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A SIGNIFICANT LATE TRIASSIC LAGERSTAETTE FROM VIRGINIA, U.S.A.

Introduction.

The nature of faunal turnover at the end of the Triassic has been the subject of much debate. Important changes have been recognized both for the marine and non-marine realms (e.g. Hallam 1981; Benton 1991). For the marine both invertebrate and vertebrate records have been included in the analyses, but significantly the main analyses of terrestrial faunal changes at the end of the Triassic have been restricted to vertebrates. This is for the most part due to the limited occurrences and documentation of terrestrial invertebrates, particularly insects.

An exceptionally large part of the fossil record of insects is restricted to lagerstätten, and Labandeira and Sepkoski (1993) noted that there is an uneven temporal distribution of such rich insect-bearing deposits. For instance insect diversity appears to sharply increase in the Upper Jurassic, and likewise in the Middle Tertiary. However Labandeira and Sepkoski believe these diversity spikes are artificial, and result from the occurrence of one or two incredibly rich and exceptionally well known insect assemblages for those particular instances in geologic history. In other words a dearth of insect-producing sites in the Cretaceous has given the false impression of low insect diversities which have been further exaggerated by excellent lagerstätten from the preceding and succeeding time intervals. Labandeira and Sepkoski believe that as older ambers and compression fossils are studied further, then many families first represented in the Tertiary will have their ranges extended back to the Mesozoic, thereby flattening out these sharp rises in diversity. Likewise, although peaks in fossil insect diversity during the Late Carboniferous and middle Permian were noted by Labandeira and Sepkoski (1993), they considered the diversity minimum between these two peaks to be artifactual. Moreover Labandeira and Sepkoski (1993) showed that there is a relatively low extinction rate among insect families, and consequently it is theoretically possible to trace families from one lagerstätten to another, which in turn should provide a reasonably continuous record of insect diversity.

By contrast, Labandeira and Sepkoski (1993) suggested that the apparent low diversity levels of insects during the Triassic could reflect a real phenomenon. They invoked the end Permian mass extinction as a possible cause of the apparent paucity of Triassic insects.

The Distribution of Triassic Insect Localities

For a long time the only areas in the world for which there were any detailed descriptions of Triassic insects pertained to a few localities in New South Wales and Queensland,

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Australia (e.g. Tillyard 1918, 1921; Riek 1954, 1955) and Kirghizistan and Kazakhstan (Martynov 1958; Rohdendorf 1961; Sharov 1968).

In the last thirty years additional rich terrestrial invertebrate assemblages have been documented from the Triassic of the Vosges, France, (e.g. Gall 1996 and papers therein), the Molteno Formation, South Africa (Anderson and Anderson 1970, 1993; Anderson et al. 1996) and the Newark Supergroup, U.S.A. (Olsen et al. 1978; Fraser et al. 1996), but until very recently there were no published details of any of these three assemblages (and there were consequently insufficient details available on these particular assemblages for Labandeira and Sepkoski's study). Interestingly it is the putatively depauperate Newark Supergroup that is yielding significant data suggesting a very different picture of Late Triassic insects, and one particular assemblage is examined here.

The Virginia Solite Quarry

The Solite Quarry in the Dan River basin of the Newark Supergroup contains excellent exposures of the Cow Branch Formation. They consist of a series of lacustrine deposits showing cyclical changes in depth that were apparently under the control of variations in the earth's orbit (Milankovitch cycles) (Olsen et al. 1978, Olsen 1986).

Fossils, including insects, were first reported from the Quarry by Olsen et al.(1978). Consisting of black shales the richest strata are microlaminated units showing no evidence of bioturbation. These have been interpreted as "deep" lake deposits (Olsen et al. 1978; Olsen et al. 1989, etc.).

However based on geochemical evidence, such an interpretation has been questioned for similar deposits elsewhere in the Newark Supergroup (Niemitz and Cox 1996). A paucity of quartz in the main insect-bearing units is indicative of alkaline conditions. Furthermore, the abundance of conchostracans, which today are commonly found in ephemeral lakes in arid environments, is also perhaps suggestive of alkaline conditions at the time of deposition.

The Diversity of the Solite Insects

The insects (Fig. 1), are preserved as two-dimensional, carbonaceous images. Microscopic details are preserved with remarkable fidelity so that even microtrichia (approximately 1μm long) are sometimes present. Furthermore color patterns are preserved on some specimens. As incredible as it now seems, Meyertons (1963) considered the deposits to be unfossiliferous.

Any analysis of biogeographic correlations is going to be strongly biased towards those deposits that are very productive. In this case, comparison of the Solite fauna is slanted to either the rich Russian, French or Australian deposits. As one might expect, due simply to geographic proximity, the Solite fauna would seem to be related to insect faunas from the Triassic and Jurassic of Europe and Russia. Initial observations indicate that connections with the forms from the Jurassic of Germany and Kazakhstan are the Boholdoyidae, Elcanidae, Locustopsidae, Procramptonomyiidae, and Staphylinidae. Connections with the Triassic of Russia are the Locustopsidae, and Schizophoridae. During the Carnian, the continents of Eurasia, North and South America, and Africa were largely contiguous. India and Antarctica were contiguous with eastern Africa, and Australia lay isolated on Antarctica's northeastern shelf. No doubt as a result of this geological isolation of

Australia, even in the late Triassic faunal provinces were manifest that distinguished Laurasia from Gondwana. Nevertheless, the dipteran *Crosaphis* is common to Australia and the Solite Quarry, and it is interesting to note the presence of the seed genus *Fraxinopsis* in the Solite Quarry, and in the Molteno, South Africa and the Ipswich Series, Australia (Axsmith et al. 1997).

Out of approximately 21 insect families from the Solite Quarry fossils, 15 can be identified with certainty, and seven (almost 50%) of those are extant families. At the very least, one third of the families from this deposit are extant. By contrast Labandeira and Sepkoski (1993: fig. 3) reported only 5% to 20% of the insect families in the Triassic as a whole being extant. If the Solite insect fauna does indeed contain a higher proportion of living families than in other deposits, this would imply that the stasis of insect clades is greater than previously hypothesized.

Other Arthropods

In addition to the insects, crustaceans, conchostracans, and spiders have been recorded from the deposits. Conchostracans are particularly abundant, and consist of at least two genera. However the only crustacean is represented by a rather poorly preserved portion of the abdomen, and to date only two specimens of spiders are known, neither of which clearly preserves the body.

Vertebrates

A partial skeleton of a most unusual new form of gliding reptile has recently been recovered. Although not yet prepared, the specimen clearly shows elongated thoracic ribs which presumably supported a gliding membrane, and in this respect it is very reminiscent of *Icarosaurus, Kuehneosaurus* and *Coelurosauravus*.

However unlike *Icarosaurus* and *Kuehneosaurus* the new form has an elongate neck and lacks the elongated transverse processes on the thoracic vertebrae, and consequently the thoracic region is remarkably slender. The posterior part of the animal is missing, but a second rather poorly defined specimen, that is complete posteriorly, is probably referable to the same taxon.

The prolacertiform reptile, *Tanytrachelos ahynis* was first described from the Solite Quarry by Olsen (1979).The closest relatives of *Tanytrachelos* are *Tanystropheus* from the Middle Triassic of Italy and Switzerland (Wild 1973) and *Langobardisaurus* from the Norian of Italy (Renesto 1994). An in depth cladistic analysis of *Tanytrachelos*, *Tanystropheus, Langobardisaurus,* and other prolacertiforms, using a variety of archosauromorphs as outgroups, is in progress.

There are a variety of fishes represented by articulated material, including a giant coelacanth, semionotids and redfieldiids, plus fragments of sharks (spines and teeth).

Plants

A diverse flora is preserved in the Solite sediments, including gymnosperms, cycadeoids, ginkgophytes and ferns. The variety of seeds and ferns are particularly notable. Conifers are very common and are represented by cones and foliage shoots. They include *Pagiophyllum*, *Brachyphyllum*, *Podozamites*, *Compsostrobus*, and *Hirmeriella*. Bennettitaleans include *Pterophyllum*, *Zamites*, and *Sphenozamites*.

Trace Fossils

While the beds producing the insects and the majority of the reptiles show no indication of bioturbation, high up in each cycle a variety of invertebrate traces, including burrows, and tetrapod footprints can be found. The latter include *Rhynchosauroides*, *Gwyneddichnium*, *Grallator* and *Atreipus* (Olsen and Baird 1984). Recently, new trackways, including a possible new dinosaur ichnotaxon, have come to light as the active quarry has been expanded.

Coprolites and gastric ejecta are very abundant in the fish-producing strata, and sometimes contain conchostracans and fish bone.

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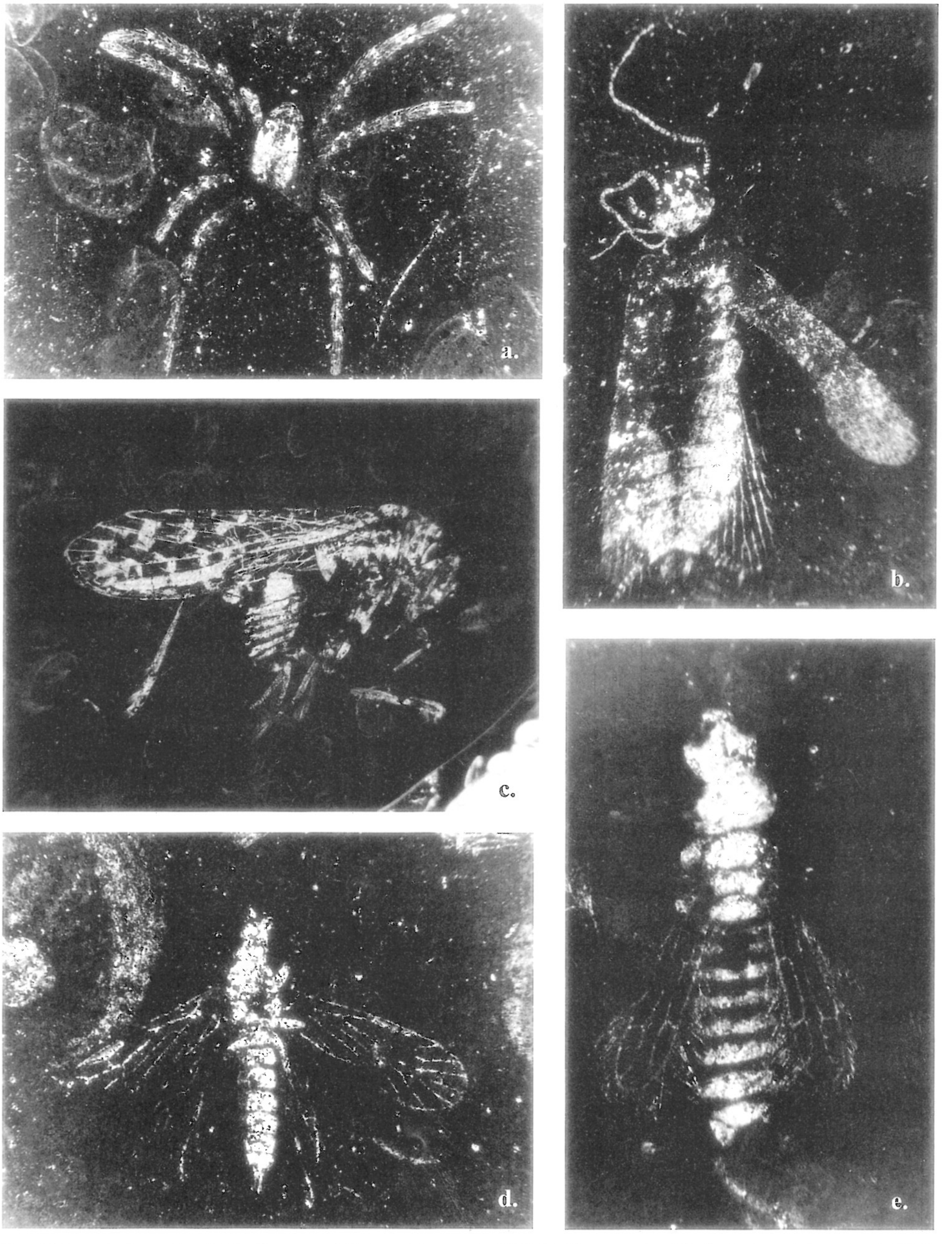

Fig. 1) Insects from the Solite Quarry. a) Spider (Araneae) X10. b) Cockroach ([Blattodea] undetermined) X17. c) Orthoptera s.s.: Elcanidae X7. d) Sternorrhyncha?: Archaescytinidae X15. e) Thysanoptera (thrips) X25.