

A Triassic Lagerstätte from eastern North America

Nicholas C. Fraser*, David A. Grimaldi†, Paul E. Olsen‡ & Brian Axsmith§

* Virginia Museum of Natural History, 1001 Douglas Avenue, Martinsville, Virginia 24112, USA

† American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA

‡ Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964, USA

§ Department of Botany, University of Kansas, Lawrence, Kansas 66045, USA

THE end of the Triassic period is pivotal in the evolution of modern ecosystems¹. Despite this, the Triassic remains one of the poorest known periods in the evolutionary history of the terrestrial arthropods. Here we report on fossiliferous shales preserving a nearly complete marginal lacustrine community from the Virginia–North Carolina border that sheds considerable light on this critical interval. Three species of insect were previously described from this locality, but the full extent and significance of its diversity have only now been discovered: we report here the oldest definitive records for three orders of insect and numerous families and superfamilies. Furthermore, in addition to new taxa, the flora is shown to contain an unusual diversity of forms, some of which have only been previously reported either from Europe or the Southern Hemisphere. The abundance of complete insects and the preservation of soft-part anatomy on some of the vertebrates elevates the site to one of the most significant Lagerstätte in the world.

A series of markedly cyclical lacustrine sediments of the Carnian Cow Branch Formation are exposed at the Solite Quarry, Cascade, Virginia, USA² (Fig. 1), and these are fossiliferous throughout. The cycles are thought to represent periodic changes in lake depth under the control of known variations in the Earth's orbit (Milankovitch cycles)³. The sediments deposited in the shallowest water contain footprints and abundant plant fragments, together with mud cracks and ripple marks. However, the richest horizons are microlaminated, organic-rich shales deposited in the deepest water, and it is in these sediments that a great diversity of insects has been found. Articulated remains of the tanystropheid reptile, *Tanytrachelos*, complete with impressions of soft tissue, also occur in these horizons, together with the best preserved plant remains.

Although over 30 cycles are exposed in the two main quarries, one cycle has proved to be particularly productive and most of the insects have been recovered from a thin band of microlaminated sediments at the base of this unit. Nevertheless, at least three other cycles have yielded insect remains. The depositional environment has been interpreted as a chemically stratified (meromictic) lake with a well-oxygenated epilimnion but an anoxic hypolimnion⁴. The anoxic bottom waters would have been largely devoid of life, as evidenced by the lack of bioturbation and decay. The matrix is an exceptionally fine-grained black shale, and the insects are preserved as two-dimensional silvery images. Microscopic details are preserved with great fidelity and the resolution of preserved detail is ~1 µm. Even microtrichiae on the body and wings of insects 2 mm long are sometimes preserved.

A complete list of the insect groups represented in the Solite assemblage is given in Table 1b. The most abundant insects are aquatic heteropterans (water bugs). Two families, the Belostomatidae and the Naucoridae, are

represented by numerous nymphal and adult specimens (Fig. 2a). These are the oldest definitive records of nepomorph Heteroptera, which include many of the predatory aquatic Heteroptera.

After the water bugs, auchenorrhyncans (leaf-hoppers) are the most common order of insect in the assemblages. Typically the wing venation in the new specimens (Fig. 2b) most closely resembles the Archescytinidae, which is known from the Permian period of Kansas, Russia and New South Wales. Two isolated wings exhibit a very unusual venation (Fig. 2c), which by elimination are considered most likely to belong to auchenorrhyncans.

A single specimen of Thysanoptera (thrips) (Fig. 2d, e) preserves short wings that end at the anterior margin of the penultimate tergite. Marginal fringes are present on both the forewings and hindwings. *Pemthrips longipennis* has been described as the oldest thrips⁵, but this referral is based purely on the body form and wing shape. In *Pemthrips*, the wings extend well beyond the apex of the abdomen and they lack the fringed margins—conditions not found in any modern thrips. Consequently, the Solite thrips is the oldest definitive specimen in this order. Furthermore, the next oldest thysanopteran, *Liassothrips crassipes*, from the Jurassic period of Russia, is very poorly preserved⁶: the wings are missing or it may even be a nymph. The only other well-preserved Mesozoic thysanopteran occur in Aptian (Lower Cretaceous) amber from Lebanon⁷.

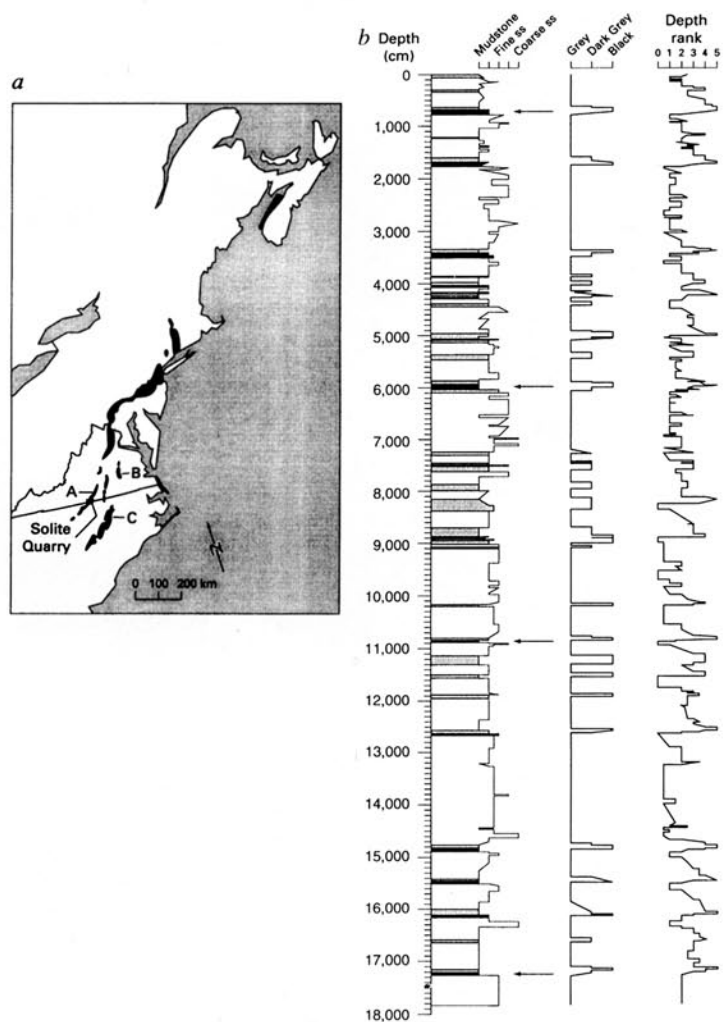


FIG. 1 a, Map showing the Triassic basins of the Newark Supergroup and the Solite Quarry. A, Dan River/Danville basin; B, Richmond basin; C, Deep River basin. b, Geological section through the first of the two main quarries. Arrows indicate cycles known to produce insect remains.

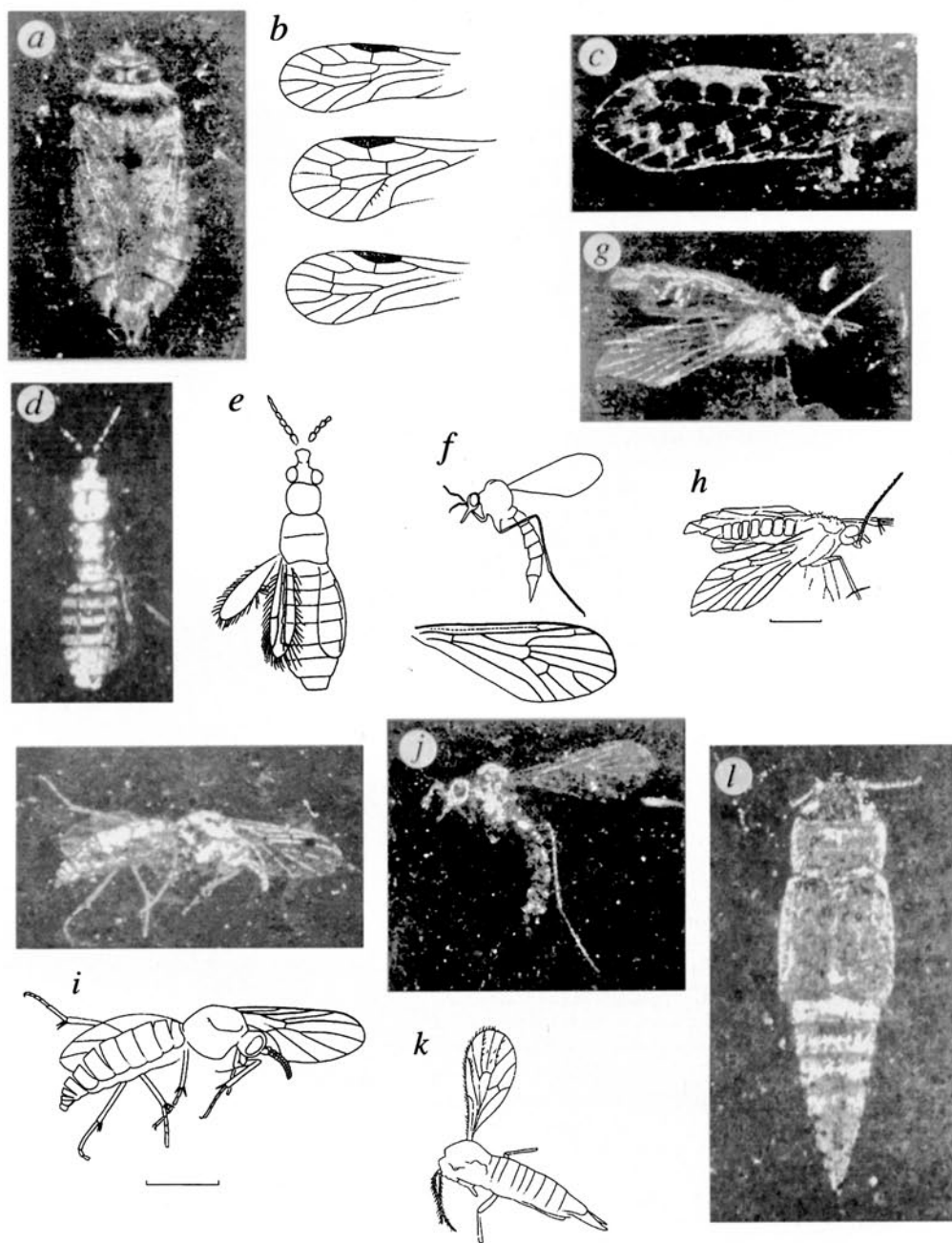
A single complete specimen of a trichopteran (caddis-fly) is known from the Solite assemblage (Fig. 2g, h). Although trichopteran have been described from the Permian and Triassic of Russia⁸, in none is the body as well preserved as the present specimen, and the wing venation of those is considerably more primitive than the new form and later Mesozoic taxa.

The oldest definitive dipteran (fly) is from the Lower/Middle Triassic of France⁹, but the dipterans in the Solite assemblage constitute the next oldest record of this order, and are very diverse, with at least six families represented. Three of these were recognized in the original material collected from the quarry in the 1970s (ref. 10), although their precise referrals need to be revised. For instance, Krzeminski¹⁰ placed *Alinka* in

the Brachycera, but the wing venation is actually characteristic of the Bibionomorpha (March flies), and only nematocerous flies have been identified so far. Tipulids have the oldest fossil record of all the dipteran families, which may reflect their status as the sister group to all other flies. They are represented in the Solite assemblage by excellent specimens of *Architipula youngi* (Fig. 2f, j).

Of the new material, a particularly important find is of two individuals of *Crosaphis*, which was originally described from an isolated wing from the upper Triassic of Australia¹¹. There has been considerable uncertainty concerning the ordinal assignment of *Crosaphis*. First described as an aphidoid hemipteran¹¹, then referred to the coccoids (scale insects) by Heie¹² and the Diptera by Kovalev¹³, these referrals did not receive wide acceptance

FIG. 2 Insects from the Solite assemblage. a, One of the numerous belostomatid specimens (VMNH 727), magnification $\times 4.6$. Like living belostomatids, the Solite belostomatids have hind tarsi with a fringe of setae and coriaceous forewings. The forewings differ from modern forms, however, by the intricate, reticulate wing venation: the most primitive condition seen so far in this group. b, Variation in forewing venation pattern observed in three different specimens of auchenorrhynchan. In all examples the wing venation most closely resembles that of the Archescytinidae. However, typically in archescytinids the forewings and hindwings are similar in size, but in the new specimens the hindwing is much narrower than the forewing. c, Isolated wing (VMNH 728) attributed to an auchenorrhynchan, magnification $\times 6$. The venation is very odd for its single longitudinal vein running parallel to the length of the wing, from which obliquely split off a row of eight veins parallel to each other. The wing is patterned, with a sclerotized costal area and clouds over each crossvein, and is unlike any other previously described. d, e, The single thysanopteran specimen (VMNH 729), magnification $\times 25$, which preserves the antennae, head, thorax, abdomen and two pairs of wings in their entirety. The rudimentary venation on the forewing is not unlike that of some primitive, modern-day thrips. f, *Architipula youngi* (VMNH 732), magnification $\times 10$. g, VMNH 730, an almost complete trichopteran, magnification $\times 15$. h, Camera lucida drawing of the trichopteran showing details of the head, body, some legs and most of the wings. Note in particular the characteristic tibial spurs and microtrichiae; scale bar, 1.0 mm. i, One of the two specimens of *Crosaphis*, VMNH 731; scale bar, 1.0 mm. j, *Architipula youngi* (VMNH 732) showing details of the wing venation pattern. k, A psychodid fly, VMNH 733, magnification $\times 14$, showing the head, antennae with long setulae, body, some legs and a complete wing. Diagnostic features of the wing essential for accurate placement are clearly preserved and include the wing apex broadly rounded, vein Sc turned abruptly costad, veins M1 and M2 forked, forked cubital vein,



and veins with long setae. l, One of the three staphylinid beetles, VMNH 734, in the Solite assemblage, magnification $\times 30$. Microtrichiae on the head, thorax and elytra are beautifully preserved. The specimens have been assigned to the Staphylinidae on the basis of the distinctively short elytra (exposing six or seven abdominal tergites), and the pronotal and head shapes.

TABLE 1 List of taxa from the Solite Quarry

(a) Plant taxa	(b) Insect taxa
Lycopodiales (lycopods)	Auchenorrhyncha (plant hoppers, leaf hoppers)
<i>Lepidodendron</i> type	Archescytinidae
<i>Lepacyclotes</i> sp.	Wing from undetermined family
ArthropHYTA (scouring rushes)	Blattodea (cockroaches)
<i>Neocalamites</i> cf. <i>knowtonii</i>	undetermined family
Pteridophyta (ferns)	Coleoptera (beetles)
<i>Lonchopteris virginiensis</i> (cf. <i>Cynepteris synorensis</i>)	Schizophoridae
<i>Cyathoforma</i> sp.	Staphylinidae
<i>Dictyophyllum</i> sp.	Diptera (flies)
<i>Wingatea</i> sp.	Tipulidae (crane flies)
cf. <i>Achrostichites linnaeae</i>	Crosaphidae
Ginkgophyta (ginkgos)	Procramptonomyiidae
<i>Sphaenobaeria</i> sp.	Psychodidae (moth flies)
<i>Metreophyllum</i> sp.	Eoptychopteridae
Coniferales (conifers)	Heteroptera (sucking bugs)
cf. <i>Hirmeriella</i> sp.	Belostomatidae
<i>Pagiophyllum simpsoniae</i>	Naucoridae
<i>Pagiophyllum diffusum</i>	Orthoptera
<i>Pagiophyllum</i> sp.	undetermined family
<i>Brachyphyllum</i> sp.	Thysanoptera (thrips)
cf. <i>Compsostrobos neotericus</i>	undetermined family
cf. <i>Elatocladus</i>	Trichoptera (caddis-flies)
<i>Podozamites</i> sp.	Undetermined family
Anthophyta	(c) Fish taxa
Bennettitales (cycad-like seed plants)	Actinopterygii
<i>Zamites powelli</i>	Palaeonisciformes
<i>Pterophyllum</i> sp.	<i>Turseodus</i> sp.
<i>Sphenozamites</i> sp.	<i>Synorichthys</i> sp.
Cycadales (cycads)	<i>Cionichthys</i> sp.
cf. <i>Zamiostrobus lissocardus</i>	Semionotidae
Incertae sedis	<i>Semionotus</i>
<i>Pannaulika triassica</i>	Sarcopterygii
<i>Fraxinopsis</i> sp.	Coelacanthini
<i>Pelourdea</i> sp.	<i>Diplurus</i> cf. <i>Newarki</i>
Seeds with dispersal hairs	cf. <i>Pariostegus</i>

because of the fragmentary nature of the material¹⁴. The new specimens, preserved in entirety (Fig. 2i), show *Crosaphis* to be indeed a dipteran, specifically in the family Anisopodidae (woodgnats) and related to the living genus *Mycetobia*. The similarity in the wing venation between the Australian and Solite specimens is striking, especially in light of the great palaeocontinental distances separating the two Triassic deposits.

Another important find is a single specimen (Fig. 2k) in the living superfamily Psychodoidea (moths and sandflies). The specimen either represents a new family very closely related to the Psychodidae, or it is the most primitive known member of the family. The next oldest specimens in this group were recently described from the Jurassic period of Germany¹⁵.

With representatives of four living infraorders of the Diptera found so far in the Solite assemblage (Bibionomorpha, Psychodomorpha, Tipulomorpha and Ptychopteromorpha), this deposit has uniquely revealed an ancestry of the Diptera more ancient than commonly believed. The placement of *Permotipula*, from the Permian of Australia, as the oldest dipteran or closest relative now seems less controversial¹⁶.

Like the Diptera, the Coleoptera from the Solite assemblage are the oldest beetles from the New World (the oldest beetles are from the Permian of Russia¹²). A single large Solite specimen is in the extinct family Schizophoridae, and in fact possesses features clearly allied to taxa from the Triassic of Russia¹⁷. The Schizophoridae belongs to an assemblage of 12 families, the Cupedoidea, of which all except one are extinct. The cupedoids were the dominant coleopteran in the late Palaeozoic and early Mesozoic eras. More exciting are three specimens unquestionably belonging to the huge living family, the Staphylinidae (rove beetles; about 30,000 species have been described) (Fig. 2l). Before this find the oldest staphylinids were from the Jurassic of Russia, to which the Solite specimens bear a distinct resemblance¹⁸. Modern staphylinoids are predominantly inhabitants of

forest leaf litter.

Despite lacking cuticle (typically a diagnostic feature of fossil plants), the plant remains (Fig. 3a–d, f) show a remarkable diversity (Table 1a). Ferns, cycadeoids and conifers predominate, and for a single palaeobotanical site, the Solite quarry is as rich as any in the world. The ferns in general are biostratigraphically and palaeogeographically significant. A single specimen is referable to *Wingatea* (Fig. 3a), a form well documented from the upper Carnian Deep River basin and the Chinle^{19,20}. However, the presence in the Solite assemblages of *Lonchopteris virginiensis* (= *Cynepteris synorensis*) and *Cyathoforma* is much more consistent with the floral assemblages from the slightly older (Julian and Tuvalian) Richmond basin and the Santa Clara Formation of New Mexico, rather than the Deep River basin and Chinle (where *Cynepteris lassiphora* is the typical form).

Specimens of ginkgophyte foliage show a remarkable similarity to *Metreophyllum*. *Metreophyllum* has been described only from the Permian of South Africa. It is essentially very like the European Jurassic genus *Eretmophyllum*, but significantly larger. The new find is the first record of an *Eretmophyllum*–*Metreophyllum* type of foliage for North America, and it hints at a possible Pangaea distribution.

Bennettitales, which could represent early members of the anthophyte radiation, are well represented by articulated fronds and leaf fragments (Table 1a). The referral of *Pannaulika*, previously described from the quarry, to the angiosperms²¹ is potentially even more significant. Although there is cause for some scepticism regarding this determination, the looping tertiary venation pattern is certainly angiosperm-like. Although the dipteridaceous fern *Dictyophyllum* also exhibits a somewhat angiosperm-like venation, it is quite unlike that of *Pannaulika* (Fig. 3f).

Two specimens of a rather unusual seed are here referred to the genus *Fraxinopsis* (Fig. 3c, d). The multiple parallel veins on the

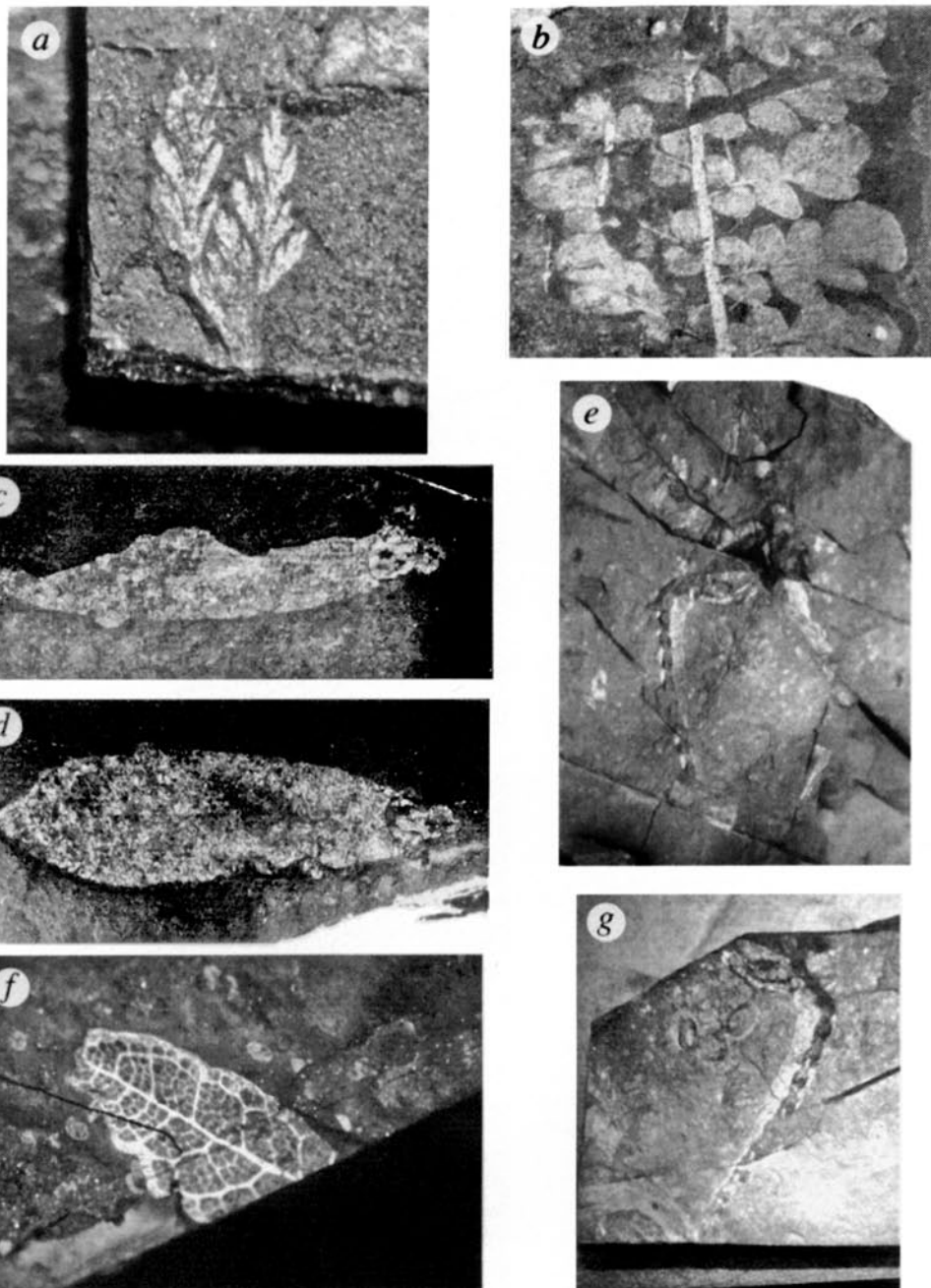


FIG. 3 a, Foliage referred to *Wingatea* (VMNH 735), magnification $\times 6$. b, A previously undescribed fern-like foliage (VMNH 736), magnification $\times 2$. It is represented by many specimens and is notable for the much enlarged apical pinnule. c, d, The two specimens of seed referred to *Fraxinopsis* VMNH 737 (c) and VMNH 738 (d). e, The caudal portion of a *Tanytrachelos* tail showing the vertebrae and myotome muscle blocks (VMNH 739), magnification $\times 1.0$. f, *Pannaulika triassica* (VMNH 201) magnification $\times 2.8$. g, *Tanytrachelos ahynis*, counterpart of VMNH, 739, magnification $\times 1.0$.

seed lamina are very characteristic, and this should therefore be regarded as the first occurrence of this taxon from Laurasia.

The aquatic prolacertiform tetrapod *Tanytrachelos* has already been described from many articulated specimens from the Solite Quarry. But many more specimens have been recovered in the latest excavations, and these include some spectacular individuals complete with ghosts of the myotome muscle blocks on the tail (Fig. 3e, g) and ligaments in the webbed hind foot. Fragmentary remains of two as-yet undescribed tetrapods have also been found. In addition to the fishes previously described (Table 1c), we have also recovered an isolated shark tooth which, at 8 mm, is much larger than most freshwater shark teeth.

Besides the spectacular preservation and the number of unique taxa, the new finds have a bearing on debates about the modes of terrestrial evolution across the Triassic–Jurassic boundary. In an analysis of insect diversity over time, Labandeira and Sepkoski²² indicated that the Triassic was a period of unexpectedly low diversity, and they suggested that this reflected either increased extinctions or slowed diversification. With the finding of seven

new, earliest records of living insect families/orders from the Solite assemblage, based on just over 200 specimens, this suggests that a 'Triassic minimum' of insect diversity is a sampling artefact due to the paucity of Triassic deposits.

The homogeneity of Early Jurassic terrestrial vertebrate faunas has been widely recognized^{23–25}, but in the Late Triassic, despite the presence of a single supercontinent, Pangaea, some localization (partitioning) of vertebrate faunas has been reported, with particularly marked distinctions between Northern (Laurasian) and Southern (Gondwanan) Hemispheres. This same separation has also been recognized for plants²⁶. However, some doubt was cast on this broad distinction by the discovery of some typical Gondwanan vertebrates (traversodont eucynodonts) together with more typical Laurasian elements (phytosaur) in a rich Late Triassic (late Carnian) site near Richmond, Virginia²⁷. On this basis, it was postulated that the apparent variations between north and south were at least in part attributable to age differences. The new finds (in particular *Fraxinopsis* and *Crosaphis*) blur even further the broad distinctions between the Laurasian and

Gondwanan realms. In addition, the new finds call into question some of the perceived age and palaeogeographic differences between the floral assemblages from different parts of North America. □

Received 5 December 1995; accepted 9 February 1996.

1. Padian, K. *The Beginning of the Age of Dinosaurs* (Cambridge Univ. Press, 1986).
2. Olsen, P. E., Remington, C. L., Comet, B. & Thomson, K. S. *Science* **201**, 729–733 (1978).
3. Olsen, P. E. *Science* **234**, 842–848 (1986).
4. Olsen, P. E. *A.G.U. Guidebook* **1351**, 1–173 (1989).
5. Martynov, A. V. *C. r. Acad. Sci. URSS* **3**, 333–335 (1935).
6. Priesner, H. & Quievreux, F. *Bull. Soc. géol. Fr.* **5**, 471–477 (1935).
7. zur Strassen, R. *Stuttg. Beitr. Naturk. A* **267**, 1–51 (1973).
8. Riek, E. F. *Rec. Aust. Mus.* **23**, 55–87 (1952).
9. Martynova, O. M. *Mater. Osnov. Paleont.* **2**, 69–94 (1958).
10. Krzeminski, W. *Bull. Soc. ent. Suisse* **65**, 39–59 (1992).
11. Evans, J. W. *Mem. Qd Mus.* **16**, 145–152 (1971).
12. Heie, O. E. *Entmol. scand. Suppl.* **15**, 401–415 (1981).
13. Kovalev, C. G. in *Entomologicheskoe obozrenie* **62**, 800–805 (1983).
14. Carpenter, F. M. *Treatise on Invertebrate Paleontology Part R (Arthropoda)* 4(4) (Geological Society of America, Lawrence, Kansas, 1993).
15. Ansoerge, J. *Paläont. Z.* **68**, 199–210 (1994).
16. Willman, R. *Naturwissenschaften* **76**, 375–377 (1989).
17. Ponomarenko, A. G. *Trudy paleont. Inst.* **125**, 1–240 (1969).
18. Tichomirova, A. L. in *Yurskie Nasekomye Karatau* (ed. Rohdendorf, B. B.) 139–156 (Akademiya nauk SSSR, Moscow, 1968).
19. Ash, S. R. *Prof. Pap. U.S. geol. Surv.* **613D**, D1–D52 (1969).
20. Ash, S. R. in *Biostratigraphy of Fossil Plants* (eds Dilcher, D. L. & Taylor, T. N. T.) 153–170 (Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, 1980).
21. Comet, B. *Mod. Geol.* **19**, 81–99.
22. Labandeira, C. C. & Sepkoski, J. J. *Science* **261**, 310–315 (1993).
23. Shubin, N. H. & Sues, H.-D. *Paleobiology* **17**, 214–230 (1991).
24. Shubin, N. H., Olsen, P. E. & Sues, H.-D. in *In the Shadow of the Dinosaurs* (eds Fraser, N. C. & Sues, H.-D.) 242–250 (Cambridge Univ. Press, 1994).
25. Olsen, P. E. & Galton, P. M. *Palaeont. afr.* **25**, 97–110 (1984).
26. Bamard, P. D. W. *Spec. Pap. Palaeont. Ass.* **12**, 175–187 (1973).
27. Sues, H.-D. & Olsen, P. E. *Science* **249**, 1020–1022 (1990).

ACKNOWLEDGEMENTS. We thank C. H. Gover and the Virginia Solite Corporation for access to the site and their unstinting support of the research, and A. Davies, C. Hampton, J. MacCarthy and T. Stallings for assistance in the excavations. Field work was financed by the National Geographic Society.

CORRESPONDENCE and requests for materials to be addressed to N.C.F.