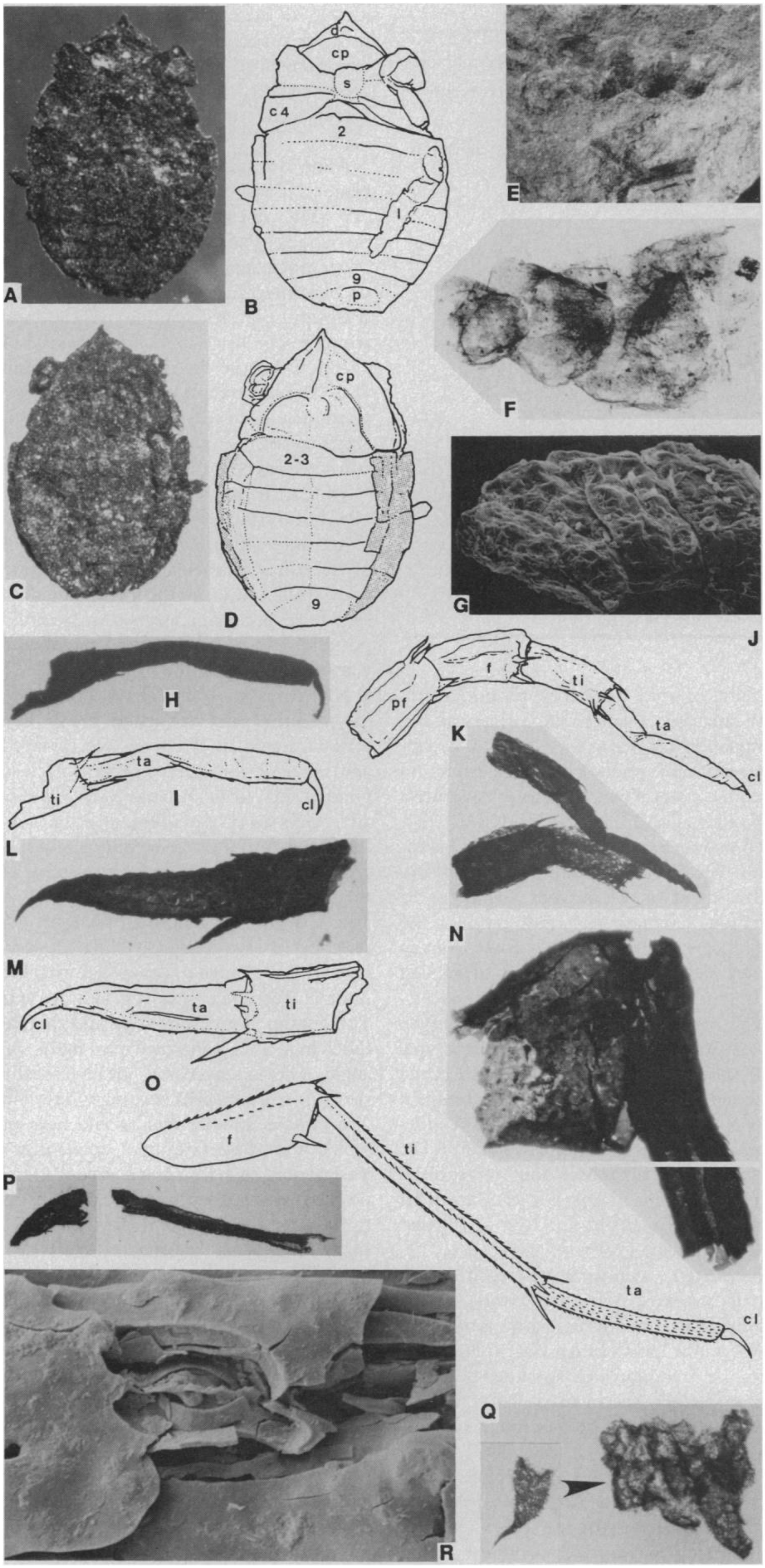

Fig. 1. Terrestrial biota from the Ludlow Bone Bed Member of Silurian (Přídolí) age, Ludford Lane, Ludlow, England. All photographs taken in incident light unless stated otherwise. (**A–D**) Trigonotarbid arachnid, (A) ventral view (×31), (B) drawing of (A), (C) dorsal view (×31), (D) drawing of (C); (**E** and **F**) kampecarid myriapod, (E) in rock, with bifurcating sterile axis of rhyniophytoid *Hostinella* below (×4.4), (F) anterior (?4) attached somites, isolated from the rock, anterior to left, transmitted light (×27); (**G**) SEM photograph of distal five segments of ?antennal appendage (possibly centipede) from series of 15 segments, note rows of setae at distal borders of segments (×170); (**H, I,** and **L** to **P**) ?scutigeromorph centipede type 1 (sawblade), (H) posterior leg, end of tibia, tarsus, and claw (×30), (I) drawing of (H), (L) anterior leg, end of tibia, tarsus, and claw (×37), (M) drawing of (L), (N) end of femur and basal part of tibia (×60), (O) reconstruction of femur to tarsus of a typical leg, (P) end of femur and nearly complete tibia (×21); (**J** to **K**) ?scutigeromorph centipede type 2 (hairy), (J) drawing of (K), (K) pre-femur, femur, tibia, tarsus, and claw, transmitted light (×33); (**Q**) posterior end of unknown arthropod, with pair of cerci and ornament of minute spinules, transmitted light (×44); (**R**) SEM photograph of stoma on sterile axis (×750). In (K), (P), and (Q), the two parts of the fragile specimens were previously joined but were disturbed during mounting. Abbreviations: cl, claw; cp, carapace; d, doublure; c4, coxa of fourth leg; f, femur; s, sternum; l, leg (poorly preserved); p, pygidium; pf, pre-femur; ta, tarsus; ti, tibia; numerals on (B) and (D) refer to opisthosomal sternites (B) and tergites (D).

thropod invasion of the land may have been closely coupled with that of the plants, rather than lagging behind as some authors have suggested (*4*).

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17. (i) *Gaspea palaeoentognathae* is preserved fully three dimensionally, and its cuticle appears from the published SEM photographs (*16*) to lack any impressions of sedimentary particles from the matrix. (ii) The presence of separated compound eyes was cited as evidence that *Gaspea* does not belong to any modern archeognathan taxon. However, the head capsule of the specimen is collapsed, with a large open tear between the eyes. The authors present no evidence that the eyes were originally separated, and therefore it is possible that the specimen could belong to an extant taxon. In addition, the sample from which the specimen came was collected from a seashore where bristletails abound; their occasional contamination of samples would be expected. (iii) The Gaspé archeognathan is a single occurrence of head and thorax of one individual; no other specimens have been found in the deposit, despite the considerable amount of material macerated in the search for plant fossils (*19*).
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Hydroxyl Radical Photoproduction in the Sea and Its Potential Impact on Marine Processes

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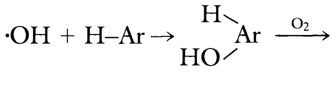
Photochemical production rates and steady-state concentrations of hydroxyl radicals (·OH) were measured in sunlight-irradiated seawater. Values ranged from 110 nanomolar per hour and 12×10^{-18} molar in coastal surface water to 10 nanomolar per hour and 1.1×10^{-18} molar in open ocean surface water. The wavelengths responsible for this production are in the ultraviolet B region (280 to 320 nanometers) of the solar spectrum. Dissolved organic matter (DOM) appears to be the main source for ·OH over most of the oceans, but in upwelling areas nitrite and nitrate photolysis may also be important. DOM in the deep sea is degraded more readily by ·OH (and its daughter radicals), by a factor of 6 to 15, than is DOM in open-ocean surface water. This finding may in part bear on major discrepancies among current methods for measuring dissolved organic carbon in seawater.

THE HYDROXYL RADICAL (·OH) IS the most reactive, photochemically produced free radical in the environment (*1–3*). It plays a central role in atmospheric chemistry (*4*), but its role in aquatic environments is less clearly understood (*3, 5*). Flash photolysis studies (*2*) demonstrated that ·OH is formed in seawater, and a few model calculations of ·OH production rates and concentrations in surface seawater have been reported (*6, 7*). However, there have been no actual measurements. We evaluated photoproduction of ·OH in seawater by two independent, well-characterized reactions. The first is based on H atom abstraction from an aliphatic alcohol, methanol (CH_3OH), by ·OH. The formation rate of the main stable product, formaldehyde (CH_2O) (*8, 9*), is then measured:

$$\cdot OH + CH_3OH \rightarrow \cdot CH_2OH + H_2O$$

$$\cdot CH_2OH + O_2 \rightarrow CH_2O + HO_2\cdot$$

The other reaction, which is more specific for ·OH, is based on addition of ·OH to the aromatic (Ar) ring of benzoic acid. The formation rates of the addition products *o*-, *m*-, *p*-hydroxybenzoic acids (*1, 8, 10*) are then measured:



$$\cdot OH + H{-}Ar \rightarrow \overset{H}{\underset{HO}{\diagdown\!\!\diagup}}Ar \xrightarrow{O_2} HO{-}Ar + HO_2\cdot$$

Similar, but less sensitive, techniques have been used to determine ·OH production rates in freshwaters (*6, 7, 10*). However, to our knowledge, these techniques have not been previously applied to seawater.

Details of experimental procedures and controls have been presented elsewhere (*11*). Samples (filtered and unfiltered) were irradiated in quartz flasks with natural sunlight (4 hours, solar noon, cloudless sky, 26°N). Production rates of both CH_2O and hydroxybenzoic acids were measured by liquid chromatography with ultraviolet (UV) detection. Formaldehyde was determined with about a 20-fold greater sensitivity as its 2,4-dinitrophenyl hydrazone (*12*). The reproducibility ($\pm 1\sigma$ SD for repeated measurements on the same sample) of ·OH production rates for coastal water ($n = 10$) was <5% for the CH_3OH probe and about 10% for the benzoic acid probe. Production rates obtained with these two different probe scavengers agreed to within ± 20% (1σ SD) for all seawater and freshwater samples tested (*11*). Because of its much higher sensitivity, we used the CH_3OH probe to measure ·OH production rates in open ocean samples where we anticipated much lower production rates than for the coastal samples. Photoproduction rates for ·OH were converted to steady-state concen-

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