THREE-DIMENSIONALLY MINERALIZED INSECTS AND MILLIPEDES FROM THE TERTIARY OF RIVERSLEIGH, QUEENSLAND, AUSTRALIA

by IAN J. DUNCAN, DEREK E. G. BRIGGS *and* MICHAEL ARCHER

ABSTRACT. An assemblage of three-dimensionally preserved insects and millipedes from the late Oligocene/ early Miocene limestones of Riversleigh (north-west Queensland) augments a sparse Tertiary insect record from Australia. The fauna includes four species of Coleoptera, one of Trichoptera represented only by the larva, and a myriapod. The arthropods are uncompacted and have been replicated in calcium phosphate. Early phosphatization has preserved original structures such as the overlapping layers and helicoidal pore canals of the procuticle, and wrinkles in the arthrodial membrane. The most remarkable preservation is of the ocular apparatus. The hexagonal lenses and their rhabdom emplacements are preserved in the Coleoptera. The trichopteran larva displays an unusual form of compound eye, consisting of large, separate circular lenses. Where the cornea has been lost, an irregular lattice of 'cups' is exposed. This is the first example of this 'schizochroal'-type eye reported in a fossil insect. Bacteria and fungi associated with the decay of the insects are themselves mineralized.

DESPITE the great success of insects through time in terms of both abundance and diversity, surprisingly little is known about the fossil insects of Australia. The majority of remains so far uncovered consist of wings or indeterminate fragments. Only rarely are wings attached to bodies and even when this occurs, most fossils are preserved in a crushed and distorted condition (Riek 1970a). Approximately 350 fossil species in 19 orders have been described from Australia, covering a period extending from the Upper Permian to the Pliocene (for reviews see Riek 1970a, 1970b; Jell and Duncan 1986). However, this record includes only three significant Tertiary insect deposits besides those at Riversleigh (Text-fig. 1): Redbank and Dinmore, southern Queensland (Riek 1967) and Vegetable Creek, NSW (Riek 1954). The information provided by these sites is limited by the quality of the fossil material. The Lower Tertiary Redbank assemblage is dominated by Coleoptera and Homoptera, but Blattodea, Hemiptera-Heteroptera, Neuroptera, Mecoptera and Diptera are also represented (Riek 1970a). Insects are much rarer in the Dinmore assemblage, with single wings of an orthopteran, an isopteran, a homopteran and an odonatan comprising the total fauna (Riek 1970a). The Vegetable Creek fauna is restricted to immature aquatic insects, predominantly Ephemeroptera and Diptera. Only beetle elytra have been recovered from other Tertiary sites (Riek 1970a). The remarkable three-dimensionally preserved insects from Riversleigh represent an important addition to this Tertiary record.

THE RIVERSLEIGH FAUNA

Riversleigh's major importance is the data that it provides on the Tertiary mammals of Australia (Archer and Bartholomai 1978; Archer and Clayton 1984), nearly trebling the species of this age previously recorded for the entire continent (Archer *et al.* 1994a, 1994b, 1995). The insects were first discovered in the course of processing the vertebrate-packed limestone in search of small bones and teeth. Acetic acid digestion may have introduced a bias, as specimens which are not phosphatized would have been destroyed. Specimens which preserve organics were recovered from other Riversleigh sites (D. A. Arena, pers. comm.). Coleopteran specimens are rare. At least four different species, each belonging to a different family, have been found. Fragmentary larval specimens of a
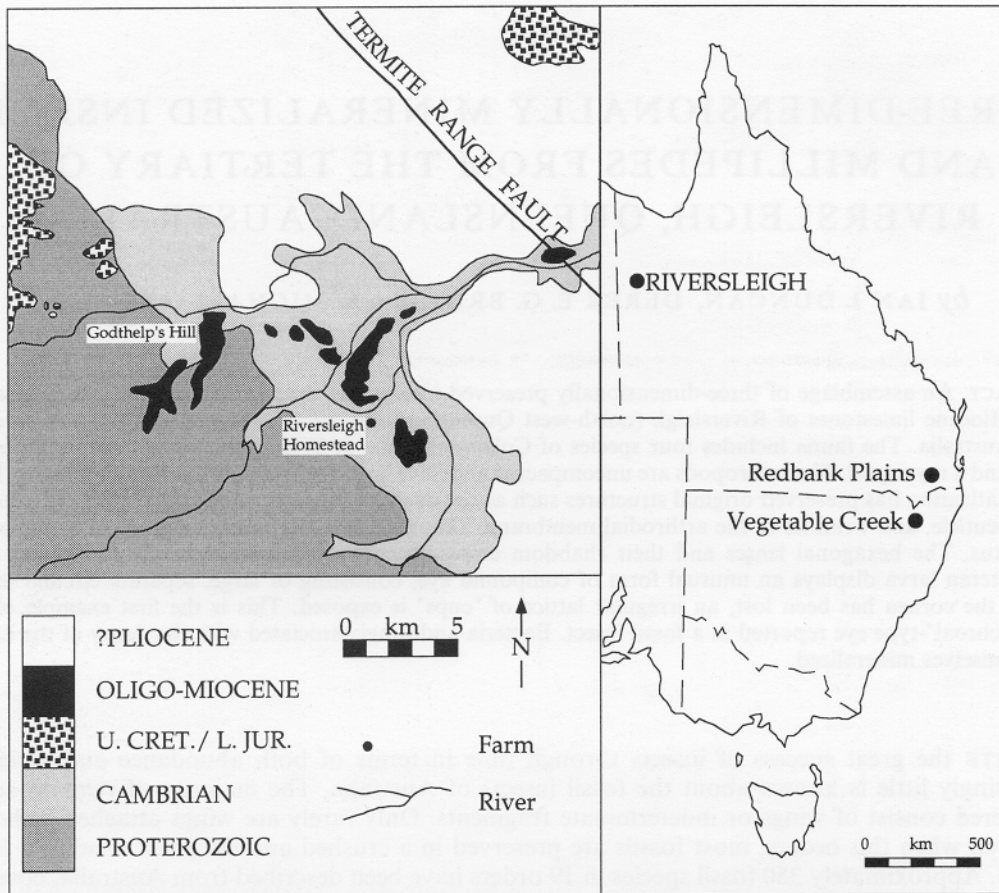
TEXT-FIG. 1. Location map. Left, detail of Upper site, Godthelp's Hill and geology of the surrounding area. Right, locations of Riversleigh and principal Tertiary insect-bearing *Lagerstätten* in eastern Australia (after Megerian 1992).

single species of Trichoptera are much more common. A myriapod, and a previously documented isopod (Archer *et al.* 1994a), complete the arthropod fauna as presently known.

Locality and stratigraphy

Although Riversleigh was originally thought to represent a single, distinct mid Miocene assemblage (Tedford 1967), fossils have now been recovered from over 100 different sites, ranging in age from late Oligocene to near present day (Archer *et al.* 1989, 1994a, 1994b, 1995). For a detailed discussion of the stratigraphy, see Megerian (1992).

The arthropods reported here were recovered from one locality, the Upper Site of Godthelp's Hill (Text-fig. 1). Arthropods are also known from other Riversleigh sites (Camel Sputum and Dunsinane sites). At the Upper Site, the vertebrate fauna is particularly diverse, with almost twice the number of marsupial species as any surviving Australian ecosystem, as well as a diverse range of birds, reptiles and amphibians (Archer *et al.* 1989, 1994a). The Upper Site is interpreted as a former shallow (*c.* 1 m deep), lime-rich pool in a rain forest (Archer *et al.* 1994a), where levels of calcium carbonate were sufficient to result in the precipitation of a thin peripheral crust.
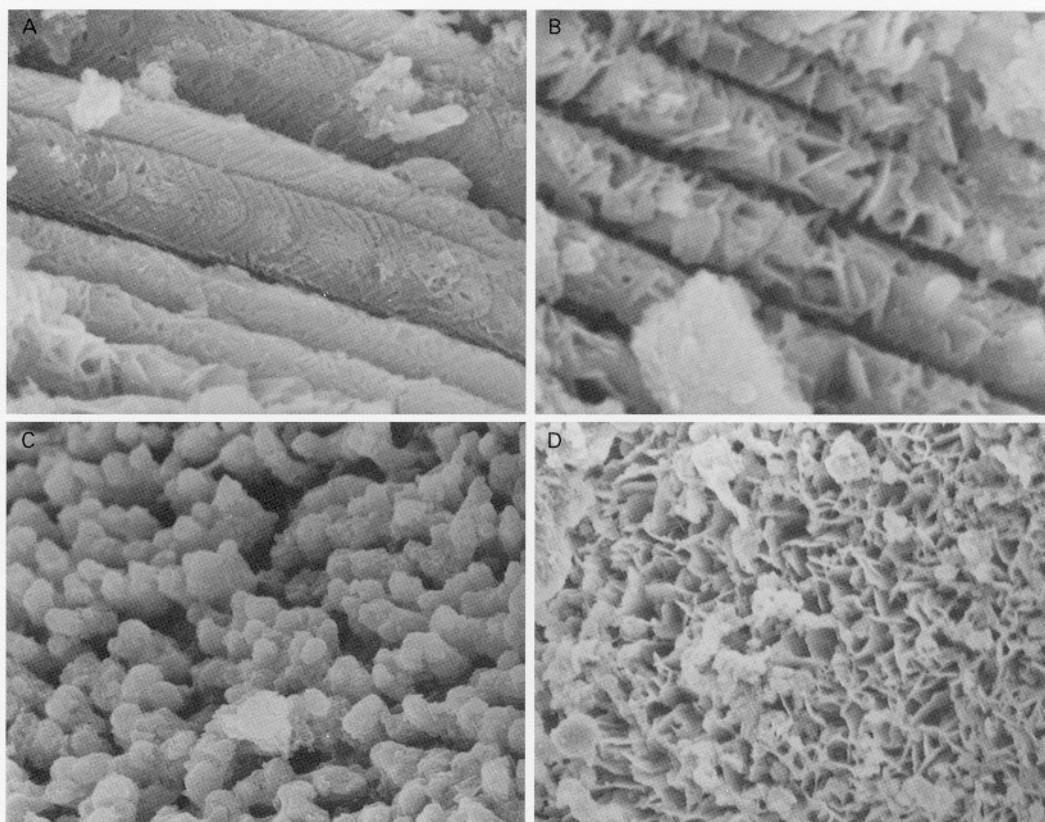
TEXT-FIG. 2. Micro-environments of preservation in a trichopteran larva (QM F34592). A, cuticular fragment from within the tail assemblage displaying distinct chevron structures arranged in parallel rows; structural detail is lost to the lower right; ×65000. B, cuticle a few micrometres distant to 'A'; the structures have been replicated by plates of calcium phosphate such that the gross structure is retained while the detail is lost; ×65000. C, 'nodular' surface of the dorsal cuticle; ×25000. D, replacement of the nodules within a few micrometres of 'C' with plates of calcium phosphate; ×30000. Specimens are gold coated.

Accumulations of piles of crystalline shards, interspersed with animal remains, are common in many of the Riversleigh deposits. The crystal crust may have given the appearance of firmness, only to give way under the weight of an animal that strayed onto it, which then drowned. The Upper Site limestone is characterized by black, iron-rich bands that may reflect periods of anaerobic conditions, where an absence of oxygen inhibited scavengers, contributing to the lack of disarticulation of the vertebrate remains. Wrinkled sheets, interpreted as algal mats, have also been recovered from acid residues (Archer *et al.* 1994*a*). The trichopteran larvae are found in tube-like extensions of this mat-like material. The range of vertebrates found at the Upper Site suggests that all the surrounding micro-environments are represented, from tree tops (many possums) to the forest floor (wynyariids, macropopoids, perameloids, etc.), and the water itself (frogs) (Archer *et al.* 1994*a*).

TAPHONOMY

The most striking feature of the Riversleigh arthropods is their preservation in three dimensions. However, only the more recalcitrant tissues have survived; the internal soft tissues have decayed.
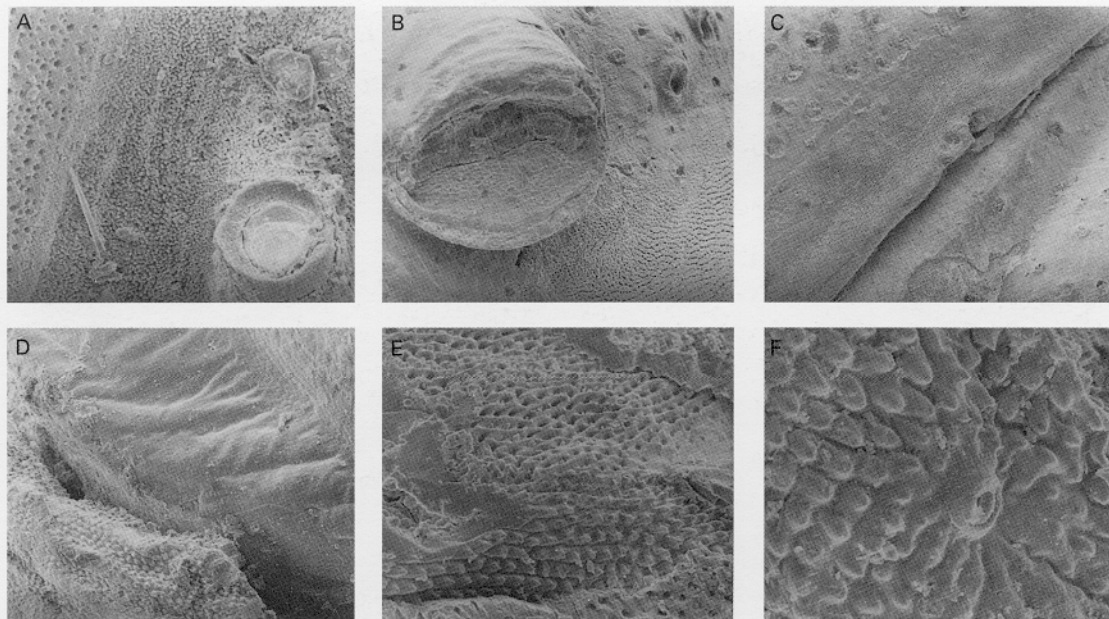
TEXT-FIG. 3. Ornamentation of cuticle of trichopteran larva (QM F34587). A, prescutum with irregular pattern of pits; a spiracle is also present; × 4500. B, interface between the scutum, showing sites of hair emplacement in its upper half, and the scutellum; the scutellum is more regularly patterned than the prescutum; × 5000. C, scutum and scutellum, overlapping the next segment (to the right); × 4000. D, limb of first thoracic segment, surrounded by arthrodial membrane; × 700. E, arthrodial membrane; × 1750. F, close-up of hair emplacement; × 2250.
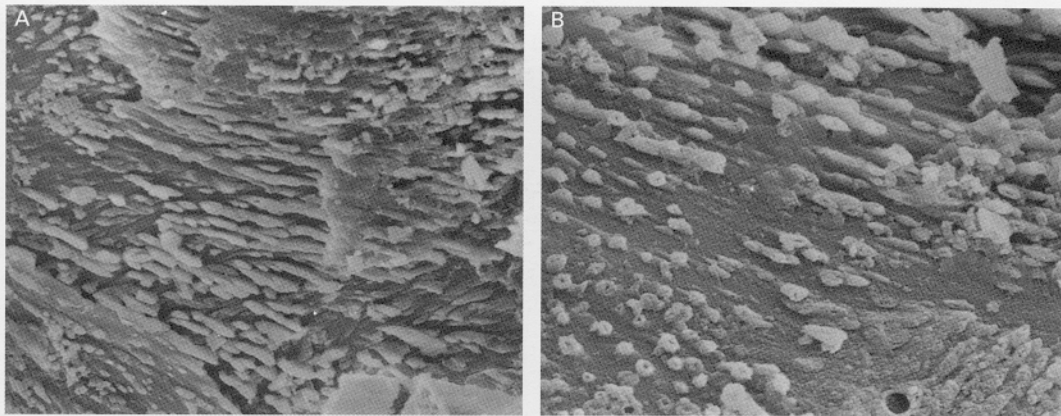
TEXT-FIG. 4. Underlying arrangement of microfibrils within the cuticle of coleopteran species C (QM F34582). A, longitudinal arrangement of microfibrils; × 13000. B, longitudinal and cross sectional arrangement of microfibrils; × 32500.

The overlapping layers that make up the cuticle are preserved, as are the ocular framework, rhabdom and individual lenses of the eye. Microprobe analysis confirms that the specimens are preserved in carbonate-fluorapatite. Some specimens are infilled with detrital matter that appears to have been phosphatized contemporaneously.
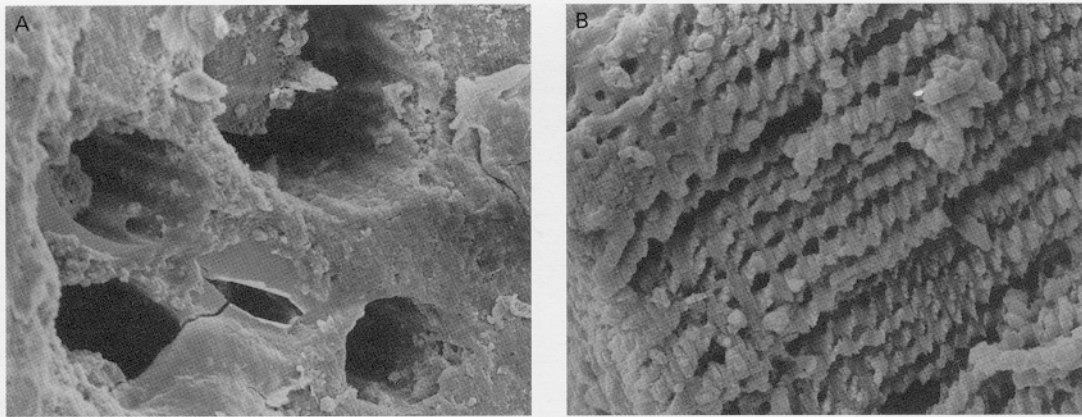
TEXT-FIG. 5. Canals within the cuticle of the trichopteran larva (QM F34591). A, series of parallel canals exposed in tail segment; ×9000. B, helicoidal pore canals (cf. Bouligand 1965) in a cuticle fragment; ×27500.

Cuticle

Structures less than 1 μm in dimensions are preserved on the surface of the cuticle (Text-fig. 3). The distinctive arrangement of the microfibrils (Text-figs 4, 9A) is evident in section, as is the helicoidal structure observed by Bouligand (1965) and Neville *et al.* (1969) in living insects (Text-fig. 5B). The orientation of the crystals follows that of the structural proteins and other biomolecules within the cuticle, emphasizing the high fidelity of replication by calcium phosphate. Parallel canals can be discerned within the tail segment of one of the larvae (Text-fig. 5A).

The cuticle of the trichopteran larva displays distinct chevron structures arranged in parallel rows (Text-fig. 2A) just a few micrometres distant from a point where the cuticle has been replaced by plates of phosphate that replicate the gross structure but obliterate the detail (Text-fig. 2B). A similar phenomenon is evident where the nodular patterning of the larval cuticle (Text-fig. 2C) is replaced within a few micrometres by plates of phosphate (Text-fig. 2D). This indicates that the conditions under which decay and mineralization took place varied on a sub-millimetre scale (see Martill 1988; Briggs and Kear 1994).

Eye

Perhaps the most striking evidence of the fidelity of preservation occurs in the eyes (Text-fig. 6; Duncan and Briggs 1996). The insect compound eye is composed of arrays of ommatidia – the basic visual unit (Snodgrass 1935; Text-fig. 6F). Each ommatidium is composed of a dioptric apparatus and rhabdom, isolated from the next ommatidium by pigment cells; the dioptric apparatus of lens and crystalline cone controls the focusing of light. The cuticle of this apparatus is composed predominantly of chitin, which differs ultrastructurally from that surrounding it (Neville 1970). The rhabdom contains the visual pigments that trigger impulses in the optic nerve (Snodgrass 1935). The entire ocular apparatus of the Riversleigh specimens is replicated in calcium phosphate.

The eyes exhibit varying degrees of alteration through decay and diagenesis. Where the lenses (diameter 30 μm) are preserved, the characteristic hexagonal-packing arrangement of the compound eye is apparent (Text-fig. 6A, I). With the deflation of an individual lens through decay, crystal aggregates are evident in the interior. Where the dioptric apparatus is lost, the rhabdom emplacement is exposed (Text-fig. 6B, D, K). In cross section the rhabdoms can be discerned
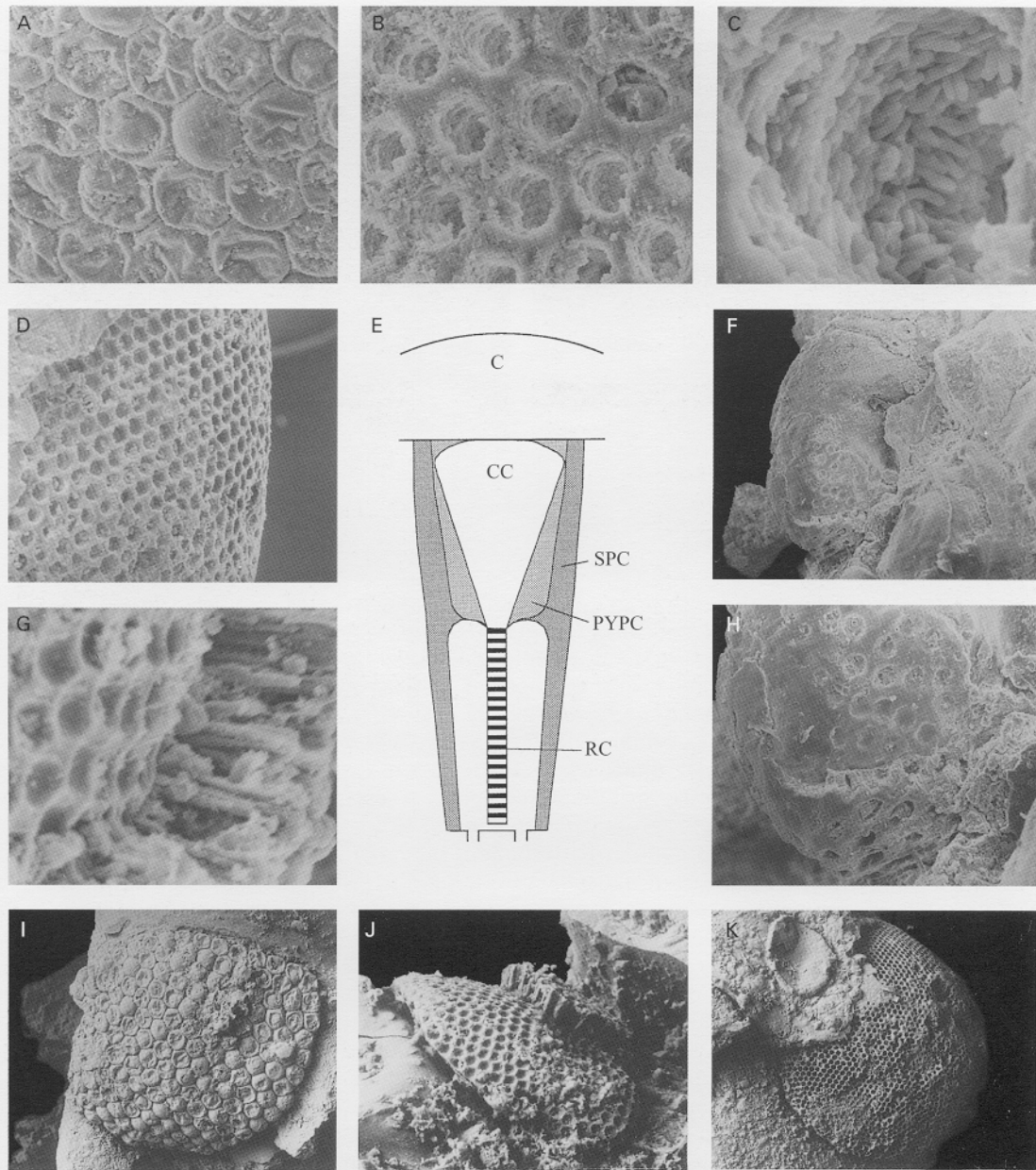
TEXT-FIG. 6. Compound eyes. A, I, coleopteran species A; B–D, K, coleopteran species B; G, J, coleopteran species C; F, H, trichopteran larva. A, lenses displaying characteristic hexagonal packing (QM F16648); ×2500. B, framework of pigment cells revealed by loss of dioptric apparatus (QM F34583); ×7000. C, walls of rhabdomal emplacement lined with bacteria (QM F34583); ×20000. D, framework of the eye (QM F34583); ×1500. E, schematic of ommatidium of apposition eye. Abbreviations: C, corneal lens; CC, crystalline cone; PYPC, primary pigment cells; SPC, secondary pigment cells; RC, retinal cells; R, rhabdom. F, 'schizochroal-type' eye (QM F34584); ×2750, G, cross section through rhabdomal emplacement showing ommatidial cups (QM F34582); ×2000. H, close-up of 'schizochroal-type' eye, showing ommatidial cups (QM F34584); ×2750. I, complete eye (QM F16648); ×720. J, complete eye (QM F34582); ×2500. K, complete eye (QM F34583); ×480.
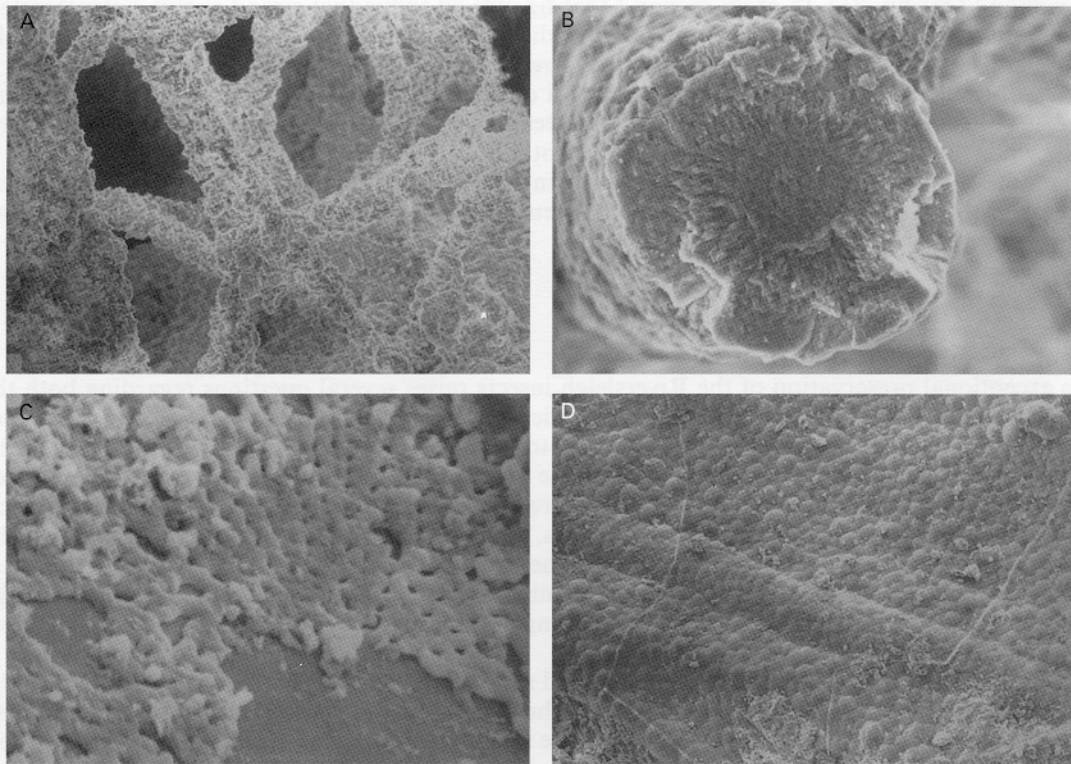
TEXT-FIG. 7. Fossil fungi and bacteria. A, fungal hyphae criss-crossing the interior of head and thorax of larva (QM F34584); ×1750. B, cross section through single fungal strand (QM F34584); ×9000. C, fungal colony covering sternite of larva (QM F34592); ×225000. D, bacterial mat covering surface of coleopteran wing (QM F34595); ×600.

extending radially from the surface of the eye (Text-fig. 6G, J). With the rhabdoms stripped away, the ommatidial cups, the concave receptacles of the ocular apparatus, are evident. The pigment cells that once lined the rhabdom interior of one specimen have been destroyed by bacteria, which are now preserved as rod-like protuberances from the walls (Text-fig. 6C). Bacteria are also preserved enshrouding the hind wings of a beetle (Text-fig. 7D). Mineralized bacteria have been reported from other localities (e.g. Messel; Wuttke 1983).

The trichopteran larva displays an unusual form of compound eye consisting of large, separate circular lenses rather than the more usual closely packed hexagonal type (Text-fig. 6F, H). Where the cornea and dioptric apparatus have been lost, an irregular arrangement of 'cups' is exposed. This 'schizochroal-type' eye occurs in only a small number of living insects (Kinzelbach, 1967; Clarkson 1979; Paulus 1979; see Horváth *et al.* 1997 for a review), where it is thought to maximize light reception. Caterpillars of the Lepidoptera, the sister group of Trichoptera, normally have six isolated biconvex lenses, widely distributed on each side of the head. Coleopteran and megalopteran larvae can have up to six well-separated stemmata on each side of the head, the Neuroptera and Raphidioptera up to seven, and the Strepsiptera five. Larvae of most Mecoptera have dispersed faceted eyes consisting of 30–35 typical ommatidia.

Fungi

A trichopteran larva preserves fungal hyphae in the head capsule and trunk (Text-fig. 7A). Individual strands criss-cross the interior of the insect displaying a simple lateral dichotomous

branching (Text-fig. 7A). In cross section (Text-fig. 7B) an individual strand shows a structureless core (12 μm in diameter) surrounded by a layer displaying a distinct radial pattern (17 μm broad). The outer layer represents a crystalline overgrowth around the original fungal strand, which is presumably represented by the core which has a diameter (12 μm) comparable to that of modern hyphae (10 μm). Extant hyphae consist of an outer wall of hemicellulose or chitin around a cavity, the strands forming a filamentous system (Talbot 1971).

An unusual fungal growth is also noted covering the external surface of a larval segment, where a number of strands appear to radiate from a central point, each joined by short lengths to form a distinctive meshwork (Text-fig. 7C).

Environmental conditions

The exceptional preservation of the Riversleigh insects raises several questions regarding both the rate and mechanism of mineralization. Most models for the preservation of non-mineralized tissues require rapid burial, anoxicity, or both, in order to preclude scavenging (Seilacher et al. 1985). The presence of a surface crust and algal mats at the Upper Site at Riversleigh would have inhibited circulation and promoted anoxicity. Only the more recalcitrant tissue (i.e. cuticle, or calcified cuticle in the case of the myriapod) is preserved and this, coupled with the presence of bacteria within the rhabdom emplacements and fungal hyphae in the head capsule of one of the specimens, suggests that decay proceeded for some time prior to mineralization. The fungal strands criss-cross the interior of some specimens indicating that the fungus colonized the carcass *after* the internal tissue was lost through decay.

It is clear that the limited number of arthropod species recovered from this site cannot reflect the total diversity of this rain forest environment. Those taxa (and life stages) that are preserved, and survived the acid digestion, are probably the more readily phosphatized elements of the biota. Their higher preservation potential may reflect the original biochemistry of the cuticle.

Other examples of three-dimensionally preserved insects

Three-dimensional preservation normally relies on sufficiently early mineralization to prevent collapse through decay, and to protect the fossil from overburden-induced compaction. Thus insects preserved as organic remains are rarely three-dimensional, except in conservation traps (*sensu* Seilacher et al. 1985) such as amber (Poinar and Hess 1982; Henwood 1992, 1993; Grimaldi et al. 1994) and asphalt (Miller 1983; Stock 1992; Stankiewicz et al. 1997). The insects of the Oligocene Bembridge Marls, Isle of Wight, England (Jarzembowski 1980) are an exception. Here they are preserved essentially as a void left by the decayed internal tissues, lined with the cuticle, which is represented by a micrometre-thick, highly altered, organic layer.

Most three-dimensionally preserved insects occur in early diagenetic concretions, such as the siderite nodules that are known from a variety of Carboniferous sites (see Bolton 1905; Woodward 1907; Heyler 1980; Baird et al. 1985a, 1985b), notably at Mazon Creek in north-eastern Illinois (Richardson 1956; Johnson and Richardson 1966; Nitecki 1979; Baird et al. 1985a). These Carboniferous insects rarely preserve ultrastructural details of the cuticle (see Baird et al. 1985a) in contrast to those preserved in Tertiary concretions. Calcareous nodules from the Miocene of Barstow, California (Palmer 1957) exhibit micrometre-scale replication of the cuticle and internal tissue by a suite of minerals including quartz, apatite, celestite, gypsum and zeolite (Park 1995). The concretions of the Eocene London Clay, England, which are composed of pyrite, apatite or calcite (Britton 1960; Allison 1988), have yielded various beetles (Britton 1960), and a pyritized maggot (Rundle and Cooper 1971) which preserves surface details of the cuticle, but not the internal tissues. Phosphatic concretions from the mid Tertiary Dunsinane Site at Riversleigh, preserve insects (D. A. Arena, pers. comm.).

The Riversleigh insects are exceptional in that phosphatization of the cuticle has led to three-dimensional preservation without the formation of a concretion. Phosphatized insects have also been reported from the Eocene Quercy Phosphorites of France (Handschin 1944), and the Oligocene fissure fillings of Ronheim, Germany (Hellmund and Hellmund 1996), but in both cases crystallization is coarser than at Riversleigh and less detail is preserved. A similar style of preservation in calcite is known from the Miocene volcanic deposits of Rusinga and M'fwangano Islands, Lake Victoria, Kenya (Leakey 1952, 1963) but only the gross morphology of taxa with thickened cuticles, such as millipedes and beetles, is preserved. Calcified millipedes are also known from Holocene cave deposits in the West Indies (Donovan and Veltkamp 1994), but the cuticle is likely to have been biomineralized in life.

SYSTEMATIC PALAEONTOLOGY

The morphological terminology and classification used here is that of *The Insects of Australia* (C.S.I.R.O. 1992). An open nomenclature is employed, as identification to the lowest taxonomic level is impossible due to the incomplete nature of the specimens. The specimens of Coleoptera lack appendages, including wings and elytra. In some cases only the head and thorax have been recovered. Thus identification must be based primarily upon the emplacement of the coxae and features of the head. No complete specimen of the trichopteran larva has been found. Details are often obscured by debris adhering to the ventral surface which cannot be removed without damage to the specimen. The only myriapod specimens are undifferentiated segments.

The specimens are held in the Queensland Museum, Brisbane, to which the abbreviation QM refers.

Phylum ARTHROPODA
Superclass HEXAPODA Latreille, 1825
Class INSECTA Linné, 1758
Subclass PTERYGOTA Brauer, 1885
Division ENDOPTERYGOTA Sharp, 1899
Order COLEOPTERA Linné, 1758
Suborder POLYPHAGA Emery, 1886
Superfamily CURCULIONOIDEA Latreille, 1802
Family CURCULIONIDAE Latreille, 1802?

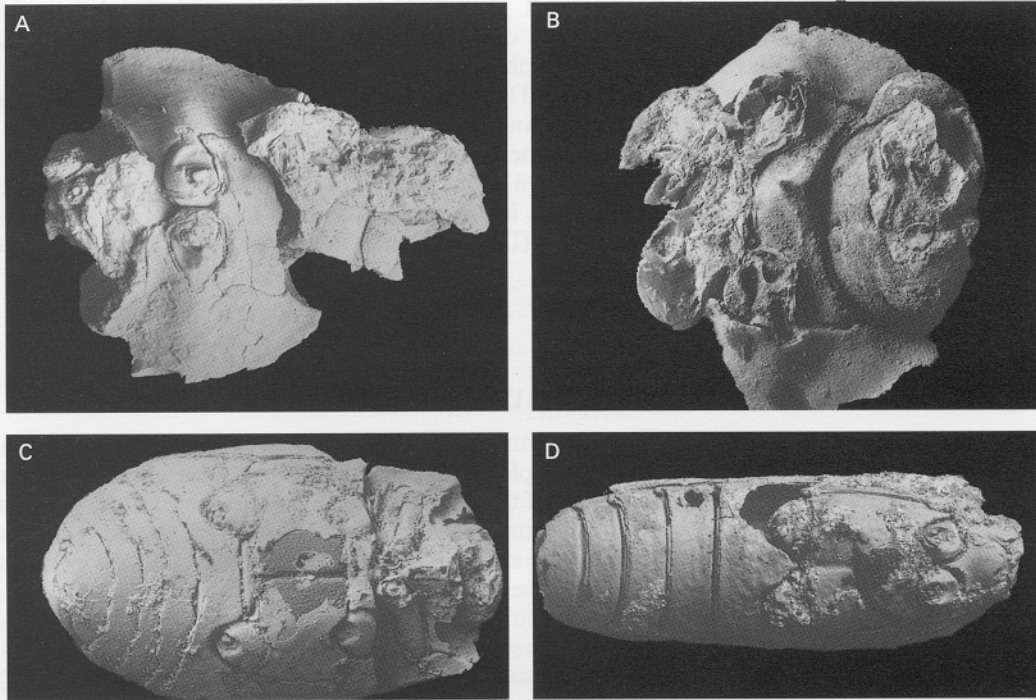Coleopteran species A

Text-figures 6A, I, 8A

Material. QM F16648, QM F34585, incomplete adults with only damaged head and prothorax present.

Description
Head. The head is large and produced forward into a rostrum, which is longer than broad. The compound eyes are large, bulging and situated dorsolaterally at the base of the rostrum.

Thorax. The prothorax is broad, half as long as wide, with gently convex lateral margins. The anterolateral corners of the pronotum project to form protective 'shoulders' about the head. The prosternum is bounded laterally by concave sternopleural sutures. The posterior margin of this plate curves round and between the fore coxae. The first pair of coxae are contiguous and meet along the midline. They are globular in shape and incorporate a lateral facing concavity to accommodate the femur.

Dimensions. Maximum length of head and prothorax: 5 mm.

TEXT-FIG. 8. Coleoptera. A, species A, undetermined curculionid (QM F16648); ×100. B, species B, undetermined polyphagan (QM F34583); ×120. C, species C, undetermined histerid (QM F34582); ×120. D, species D, undetermined ommatid (QM F34595); ×60.

Remarks. This species is referred to Curculionidae on the basis of its stout rostrum, large eyes toward the rostral base and contiguous, projecting, fore coxae. The incompleteness of the specimens prevents a more detailed interpretation.

Superfamily and Family indet.

Coleopteran species B

Text-figures 6B–D, K, 8B

Material. QM F34583, an incomplete adult, with only head and prothorax intact; QM F34586, an incomplete adult, consisting only of the pronotum.

Description. The body is highly convex in cross section.

Head. The head is hooded by the pronotum (Text-fig. 8B) and is all but concealed from above. The anterior margin is gently convex. The large, bulbous compound eyes are ventrolateral in position, and approach the anterior margin (Text-fig. 6K). The mouth is hypognathous.

Thorax. In plan view, the prothorax is a longitudinally elongate semicircle. The anterior margin is convex. On the ventral surface the sternopleural suture of the prosternum runs from the lateral margins of the head to the

coxae of the first limbs. These sutures mark the lateral margins of the prosternum, which is bounded anteriorly by the head and posteriorly by the transverse suture of the mesosternal plate. The plate rises to an elevated process between the first pair of limbs. The sternopleural sutures of the mesothorax form a gently curved semicircular outline. The thorax slopes rapidly from the sternopleural sutures to the lateral margin of the prothorax.

Dimensions. Maximum length of head and pronotum: 5 mm.

Remarks. The specimens show a number of characters that support assignment to the Polyphaga: notopleural sutures are absent on the prothorax, the ventral portion of the notum (hypomeron) is joined directly to the sternum on each side along the notosternal suture, and the pleuron is reduced and concealed. Insufficient detail is preserved to allow a more detailed taxonomic assignment.

Superfamily HYDROPHYLOIDEA Latreille, 1802
Family HISTERIDAE Latreille, 1802

Coleopteran species C

Text-figures 4A–B, 6G, J, 8C

Material. QM F34582, an almost complete adult, with only mid and hind legs missing.

*Description*. The outline of the body is a near perfect oval.

Head. The head is small (less than one-eighth body length) and sub-rectangular in outline, almost half as long as wide. It is sunk deeply into the pronotum and is concealed when viewed from above. The eyes are flattened and occupy the entire lateral margin of the head, approaching the anterior margin (Text-fig. 6J). The mouth is hypognathous.

Thorax. A distinct pronotum, narrower than the meso- and metathorax, hoods the head. When viewed from above it appears rectangular in outline, and extends laterally beyond the head. The outline of the pronotum tapers gently from the posterior to the anterior margin. On the anterior margin of the prosternum is a raised median process which becomes a ridge running the length of the prosternum, decreasing in height as it does so. The first pair of limbs immediately flanks this ridge. The fore coxae, although partially obscured by the encrusted tibia, appear both large and transverse. Fore trochantins appear absent. The pronotum and the mesonotum are united along a transverse suture. The mesosternum is bound laterally by the coxae of the second pair of limbs, which appear to open laterally. Its anterior margin is marked by the boundary between the pronotum and the mesonotum, its posterior by the metasternal transverse anterior suture. The metasternal surface is divided along the midline by the longitudinal suture. Both the fore and hind coxae incorporate a concavity to accommodate the femur.

Abdomen. The abdomen tapers gently posteriorly, forming a rounded pygidium. The elytra are truncate leaving the propygidium and pygidium exposed. There are five ventrites.

Dimensions. Maximum length of beetle: 5 mm.

Remarks. The ovoid body shape, truncate elytra exposing two complete tergites, and head all but concealed by the pronotum, are indicative of superfamilies Hydrophyloidea and Staphylinoidea. A median metasternal suture is unknown in the latter. The separation of the mid-coxae by more than the width of one coxa, and the wider separation of the hind coxae, indicate that the species belongs to the family Histeridae, and not Hydrophilidae.
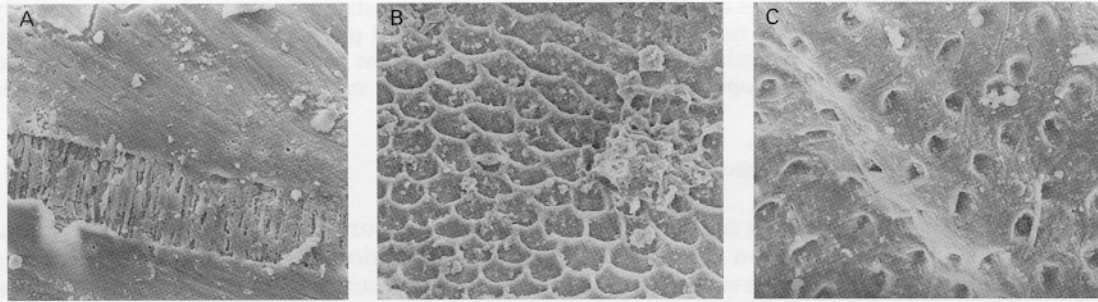
TEXT-FIG. 9. Cuticle and wing of ommatid (coleopteran species D) (QM F34595). A, break in cuticle reveals distinct alignment of microfibrils; ×9000. B, terrace-like pattern of cuticle between wings on ventral surface; ×6000. C, close-up of wing; ×6000.

Suborder ARCHOSTEMATA Kolbe, 1908
Superfamily CUPIDOIDEA Latreille, 1802
Family OMMATIDAE Newman, 1839

Coleopteran species D

Text-figures 7D, 8D, 9A–C

Material. QM F34595, an almost complete adult, missing head and prothorax, with the wings covering much of the dorsal surface of the body (Text-fig. 8D).

Description
Thorax. The lateral margins of the mesothorax are parallel for much of their length, but begin to converge gently towards the anterior. The mesothoracic coxae are contiguous, globular in shape, with a posterior-facing concavity. A median suture divides the metasternum. The meta-coxae are also globular and adjoin the anterior margin of the metasternum, the margin of which curves between and around them. The lateral metasternal sutures diverge gently from the mesothoracic coxae, so that the metasternum increases in width posteriorly. The metathoracic coxae are larger than the mesothoracic but are not contiguous. The cuticle displays distinct lineation (Text-fig. 9A).

The dorsal surface is almost entirely shrouded by the exposed hind wings. They slope from the anterior 'shoulders' toward the midline. The gap separating them decreases in width posteriorly. It extends one-quarter of the length of the thorax, at which point the wings meet. The cuticle within the gap displays a distinct terracing (Text-fig. 9B). At the anterior margin is a small pinnacle, posterior of which is a narrow ridge which runs the length of the gap.

The remains of the wings shrouding the dorsal surface show traces of venation (Text-fig. 9C), but the detail is obscured by a coating of mineralized bacteria (Text-fig. 7D).

Abdomen. The abdomen consists of five segments, and has a distinct blunt appearance, the lateral margins tapering gently to a rounded pygidium. The first ventrite, which is the largest, curves around and between the metathoracic coxae. The other four are smaller, and all are of similar length.

Dimensions. Maximum length of specimen, 7 mm.

Remarks. This species is assigned to the suborder Archostemata on the basis of the metathoracic trochantins. The presence of five ventrites indicates that the species belongs to either Cupedidae or Ommatidae. The lack of grooves on the ventral surface to accommodate the legs precludes assignment to the former, and indicates that this species belongs to the latter.
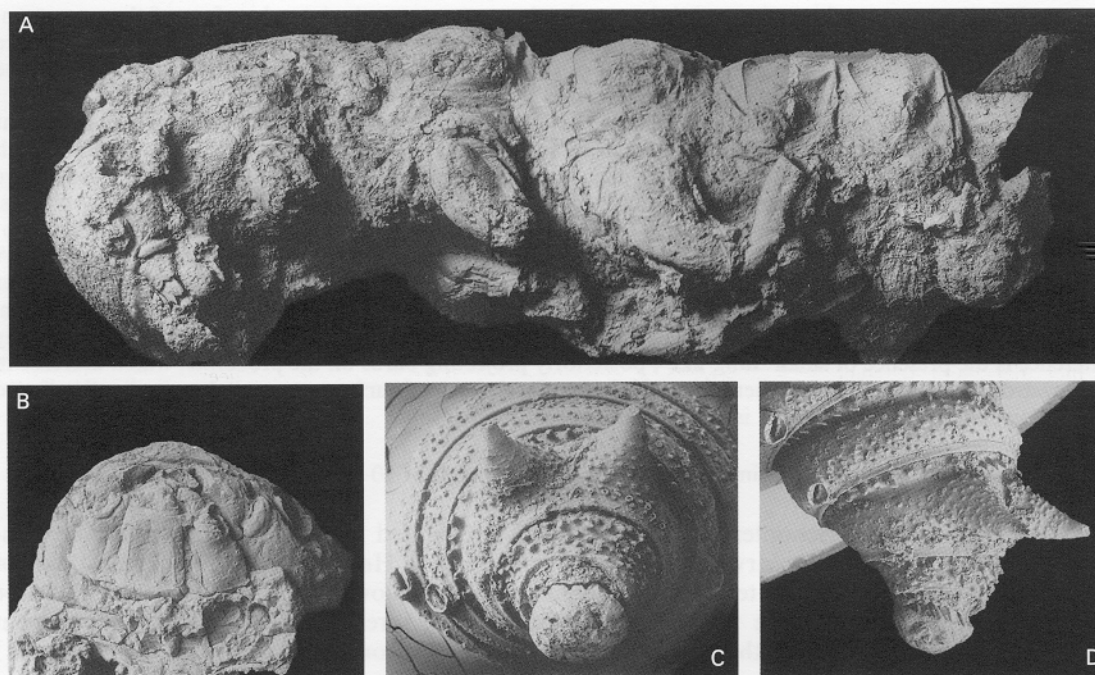
TEXT-FIG. 10. Trichopteran larva. A, composite image of head, thorax and upper abdomen (QM F34587); × 80. B, ventral view of head (QM F34593); × 100. C–D, tail assemblage (QM F34594); × 140.

Order TRICHOPTERA Kirkby, 1815

Superfamily and Family indet.

Text-figures 2A–D, 3A–F, 5A–B, 6F, H, 10A–D

Material. QM F34584, QM F34587–QM F34594, all of which are incomplete larval stages.

Description. In cross section the dorsal surface is strongly curved, whilst the ventral surface is flattened.

Head. The head is globular in shape with a slightly flattened anterior margin, and is broader than long. It is marked by two large ventrolateral antennal sockets, which protrude downwards. The scape of the antenna is large, and circular in cross section. The lateral epicranial sutures arise at the posterior margins of the head, pass around the sockets of the antennae on the lateral side and converge to form the median suture. The general outline of the suture is that of an inverted 'Y'. The epicranium is patterned by a random arrangement of setae emplacements. Five ocelli form a semicircle about a central ocellus towards the anterior margin of the head. The clypeal region, which is divided into two equal segments, is slightly produced and evenly convex over the entire margin. The sutura frontoclypealis is dorsally convex. The labrum is short and gently tapered. The mandibles are curved and opposable with a double saw-toothed edge. The ventral surface of the cranium is covered by a bilaterally symmetrical labium. Flanking this is a pair of gently convex maxillae (Text-fig. 10B). Anterior to this, also flanking the labium, is a small, flattened eye of 'schizochroal'-type (Text-fig. 6F, H).

Thorax. The thorax consists of three segments, with the pronotum being the largest (Text-fig. 10A). All are much wider than long, with the cuticle of the dorsal surface more heavily sclerotized than that of the ventral surface and the abdomen. There is a distinct ridge around the periphery of the pronotum. There are three distinct units to each tergite. The anterior prescutum (Text-fig. 3A) is relatively narrow but increases in thickness dorsally, forming a 'saddle-like' feature and patterned by an irregular arrangement of pits (Text-fig. 3B). The scutum, the largest of the three units, is patterned by a random arrangement of raised setae emplacements. The posterior scutellum is wider than the prescutum, although similarly patterned (Text-fig. 3C). The scutellum of each segment overlies the prescutum of that behind. The individual tergites are

separated by intersegmental membranes. A large spiracle is present on the lateral surface of the pronotum. There is a slight bulging of each segment laterally, just above the first pair of limbs. The limbs themselves are robust and decrease in size posteriorly. The base of each is protected by a coxal collar (Text-fig. 3D). The adjacent arthrodial membrane is distinctly patterned (Text-fig. 3E–F).

Abdomen. The abdomen bears at least nine tergites, although no complete specimen exists. There is a slight swelling of the abdomen about the fifth-last tergite and it tapers gently posterior to this. The scutellum of each tergite overlaps the prescutum of the following one, as with the thorax. The last few tergites have a distinctive appearance, the penultimate segment bearing two posteriorly projecting conical 'horns', or terminal prolegs, which are fused to the dorsal surface (Text-fig. 10C–D). The final tergite terminates in a hemispherical 'bulb' (although this may be an extrusion of internal tissue, since this 'bulb' is absent from a second specimen). A tube-like spiracle projects posteriorly from the ventral surface of each abdominal somite, although poor preservation prevents confirmation that such a spiracle is present on segment 1. The cuticle of the abdomen, including that of the tergite with the 'horns', is ornamented in a similar fashion to the thorax. The only difference is the presence of small 'fang-like', posteriorly projecting barbs on the prozonite, which decrease in size towards the ventral surface, where they are absent. On the ventral surface are small, longitudinally aligned setae. However, their arrangement is obscured by encrusting material.

Dimensions. Almost complete specimens suggest an overall length of 50–70 mm.

Remarks. The orders Trichoptera and Lepidoptera are united in the informal rank Amphies-menoptera. Accordingly, the larvae possess many similarities. However, the presence of a pair of projecting conical 'horns', or terminal abdominal prolegs, allows the Riversleigh species to be assigned with some confidence to the order Trichoptera. More detailed taxonomic assignment would require information on the position of setae or spicules on the abdomen.

<div align="center">

Class MYRIAPODA Latreille, 1796
Order JULIDA Brandt, 1833

Family indet.

</div>

Material. QM F34596 (two specimens), mid sections of the trunk composed of four and five segments respectively.

Description. The trunk consists of a number of leg-bearing rings. The sclerites of each ring are fused together and to the pleurotergal arch to form a completely cylindrical sclerite (Monozonian condition). The prozonite of one ring is overlapped by the metazonite of that preceding it. The two zonites are separated by a distinct suture. Each ring carries two pairs of limbs and constitutes a diplosegment. The coxal openings are small and project laterally. The limbs are slender.

Dimensions. Length of single ring 3 mm, diameter 4 mm.

Remarks. The presence of only disarticulated segments precludes assignment beyond the level of suborder.

provided by E. N. K. Clarkson, P. R. Wilby and A. C. Neville. E. A. Jarzembowski and P. Hammond reviewed an earlier draft. Additional SEM assistance was provided by Chris Jones of The Natural History Museum (London). IJD is a NERC research student.

REFERENCES

ALLISON, P. A. 1988. Taphonomy of the Eocene London Clay biota. *Palaeontology*, **31**, 1079–1110.

ARCHER, M. and BARTHOLOMAI, A. 1978. Tertiary mammals of Australia: a synoptic review. *Alcheringa*, **2**, 1–19.

—— and CLAYTON, G. (eds). 1984. *Vertebrate zoogeography and evolution in Australasia*. Hesperian Press, Perth, 136 pp.

—— GODHELP, H., HAND, S. J. and MEGERIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist*, **25**, 29–65.

—— HAND, S. J. and GODHELP, H. 1994a. *Riversleigh, the story of animals in ancient rainforests of inland Australia*. Second edition. Reed Books, Chatswood, NSW, 264 pp.

—— —— —— 1994b. Patterns in the history of Australia's mammals and inferences about palaeohabitats. 80–103. *In* HILL, R. (ed.). *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, 340 pp.

—— —— —— 1995. Tertiary environmental and biotic change in Australia. 77–90. *In* VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. and BURCKLE, L. H. (eds). *Paleoclimate and evolution, with emphasis on human origins*. Yale University Press, New Haven, 265 pp.

BAIRD, G. C., SROKA, S. C., SHABICA, C. W. and BEARD, T. L. 1985a. Mazon Creek-type fossil assemblages in the U.S. midcontinent Pennsylvanian: their recurrent character and paleoenvironmental significance. *Philosophical Transactions of the Royal Society, Series B*, **311**, 87–99.

—— SHABICA, C. W., ANDERSON, J. L. and RICHARDSON, E. S. Jr 1985b. The biota of a Pennsylvanian muddy coast: habitats within the Mazonian Delta Complex, northeastern Illinois. *Journal of Paleontology*, **59**, 253–281.

BOLTON, H. 1905. Notes on the geological horizon and palaeontology of the 'Soapstone Bed' in the Lower Coal Measures, near Colne, Lancashire. *Geological Magazine*, (5), **2**, 433–444.

BOULIGAND, Y. 1965. Sur une architecture torsadée répandue dans de nombreuses cuticules d'arthropodes. *Compte rendu hebdomadaire des séances de l'Académie des Sciences, Paris*, **261**, 3665–3668.

BRANDT, X. 1833. Ueber die inder Regentschaft Algier beobachteten Myriopoden. *In* WAGNER, M. (ed.). *Alger III*. Leopold Voss, Leipzig, 135 pp.

BRAUER, F. 1885. Systematische-zoologische Studien. *Sitzungsberichte der (K.) Akademie der Wissenschaften in Wien, mathematische-naturwissenschaftlichen Klasse*, **91**, 237–431.

BRIGGS, D. E. G. and KEAR, A. J. 1994. Decay and mineralization of shrimps. *Palaios*, **9**, 431–456.

BRITTON, E. B. 1960. Beetles from the London Clay (Eocene) of Bognor Regis, Sussex. *Bulletin of the British Museum, Natural History (Geology)*, **4**, 27–50.

CLARKSON, E. N. K. 1979. The visual system of trilobites. *Palaeontology*, **22**, 1–22.

COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANIZATION (C.S.I.R.O) 1992. *The insects of Australia*. Melbourne University Press, Melbourne, 1029 pp.

DONOVAN, S. K. and VELTKAMP, C. J. 1994. Unusual preservation of late Quaternary millipedes from Jamaica. *Lethaia*, **27**, 355–362.

DUNCAN, I. J. and BRIGGS, D. E. G. 1996. Three-dimensionally preserved insects from the Tertiary of Riversleigh, Australia. *Nature*, **381**, 30–31.

EMERY, C. 1886. Ueber Phylogenie und Systematik der Insekten. *Biologisches Zentralblatt*, **5**, 648–656.

GRIMALDI, D. A., BONWICH, E., DELANNOY, M. and DOBERSTEIN, S. 1994. Electron microscope studies of mummified tissues in amber fossils. *American Museum Novitates*, **3097**, 1–31.

HANDSCHIN, E. 1944. Insekten aus den Phosphoriten des Quercy. *Schweizer Paläontologische Abhandlungen*, **64**, 1–23.

HELLMUND, M. and HELLMUND, W. 1996. Phosphoritisierte Insekten- und Annelidenreste aus der mitteloligozänen Karstpaltenfüllung 'Ronheim 1' bei Harburg (Bayern, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde, Series B*, **241**, 1–21.

HENWOOD, A. 1992. Exceptional preservation of dipteran flight muscle and the taphonomy of insects in amber. *Palaios*, **7**, 203–212.

—— 1993 Recent plant resins and the taphonomy of organisms in amber: a review. *Modern Geology*, **19**, 35–59.

HEYLER, D. 1980. Fossiles du Stephanian de Montceau-les-Mines (France). *Bulletin du Société Histoire Naturelle, Autun*, **94**, 3–6.

HORVÁTH, G. and CLARKSON, E. N. K. 1993. Computational reconstruction of the probable change of form of the corneal lens and the maturation of optics in the post-ecdysial development of the Devonian Trilobite *Phacops rana milleri* Stewart 1927. *Journal of Theoretical Biology*, **160**, 343–373.

———— and PIX, W. 1997. Survey of modern counterparts of schizochroal trilobite eyes: structural and functional similarities and differences. *Historical Biology*, **12**, 229–264.

JARZEMBOWSKI, E. A. 1980. Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bulletin of the British Museum, Natural History (Geology)*, **33**(4), 237–293.

JELL, P. A. and DUNCAN, P. M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Gp), South Gippsland, Victoria. *Memoir of the Association of Australasian Palaeontologists*, **3**, 111–205.

JOHNSON, R. G. and RICHARDSON, E. S., Jr 1966. A remarkable Pennsylvanian fauna from the Mazon Creek area, Illinois. *Journal of Geology*, **74**, 626–631.

KINZELBACH, R. 1967. Zur Kopfmorphologie der Fächerflügler (Strepsiptera, Insecta). *Zoologische Jahrbücher Anatomie*, **84**, 559–684.

KIRKBY, W. 1815. *An introduction to entomology.* Longman, London, 512 pp.

KOLBE, H. J. 1908. Mein System der Coleopteran. *Zeitschrift für wissenschaftliche Insektbiologie*, **4**, 116–123.

LATREILLE, P. A. 1802. *Histoire naturelle, générale et particulière, des crustacés et des insectes.* 3. Dufart, Paris, 467 pp.

———— 1825. *Familles naturelles du régne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genre.* Dufart, Paris, 570 pp.

LEAKEY, L. S. B. 1952. Lower Miocene invertebrates from Kenya. *Nature*, **169**, 1020–1021.

———— 1963. Adventures in the search for man. *National Geographic*, **123**(1), 132–152.

LINNÉ, C. von 1758. *Systema Naturae Regna Tria Naturae: secundum classes, ordines, genera, species, cum characteribus differentiis synonymis, locis.* 10th edition, revised. Laurentius Salvius, Holmiae, 824 pp.

MARTILL, D. M. 1988. Preservation of fish in the Cretaceous of Brazil. *Palaeontology*, **31**, 1–18.

MEGERIAN, D. 1992. Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. *The Beagle*, **9**, 219–248.

MILLER, S. E. 1983. Late Quaternary insects of Rancho La Brea and McKittrick, California. *Quaternary Research*, **20**, 90–104.

MILLS, J. S., WHITE, R. and GOUGH, L. J. 1984. The chemical composition of Baltic amber. *Chemical Geology*, **47**, 15–39.

NEVILLE, A. C. 1970. Cuticle ultrastructure in relation to the whole insect. 17–39. *In* NEVILLE, A. C. (ed.). *Insect ultrastructure.* Symposium of the Royal Entomological Society of London, 5.

———— THOMAS, M. G. and ZELAZNY, B. 1969. Pore canal shape related to molecular architecture of arthropod cuticle. *Tissue and Cell*, **1**, 183–200.

NITECKI, M. H. (ed.) 1979. *Mazon Creek fossils.* Academic Press Inc., New York, 581 pp.

PALMER, A. R. 1957. Miocene arthropods from the Mojave desert, California. *Professional Papers of the U.S. Geological Survey*, **294**, 237–80.

PARK, L. E. 1995. Geochemical and paleoenvironmental analysis of lacustrine arthropod-bearing concretions of the Barstow Formation, southern California. *Palaios*, **10**, 44–57.

PAULUS, H. F. 1979. Eye structure and the monophyly of the Arthropoda. 299–383. *In* GUPTA, A. P. (ed.). *Arthropod phylogeny.* Van Nostrand Reinhold, New York, 330 pp.

POINAR, G. O. Jr 1992. *Life in amber.* Stanford University Press, Stanford, California, 349 pp.

———— and HESS, R. 1982. Ultrastruture of 40-million-year-old insect tissue. *Science*, **215**, 1241–1242.

RICHARDSON, E. S. Jr 1956. Pennsylvanian invertebrates of the Mazon Creek area, Illinois. *Fieldiana Geology*, **12**, 1–76.

RIEK, E. F. 1954. A re-examination of the Upper Tertiary mayflies described by Etheridge and Olliff from the Vegetable Creek tin-field. *Records of the Australian Museum*, **23**, 159–160.

———— 1967. Further evidence of Panorpidae in the Australian Tertiary (Insecta: Mecoptera). *Journal of the Australian Entomological Society*, **6**, 71–72.

———— 1970a. Fossil history. 168–187. *In* C.S.I.R.O. Division of Entomology. *The Insects of Australia.* 3rd edition. Melbourne University Press, Carlton, Victoria.

———— 1970b. Origin of the Australian insect fauna. *Second Gondwana Symposium – 1970*, 593–598.

RUNDLE, A. J. and COOPER, J. 1971. Occurrence of a fossil insect larva from the London Clay of Herne Bay, Kent. *Proceedings of the Geologists' Association*, **82**, 293–295.

SEILACHER, A., REIF, W.-E. and WESTPHAL, F. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London, Series B*, **311**, 5–23.

SHARP, D. 1899. Some points in the classification of the Insecta Hexapoda. *In Proceedings of the fourth International Congress of Zoology, Cambridge, England*, 246–249.

SNODGRASS, R. E. 1935. *Principles of insect morphology*. McGraw Hill, New York, 667 pp.

STANKIEWICZ, B. A., BRIGGS, D. E. G., EVERSHED, P. R. and DUNCAN, I. J. 1997. Chemical preservation of the insect cuticles from the asphalt deposits of California. *Geochimica et Cosmochimica Acta*, **61**, 2247–2252.

STOCK, C. H. 1992. *Rancho La Brea. A record of Pleistocene life in California*. Natural History Museum of Los Angeles County, Science Series, 37. 79 pp.

TALBOT, P. H. B. 1971. *Principles of fungal taxonomy*. Macmillan, London, 274 pp.

TEDFORD, R. H. 1967. Fossil mammal remains from the Tertiary Carl Creek Limestone, northwestern Queensland. *Bulletin of the Bureau of Mineral Resources, Australia*, **92**, 217–36.

WOODLAND, B. A. and STENSTROM, R. C. 1979. The occurrence and origin of siderite concretions in the Francis Creek Shale (Pennsylvanian) of northeastern Illinois. 69–104. *In* NITECKI, M. H. (ed.). *Mazon Creek fossils*. Academic Press Inc., New York, 581 pp.

WOODWARD, H. 1907. Further notes on the Arthropoda of the British Coal Measures. *Geological Magazine*, (5), **4**, 539–549.

WUTTKE, M. 1983. 'Weichteil-Erhaltung' durch lithizierte Mikroorganismen bei mitteleozänen Vertebraten aus den Ölschiefern der 'Grube-Messel' bei Darmstadt. *Senckenbergiana Lethaea*, **64**, 509–527.

IAN J. DUNCAN

DEREK E. G. BRIGGS

Department of Earth Sciences
University of Bristol
Wills Memorial Building
Queen's Road
Bristol BS8 1HQ, UK
e-mail ian.j.duncan@bristol.ac.uk
D.E.G.Briggs@bristol.ac.uk

MICHAEL ARCHER

Vertebrate Palaeontological Research
Laboratory
School of Biological Sciences
University of New South Wales
Sydney 2052, Australia