

Scientific Reports

Late Triassic extinction events

Spencer G. Lucas¹ and Lawrence H. Tanner²

¹*New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104-1375 USA, slucas@nmmnh.state.nm.us;*

²*Department of Geography & Geoscience, Bloomsburg University, Bloomsburg, PA 17815 USA, lhtann@blomu.edu*

Abstract - Accelerated biotic turnover during the Late Triassic has been misinterpreted as a single, end-Triassic mass extinction event, now regarded as one of the “big five” extinctions. However, careful examination of the fossil record indicates that the groups usually claimed to have suffered a catastrophic extinction at the end of the Triassic, including ammonites, bivalves, conodonts and tetrapods, experienced multiple or prolonged extinctions throughout the Late Triassic, and that other groups were relatively unaffected or subject to only regional effects. Instead of a single mass extinction at the end of the Triassic, the Late Triassic was an interval of elevated extinction rates, encompassing distinct extinction events at the Late Triassic stage boundaries, as well as other, within-stage extinction events.

Introduction

The decline in diversity at the Triassic-Jurassic boundary (TJB) has come to be regarded as one of the “big five” mass extinctions of the Phanerozoic. Attribution of this level of suddenness and severity to the extinction at the TJB followed Sepkoski (1982), who, based on a global compilation of families of marine invertebrates, designated this boundary as one of four mass extinctions events of intermediate magnitude (end-Cretaceous, end-Triassic, Late Devonian, Late Ordovician). Overall, this assumption of intense and sudden biotic decline at the TJB has remained unquestioned, until recently (Hallam, 2002; Tanner et al., 2004).

Here, we reject what we believe is the myth of a catastrophic extinction at the TJB. This myth is largely rooted in poor stratigraphic resolution compounded by a reliance on literature compilations as a method of identifying and gauging mass extinctions. Instead, the Late Triassic was an interval of elevated extinction rates that manifested themselves in a series of discrete extinctions throughout Norian and Rhaetian time. Significantly, no data document Late Triassic mass extinction(s) of many biotic groups, including gastropods, brachiopods, conulariids, foraminiferans, ostracods, fishes and marine reptiles (Hallam, 2002; Tanner et al., 2004). Therefore, we focus our discussion on those groups that have been perceived by some as part of a TJB mass extinction, namely ammonites, bivalves, reef organisms, radiolarians, conodonts, tetrapods and land plants.

The compiled correlation effect

Two methods have been used to analyze the data on extinctions at the TJB: (1) the compilation of global diversity from the published literature; and (2) the study of diversity changes based on the actual stratigraphic distri-

bution of fossils in specific sections. These two methods are not totally disjunct, because the global compilations supposedly reflect the actual stratigraphic distributions of the fossils in all sections. However, the global compilations contain a serious flaw—their stratigraphic imprecision (Teichert, 1988), which Lucas (1994) termed the Compiled Correlation Effect (CCE). This imprecision is largely responsible for the myth of a single, TJB mass extinction.

The CCE refers to the fact that the temporal ranges of taxa in literature compilations are only as precise as the correlations, or relative ages, of the compiled taxa. Because most published correlations are at the stage/age level, the temporal resolution of extinction events within these stages/ages cannot be resolved (Fig. 1). The result is the artificial concentration of extinctions at stage/age boundaries; a complex extinction of significant temporal duration during a stage/age is made to appear as a mass extinction at the end of the stage/age (Fig. 1).

Much of the literature on the TJB extinction fails to consider the CCE. Thus, for example, the supposedly profound extinction of ammonites at the end of the Rhaetian reflects a lack of detailed stratigraphic analysis; literature compilations assumed that any ammonite taxon found in Rhaetian strata has a stratigraphic range throughout the entire Rhaetian (Fig. 1). This gives the appearance of a dramatic ammonite extinction at the end of the Rhaetian, when in fact, there were several ammonite extinction events within the Rhaetian. Furthermore, those who did not recognize a Rhaetian Stage exacerbated the CCE, because they reduced stratigraphic resolution by considering the entire post-Carnian Late Triassic to belong to a single, Norian Stage.

Also note that the Signor-Lipps effect, which recognizes

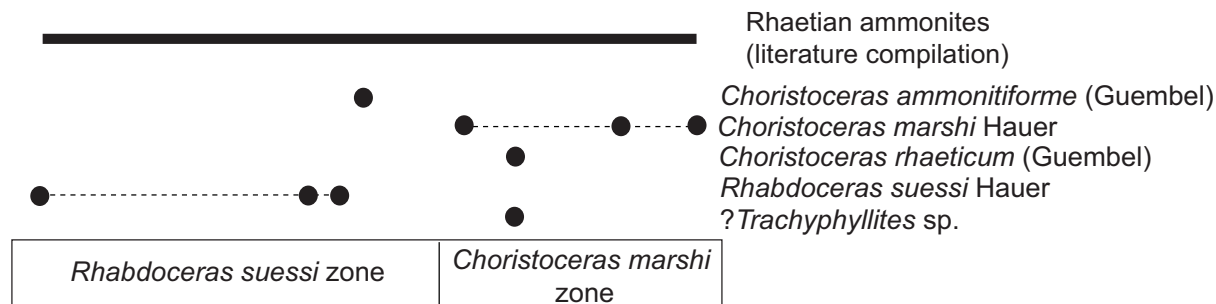


Figure 1. The actual ranges of Rhaetian ammonites in the Weissloferbach section (Austria) of the Kössen Beds (after Mostler et al., 1978) show a low diversity Rhaetian ammonite assemblage with only one taxon (*Choristoceras marshi*) present at the top of the Rhaetian section. In contrast, the low stratigraphic resolution characteristic of literature compilations indicates all ammonite ranges simply truncated at the top of the Rhaetian, a typical example of the CCE.

that in theory some actual stratigraphic ranges in the fossil record are artificially truncated, has been used by some to discount the reliability of actual stratigraphic ranges. Statistical methods even exist to “complete” these supposedly truncated stratigraphic ranges. However, we regard these methods as little more than assumption-laden ways to invent data, and prefer to rely on the actual stratigraphic ranges of fossils in well-studied sections.

Ammonites

Biostratigraphic recognition (and definition) of the TJB has long been based on a clear change in the ammonite fauna from the ornamented ceratites and their peculiar heteromorphs of the Late Triassic to the smooth psiloceratids of the Early Jurassic. Most workers agree that all but one lineage of ammonites became extinct by the end of the Triassic, and the subsequent Jurassic diversification of ammonites evolved from that lineage.

There is indeed substantial turnover in the ammonites around the TJB, and Early Jurassic ammonite assemblages are qualitatively very different from Late Triassic assemblages. However, Kennedy (1977) and Signor and Lipps (1982) correlated the drop in ammonite diversity at the end of the Triassic with a drop in sedimentary rock area, not with a mass extinction. And, Teichert (1988) listed more than 150 ammonite genera and subgenera during the Carnian, which was reduced to 90 in the Norian, and reduced again to 6 or 7 during the Rhaetian. This indicates that the most significant ammonite extinctions were during or at the end of the Norian, not at the end of the Rhaetian.

The most completely studied and ammonite-rich section in the world that crosses the TJB is in the New York Canyon area of Nevada, USA (Fig. 2). Taylor et al. (2000, 2001) and Guex et al. (2003) plotted ammonite distribution in this section based on decades of collecting and study; of 11 Rhaetian species, 7 extend to the upper Rhaetian (shown in Figure 2), and only 2 are present at

the stratigraphically highest Rhaetian ammonite level. Taylor et al. (2000) presented a compelling conclusion from these data: a two-phase latest Triassic ammonite extinction, one in the Norian followed by a low diversity Rhaetian ammonite fauna that becomes extinct at the end of the Triassic.

Another detailed study of latest Triassic ammonite distribution is in the Austrian Kössen Beds (Fig. 1; Ulrichs, 1972; Mostler et al., 1978). The youngest Triassic zone here, the *marshi* zone, has three ammonoid species, two with single level records low in the zone, and only *Choristoceras marshi* is found throughout the zone. This, too, does not indicate a sudden TJB mass extinction of ammonites. Thus, the change in ammonites across the TJB is profound, but it took place as a series of extinction events spread across Norian and Rhaetian time, not as a single mass extinction at the TJB.

Bivalves

The perception of a TJB mass extinction of marine bivalves stems from Hallam (1981), who claimed a 92% extinction of bivalve species at the TJB by combining all Norian (including Rhaetian) marine bivalve taxa, thereby encompassing a stratigraphic interval with a minimum duration of 15 million years. He then compared this to a pool of Hettangian taxa, an outstanding example of the CCE.

Johnson and Simms (1989) pointed out that better much stratigraphic resolution could be achieved on the local scale; in the Kössen beds, for example, Hallam considered all of the bivalve taxa to range throughout the Rhaetian, even though published data (e.g., Morbey, 1975) showed varied highest occurrences throughout the Rhaetian section. Furthermore, Skelton and Benton’s (1993) global compilation of bivalve family ranges showed a TJB extinction of 5 families, with 52 families passing through the boundary unscathed, certainly suggesting that there was not a mass extinction of bivalve

families. Hallam and Wignall (1997) reexamined the bivalve record for the TJB in northwestern Europe and the northern Calcareous Alps in considerable detail. They found extinction of only 4 out of 27 genera in northwest Europe and 9 of 29 genera in the Calcareous Alps, again, not indicating a mass extinction. Although Hallam (2002) continued to argue for a substantial TJB bivalve extinction, he conceded that the data to demonstrate this are not conclusive. We believe unequivocally that these data do not exist.

Indeed, detailed inspection of the Late Triassic bivalve record suggests that extinctions were episodic throughout this interval, not concentrated at the TJB. A significant extinction of bivalves, including the cosmopolitan

and abundant pectinacean *Monotis*, is well documented for the end-Norian (Dagys and Dagys, 1994; Hallam and Wignall, 1997). Detailed studies of Late Triassic bivalve stratigraphic distributions (e.g., Allasinaz, 1992; McRoberts, 1994; McRoberts and Newton, 1995; McRoberts et al., 1995) identify multiple bivalve extinction events within the Norian and Rhaetian Stages. A good example is the New York Canyon section, where bivalve genera disappear at several levels in the Rhaetian, with most bivalve turnover predating the ammonite-based TJB (Fig. 2). The pattern of bivalve extinction during the Late Triassic is thus one of multiple extinction events, not a single mass extinction at the TJB.

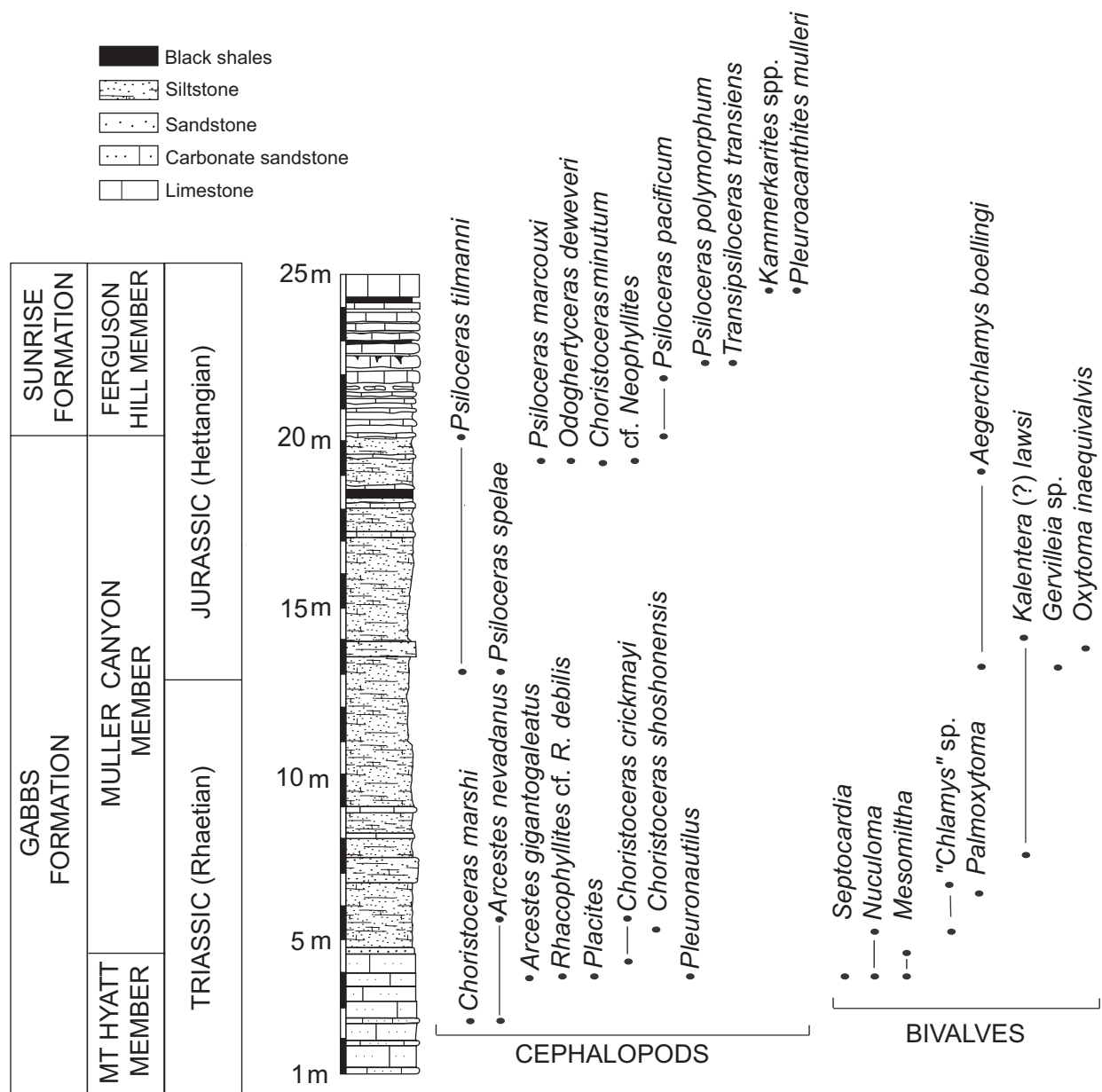


Figure 2. The actual stratigraphic ranges of ammonites and bivalves across the TJB in the New York Canyon section, Nevada (modified from Guex et al., 2003). The TJB is placed here at the lowest occurrence of *Psiloceras tilmanni*.

Reefs

The scleractinian corals, important reef builders during the Triassic, underwent a marked decline at the end of the Triassic that was followed by a “reef gap” during the Hettangian and early Sinemurian, after which corals re-diversified to become the dominant reef builders (Stanley, 1988). The extinctions in the reef community at the end of the Triassic are best documented in Tethys, where the reef ecosystem collapsed, carbonate sedimentation nearly ceased, and earliest Jurassic reefal facies are rare. Those earliest Jurassic reefs that are known (particularly in Morocco) are carbonate mounds produced by spongiomorphs and algae (e.g., Flügel, 1975). However, coral Lazarus taxa have been discovered in Early Jurassic suspect terranes of western North America, indicating the persistence of at least some corals in Panthalassan refugia during the earliest Jurassic reef gap.

Hallam and Goodfellow (1990) argued that sea level change caused the collapse of the reef system, with significant extinctions of calcisponges and scleractinian corals at the TJB. They discounted the possibility of a major drop in productivity as an explanation for the facies change from platform carbonates to siliciclastics. There is indeed a distinct lithofacies change at or near the TJB in many sections, particularly in the Tethyan realm, where facies changes suggest an interval of regression followed by rapid transgression. At the TJB section in western Austria, for example, a shallowing-upward trend from subtidal carbonates to red mudstones, interpreted as mudflat deposits, is succeeded by thin-bedded marl and dark limestone (McRoberts et al., 1997). The boundary in parts of the Austrian Alps displays karstification, suggesting a brief interval of emergence. In the Lombardian Alps the TJB is placed (palynologically) in the uppermost Zu Limestone at a flooding surface that marks the transition from mixed siliclastic-carbonate sedimentation to subtidal micrite deposition (Cirilli et al., 2003). Thus, a change in bathymetry resulted in the extirpation of reefs, which in large part caused the cessation of carbonate sedimentation. However, the evidence that this was a global event is lacking, and can be explained easily as a regional extinction driven by sea level changes.

Kiessling's (2001) compilation indicates that the decline of reefs began during the Late Triassic and that the TJB corresponds to the loss of reefs concentrated around 30°N latitude, although this article is frequently cited as documenting a TJB mass extinction of reef organisms (e.g., Pálffy, 2003). Beauvais (1984) stressed the endemism of scleractinian species during the Liassic, raising the possibility that the apparent TJB extinction of these organisms may be heavily influenced by (Tethyan?) sampling biases. Thus, a sudden extinction of reef organisms at the TJB is limited to Tethys and reflects a regional change in bathymetry, not a global mass extinction of reef organisms.

Radiolarians

At the family level, radiolarians show no decline at the

TJB (Hart and Williams, 1993), although significant species turnover is indicated (Vishnevskaya, 1997). Data from the Queen Charlotte Islands in western Canada have been interpreted to indicate a drastic extinction of radiolarians at the TJB (Tipper et al., 1994; Carter, 1994; Ward et al., 2001). Carter (1974) cites the loss of 45 radiolarian species in the top 1.5 m of the *Globolaxtorum tozeri* zone (topmost Rhaetian) on Kunga Island, above which is a low diversity Hettangian fauna in which nassellarians are rare. However, Guex et al. (2002) argue that the radiolarian extinction in the Queen Charlotte Islands section is directly associated with a stratigraphic gap (unconformity), which suggests the extinction is more apparent than real, though E. Carter (personal commun., 2003) believes there is no gap in the section. Regardless, few data indicate that this extinction was anything more than a local event.

Data from other Pacific rim locations suggest that the extinction pattern was not catastrophic. Bedded cherts from Japan, for example, display radiolarian faunas that indicate gradual replacement across the boundary with observable transition groups (Hori, 1992), though Carter and Hori (2003) recently reported a drastic change in the radiolarian fauna across the TJB in one Japanese section. Vishnevskaya (1997) indicates that about 40% of the latest Triassic radiolarian genera survived the TJB. Indeed, the greatest radiolarian extinction of the early Mesozoic occurred during the Early Jurassic (early Toarcian), not at the TJB (Racki, 2003). Moreover, occurrences of bedded cherts show no decrease from the Late Triassic to the Early Jurassic, suggesting that there was no significant radiolarian decline (Kidder and Erwin, 2001).

Conodonts

The Conodonta (a phylum or subphylum) is usually identified as one of the most significant groups to have suffered complete extinction at the end of the Triassic. This is misleading. Detailed reviews of the conodont extinction emphasize that conodonts suffered high rates of extinction throughout the Triassic (e.g., Clark, 1983; Sweet, 1988; Aldridge and Smith, 1993), and maximum conodont extinction took place at the end of the Norian. Indeed, this long appeared to be the final extinction of conodonts in North America, as the youngest conodonts on the continent were from the late Norian *suessi* zone (Clark, 1980, 1981, 1983). Conodonts, however, are now known from the Rhaetian *crickmayi* zone in Canada, though they are known only from terranes and are low in both abundance and diversity (Orchard, 1991, 2003). They are also found in the Rhaetian *marshi* zone in Europe, though diversity is low (4 species) and population sizes (based on sample abundance) also are low (Mostler et al., 1978). Thus, conodonts were mostly extinct by the end of the Norian.

Tetrapods

The idea of a substantial nonmarine tetrapod (amphibian and reptile) extinction at the end of the Triassic began with Colbert (1949, 1958), and has been more recently advocated by Olsen et al. (1987, 1990, 2002a, b), largely

Eubrontes

Upper Triassic

Australia

50 cm



Figure 3. *Eubrontes* footprints from the Upper Triassic of the Sydney basin, Australia. The drawings are of a trackway (after Staines and Woods, 1964), and the photograph of a track is after Batholomai (1966).

based on the tetrapod fossil record of the Newark Supergroup (eastern North America). Benton (1994) and Lucas (1994) rejected this conclusion, both arguing against building a case for extinction on the very incomplete record of the Newark Supergroup. Furthermore, Cuny (1995) saw no evidence of a TJB mass extinction of tetrapods in the western European tetrapod fauna.

Colbert (1958) believed that the temnospondyl amphibians, a significant component of late Paleozoic and Early-Middle Triassic tetrapod assemblages, underwent complete extinction at the TJB. However, more recent discoveries have invalidated that conclusion. Milner (1993) demonstrated a less pronounced extinction of amphibians, with only one family extinct at the end of the Triassic (plagiosaurids); he showed the disappearance of the capitosaurids, metoposaurids and laticopids at the Norian-Rhaetian boundary. Moreover, these temnospondyls are only a minor component of Late Triassic tetrapod assemblages, being of low diversity and relatively small numbers in many samples (e.g., Hunt, 1993). Temnospondyl extinction thus largely preceded the Rhaetian.

The global compilation of reptile families by Benton (1993) lists the extinction of 11 terrestrial reptile families at the TJB: Proganochelyidae, Kuehneosauridae, Pachystropheidae, Trilophosauridae, Phytosauridae, Stagonolepididae, Rausisuchidae, Ornithosuchidae, Saltoposuchidae, Thecodontosauridae and Traversodontidae. However, only two of these families, Phytosauridae and Procolophonidae, have well established

Rhaetian records (Lucas, 1994), especially given that new data indicate that the uppermost Chinle Group in the western United States is pre-Rhaetian. There is thus no evidence that most of the tetrapod families that disappeared during the Late Triassic were present during the Rhaetian; they apparently became extinct sometime earlier, during the Norian.

The Newark Supergroup body fossil record of tetrapods is inadequate to demonstrate a mass extinction of tetrapods at the TJB, so the tetrapod footprint record in the Newark Supergroup has been used to identify a TJB tetrapod extinction (e.g., Olsen and Sues, 1986; Olsen et al., 2002a,b). However, detailed stratigraphic data on the Newark footprint record (e.g., Szajna and Silvestri, 1996) indicate the disappearance of about 4 ichnogenera and appearance of 2 ichnogenera at the palynologically-determined TJB, with four ichnogenera continuing through this boundary; this does not qualify as a sudden mass extinction. Avanzini et al. (1997) described a diverse track assemblage in peritidal sediments of the Southern Alps of Italy of earliest Hettangian age, which negates the idea advocated by some of low tetrapod diversity during the earliest Jurassic.

The discussion of tetrapod footprint evidence of a TJB mass extinction by Olsen et al. (2002a, b) argued that the sudden appearance of large theropod tracks (ichnogenus *Eubrontes*) in the earliest Jurassic strata of the Newark Supergroup indicates a dramatic size increase in theropod dinosaurs at the TJB. They interpreted this as the result of a rapid (thousands of years) evolutionary response by

the theropod survivors of a mass extinction and referred to it as “ecological release” (Olsen et al., 2002a, p. 1307). They admitted, however, that this hypothesis can be invalidated by the description of *Dilophosaurus*-sized theropods or diagnostic *Eubrontes giganteus* tracks in verifiably Triassic-age strata.

Indeed, large, *Dilophosaurus*-size theropods have been known from the Late Triassic body-fossil record since the 1930s: *Liliensternus* from the Norian of Germany (estimated length of ~ 5 m) and *Gojirasaurus* from the Norian of the USA (estimated length ~ 5.5 m) (Huene, 1934; Welles, 1984; Carpenter, 1997). *Dilophosaurus* has an estimated length of 6 m, and the foot of *Liliensternus* is 92% (based on maximum length) the size of that of *Dilophosaurus*. Clearly, theropods capable of making *Eubrontes*-size tracks were present during the Norian, and the sudden abundance of these tracks in the Newark Supergroup at the beginning of the Jurassic cannot be explained simply by rapid evolution to large size of small theropods following a mass extinction.

Also, tracks of large theropod dinosaurs (ichnogenus *Eubrontes*) have long been known from the Triassic of Australia (Staines and Woods, 1964; Hill et al., 1965; Bartholomai, 1966; Molnar, 1991; Thulborn, 1998), further invalidating the “ecological release” hypothesis. These tracks (Fig. 3) are from the Blackstone Formation of the Ipswich Coal Measures near Dinmore in south-eastern Queensland, a unit of well-established Triassic age (probably late Carnian: Balme and Foster, 1996). The largest tracks are 43 cm long and 38 cm wide (Fig. 3) and closely resemble tracks of *Eubrontes giganteus* from the Newark Supergroup described by Olsen et al. (1998).

Thulborn (2003) argued that the Australian Triassic record of *Eubrontes* refutes the notion that its first occurrence is at the TJB. Olsen et al. (2003), nevertheless, claimed that the Australian *Eubrontes* tracks are actually tridactyl underprints of a pentadactyl chirothere track. However, the footprint of *Eubrontes* is mesaxonic (symmetrical around its long axis), as are the Australian *Eubrontes* tracks (Fig. 3). Tridactyl underprints of chirotheres are paraxonic (asymmetrical around their long axis). Therefore, the *Eubrontes* tracks from the Upper Triassic of Australia are correctly identified. The concept of a sudden appearance of *Eubrontes* tracks due to “ecological release” at the TJB thus was refuted decades before it was proposed by Olsen et al. (2002a, b).

PLANTS

Ash (1986) reviewed the global record of megafossil plants and concluded that changes across the TJB boundary primarily involved seed ferns, in particular, the loss of the families Glossopteridaceae, Peltaspermeaceae, and Corystospermeaceae (also see Traverse, 1988). The TJB in East Greenland is marked by the transition from the *Lepidopteris* Zone to the *Thaumatopteris* Zone, with few species in common. The former is characterized by the presence of palynomorphs including *Rhaetipollis*, while the latter contains *Heliosporites* (Pedersen and Lund,

1980), and although extinction of some species across the transition between the two zones is evident, many species continue. Thus, no catastrophic extinction is documented. This accords well with the global compilations at the species and family levels that show no substantial extinction at the TJB (Niklas et al., 1983; Knoll, 1984; Edwards, 1993; Cleal, 1993a, b). Nevertheless, McElwain et al. (1999) claimed a 95% extinction of leaf species for northern Europe (East Greenland and Scania) at the TJB, but this supposed extinction has not been confirmed over a wider area.

The palynological record provides no evidence for mass extinction at the TJB. Fisher and Dunay (1981) demonstrated that a significant proportion of the *Rhaetipollis germanicus* assemblage that defines the Rhaetian in Europe (Orbell, 1973; Schuurman, 1979) persists in lowermost Jurassic strata. Indeed, a study of the British Rhaeto-Liassic by Orbell (1973) found that of 22 palynomorphs identified in the *Rhaetipollis* Zone, only 8 disappeared completely in the overlying *Heliosporites* Zone. These authors, as well as Brugman (1983) and Traverse (1988), have concluded that floral turnover across the TJB was gradual, not abrupt. Kelber (1998) also described the megafloora and palynoflora for Central Europe in a single unit he termed “Rhaeto-Liassic,” and concluded there was no serious disruption or decline in plant diversity across the TJB.

Nevertheless, profound palynomorph extinction at the TJB has been argued from the Newark Supergroup record (Olsen and Sues, 1986; Olsen et al., 1990; Fowell and Olsen, 1993; Olsen et al., 2002a,b). Notably, the palynomorph taxa used to define the TJB in the European sections (*Rhaetipollis germanicus* and *Heliosporites reissingeri*: Orbell, 1973) are not present in the Newark Supergroup basins, so placement of the palynological TJB in these basins was initially based on a graphic correlation of palynomorph records (Cornet, 1977). More recent work identified the TJB in the Newark by a decrease in diversity of the pollen assemblage, defined by the loss of palynomorphs considered typical of the Late Triassic, and dominance by several species of the genus *Corollina*, especially *C. meyeriana* (Cornet and Olsen, 1985; Olsen et al., 1990; Fowell and Olsen, 1993; Fowell et al., 1994; Fowell and Traverse, 1995).

Nevertheless, this method of defining the system boundary is compromised by regional variations in the timing of the *Corollina* peak. In the classic Kendelbach section, for example, the peak abundance of *C. meyeriana* occurs in beds of Rhaetian and older age (Kössen Formation: Morbey, 1975), as it does in Tibet (Hallam et al., 2000). But, in Australia this peak may not occur until mid-Hettangian (Helby et al., 1987). Thus, abundance patterns of *Corollina* spp. are not a reliable indicator of the TJB. Furthermore, apparent extinction of palynomorphs in the Newark Supergroup basins does not match other megafossil data from the Newark Supergroup, which suggest that any extinction effects represented by these data are strictly local.

Prospectus

Two hundred years of fossil collecting failed to document a global mass extinction at the TJB, yet 20 years of literature compilation and the CCE did. The myth of a single mass extinction at the TJB has led to a search for the cause of the “mass extinction” (“those weapons of mass destruction must be around here somewhere”) and drawn attention away from what were actually a series of extinctions that took place throughout the Late Triassic. Research now needs to focus on these multiple extinctions and their causes, not on a single extinction event. Perhaps the most interesting question not yet addressed by most researchers is why this prolonged (at least 20 million years) interval of elevated extinction rates occurred during the Late Triassic?

References

Aldridge, R. J., Smith, M. P. 1993. Conodonta. In: Benton, M. J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 563-572.

Allasinaz, A. 1992. The Late Triassic-Hettangian bivalve turnover in Lombardy (Southern Alps). *Rivista Italiana Paleontologia Stratigrafia*, 97: 431-454.

Ash, S. 1986. Fossil plants and the Triassic-Jurassic boundary. In: Padian, K. (Ed.), *The Beginning of the Age of Dinosaurs*. Cambridge Univ. Press, Cambridge, UK, pp. 21-30.

Avanzini, M., Frisia, S., van den Driessche, K., Keppens, E., 1997. A dinosaur tracksite in an early Liassic tidal flat in northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry. *Palaios*, 12: 538-551.

Balme, B.F., Foster, C.B., 1996. Triassic (chart 7). In: Young, G.C., Laurie, J.R. (Eds.), *An Australian Phanerozoic Timescale*. Oxford Univ. Press, Melbourne, pp. 136-147.

Bartholomai, A., 1966. Fossil footprints in Queensland. *Australian Natural History*, 15: 147-150.

Beauvais, L., 1984. Evolution and diversification of Jurassic Scleractinia. *Palaeontographia Americana*, 54: 219-224.

Benton, M.J., 1993. Reptilia. In: Benton, M. J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 681-715.

Benton, M.J., 1994. Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern. In: Fraser, N.C., Sues, H-D. (Eds.), *In the Shadow of the Dinosaurs*. Cambridge Univ. Press, Cambridge, UK, pp. 366-397.

Brugman, W.A., 1983. Permian-Triassic palynology. Utrecht, State University Utrecht, 121 pp.

Carpenter, K., 1997. A giant coelophysoid (Ceratosauria) theropod from the Upper Triassic of New Mexico, USA. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 205: 189-208.

Carter, E. S., 1994, 1994. Evolutionary trends in latest Norian through Hettangian radiolarians from the Queen

Charlotte Islands, British Columbia. *Geobios Mémoire Spécial*, 17: 111-119.

Carter, E. and Hori, R., 2003. Extinction and recovery of radiolarians at the Triassic-Jurassic boundary in Queen Charlotte Islands: implications for global productivity collapse. *Geological Association of Canada, Vancouver 2003 Meeting, Abstracts Volume*, 28: CD-ROM.

Cirilli, S., Galli, M.T., and Jadoul, F., 2003. Carbonate platform evolution and sequence stratigraphy at Triassic/Jurassic boundary in the Western Southern Alps of Lombardy (Italy): an integrated approach of litho-palynofacies analysis. *Geological Association of Canada, Vancouver 2003 Meeting, Abstracts Volume*, 28: CD-ROM.

Clark, D.L., 1980. Rise and fall of Triassic conodonts. *American Association of Petroleum Geologists Bulletin*, 64: 691.

Clark, D.L., 1981. Extinction of Triassic conodonts. *Geologische Bundesanstalt Abhandlungen*, 35: 193-195.

Clark, D.L., 1983. Extinction of conodonts. *Journal of Paleontology*, 57: 652-661.

Cleal, C.J., 1993a. Pteridophyta. In: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 779-794.

Cleal, C.J., 1993b. Gymnospermophyta; in Benton, M. J., ed., *The Fossil Record 2*. London, Chapman & Hall, p. 795-808.

Colbert, E.H. 1949. Progressive adaptations as seen in the fossil record. In: Jepsen, G.L., Mayr, E., Simpson, G.G. (Eds.), *Genetics, Paleontology and Evolution*. Princeton University Press, Princeton, NJ, pp. 390-402.

Colbert, E.H., 1958. Triassic tetrapod extinction at the end of the Triassic Period. *Proceedings National Academy Science USA*, 44: 973-977.

Cornet, B., 1977. The palynostratigraphy and age of the Newark Supergroup. Ph.D. Thesis. Pennsylvania State University, University Park, PA, 505 pp.

Cornet, B. and Olsen, P.E., 1985. A summary of the biostratigraphy of the Newark Supergroup of eastern North America with comments on provinciality. In: Weber, R. (editor), *III Congreso Latinoamericano de Paleontología Mexico, Simposio Sobre Floras del Triásico Tardío, su Fitogeografía y Paleología*, Memoria. UNAM Instituto de Geología, Mexico City, pp. 67-81.

Cuny, G., 1995. French vertebrate faunas and the Triassic-Jurassic boundary.

Palaeogeography, Palaeoclimatology, Palaeoecology, 119: 343-358.

Dagys, A.S. and Dagys, A.A., 1994. Global correlation of the terminal Triassic. *Mémoire de Géologie (Lausanne)*, 22: 25-34.

Edwards, D., 1993. Bryophyta. In: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 775-778.

Fisher, M. J. and Dunay, R.E., 1981. Palynology and the

- Triassic/Jurassic boundary. Review of Palaeobotany and Palynology, 34: 129-135.
- Flügel, E., 1975. Fossile Hydrozoan—Kenntnisse und Probleme. Paläontologische Zeitschrift, 49: 369-406.
- Fowell, S.J. and Olsen, P.E., 1993. Time calibration of Triassic-Jurassic microfossil turnover, eastern North America. Tectonophysics, 222: 361-369.
- Fowell, S.J. and Traverse, A., 1995. Palynology and age of the upper Blomidon Formation, Fundy basin, Nova Scotia. Review of Palaeobotany and Palynology, 86: 211-233.
- Fowell, S.J., Cornet, B. and Olsen, P.E., 1994. Geologically rapid Late Triassic extinctions: palynological evidence from the Newark Supergroup. Geological Society of America Special Paper, 288: 197-206.
- Guex, J., Bartolini, A., Taylor, D., 2002. Discovery of *Neophyllites* (Ammonita, Cephalopoda, early Hettangian) in the New York Canyon sections (Gabbs Valley Range, Nevada) and discussion of the $\delta^{13}\text{C}$ negative anomalies located around the Triassic-Jurassic boundary. Bulletin Société Vaudoise Sciences Naturelles, 88.2: 247-255.
- Guex, J., Bartolini, A., Atudorei, V. and Taylor, D., 2003. Two negative $\delta^{13}\text{C}_{\text{org}}$ excursions near the Triassic-Jurassic boundary in the New York Canyon area (Gabbs Valley Range, Nevada). Bulletin de Géologie Lausanne, 360: 1-4.
- Hallam, A., 1981. The end-Triassic bivalve extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology, 35: 1-44.
- Hallam, A., 2002. How catastrophic was the end-Triassic mass extinction? Lethaia, 35: 147-157
- Hallam, A. and Goodfellow, W. D., 1990. Facies and geochemical evidence bearing on the end-Triassic disappearance of the Alpine reef ecosystem. Historical Biology, 4: 131-138.
- Hallam, A. and Wignall, P.B., 1997. Mass Extinctions and their Aftermath. Oxford University Press, Oxford, 320 pp.
- Hallam, A. and Wignall, P.B., 2000. Facies changes across the Triassic-Jurassic boundary in Nevada, USA. Journal Geological Society (London), 157: 49-54.
- Hallam, A., Wignall, P.B., Yin, J. and Riding, J.B., 2000. An investigation into possible facies changes across the Triassic-Jurassic boundary in southern Tibet. Sedimentary Geology, 137: 101-106.
- Helby, R.J., Morgan, R. and Partridge, A.D., 1987. A palynological zonation of the Australian Mesozoic: Memoir Association Australian Paleontology, 4: 1-94.
- Hill, D., Playford, G. and Woods, J.T. (Eds.), 1965. Triassic fossils of Queensland. Queensland Palaeontographical Society, Brisbane, 32 pp.
- Hori, R., 1992. Radiolarian biostratigraphy at the Triassic/Jurassic period boundary in bedded cherts from the Inuyama area, central Japan. J. Geosci., Osaka City Univ. 35, 53-65.
- Huene, F. von, 1934. Ein neuer Coelurosaurier in der thüringischen Trias. Paläontologische Zeitschrift, 16: 145-170.
- Hunt, A.P., 1993. A revision of the Metoposauridae (Amphibia: Temnospondyli) of the Late Triassic with description of a new genus from the western United States. Museum Northern Arizona Bulletin, 59: 67-97.
- Johnson, L.A. and Simms, M.J., 1989. The timing and cause of Late Triassic marine invertebrate extinctions: evidence from scallops and crinoids. In: Donovan, S.K. (Ed.), Mass Extinctions: Processes and Evidence. Columbia Univ. Press, New York, pp. 174-194.
- Kelber, K.-P., 1998. Phytostratigraphische Aspekte der Makroflora des süddeutschen Keupers. Documenta Naturae, 117: 89-115.
- Kennedy, W.J., 1977. Ammonite evolution. In: Hallam, A. (Ed.), Patterns of Evolution as Illustrated in the Fossil Record. Elsevier, Amsterdam, pp. 251-304.
- Kidder, D.L. and Erwin, D.H., 2001. Secular distribution of biogenic silica through the Phanerozoic: comparison of silica-replaced fossils and bedded cherts at the series level. Journal of Geology, 109: 509-522.
- Kiessling, W., 2001. Paleoclimatic significance of Phanerozoic reefs. Geology, 29: 751-754.
- Knoll, A.H., 1984. Patterns of extinction in the fossil record of vascular plants. In: Nitecki, M.H. (Ed.), Extinction. University of Chicago Press, Chicago, pp. 21-68.
- Lucas, S.G., 1994. Triassic tetrapod extinctions and the compiled correlation effect. Canadian Society Petroleum Geologists Memoir, 17: 869-875.
- McElwain, J.C., Beerling, D.J. and Woodward, F.I., 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. Science, 285: 1386-1390.
- McRoberts, C.A., 1994. The Triassic-Jurassic ecostratigraphic transition in the Lombardian Alps, Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, 110: 145-166.
- McRoberts, C. A. and Newton, C. R., 1995. Selective extinction among end-Triassic European bivalves. Geology, 23: 102-104.
- McRoberts, C.A., Furrer, H. and Jones, D.S., 1997. Palaeoenvironmental interpretation of a Triassic-Jurassic boundary section from western Austria based on palaeoecological and geochemical data. Palaeogeography, Palaeoclimatology, Palaeoecology, 136: 79-95.
- McRoberts, C.A., Newton, C.R. and Allasinaz, A., 1995. End-Triassic bivalve extinction: Lombardian Alps, Italy. Historical Biology, 9: 297-317.
- Milner, A.R., 1993. Amphibian-grade Tetrapoda. In: Benton, M. J. (Ed.), The Fossil Record 2. Chapman & Hall, London, pp. 665-679.
- Milner, A.R., 1994. Late Triassic and Jurassic amphibians: Fossil record and phylogeny. In: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of the Dinosaurs. Cambridge Univ. Press, Cambridge, UK, pp. 5-22.

- Molnar, R.E., 1991. Fossil reptiles in Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., Rich, T.H. (Eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, Melbourne, pp. 605-702.
- Morbey, J.S., 1975. The palynostratigraphy of the Rhaetian stage, Upper Triassic in the Kendelbachgraben, Austria. *Palaeontographica B*, 152:1-75.
- Mostler, H., Scheuring, R. and Ulrichs, M., 1978. Zur Mega-, Mikrofauna und Mikroflora der Kossenen Schichten (alpine Obertrias) von Weissloferbach in Tirol unter besonderer Berücksichtigung der in der suessi- und marshi- Zone auftretenden Conodonten. *Osterreichische Akademie der Wissenschaften Erdwissenschaftliche Kommission Schriftenreihe 4*, 141-174.
- Niklas, K.J., Tiffney, B.H. and Knoll, A.H., 1983. Patterns in vascular land plant diversification: A statistical analysis at the species level. *Nature*, 303: 614-616.
- Olsen, P.E. and Sues, H-D., 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic-Jurassic tetrapod transition. In: Padian, K., (Ed.), *The Beginning of the Age of Dinosaurs*. Cambridge Univ. Press, Cambridge, UK, pp. 321-351.
- Olsen, P.E., Fowell, S.J. and Cornet, B., 1990. The Triassic/Jurassic boundary in continental rocks of eastern North America; a progress report. *Geological Society of America Special Paper*, 247: 585-593.
- Olsen, P.E., Shubin, N.H. and Anders, M.H., 1987. New Early Jurassic tetrapod assemblages constrain Triassic-Jurassic tetrapod extinction event. *Science*, 237: 1025-1029.
- Olsen, P.E., Smith, J.B. and McDonald, N.G., 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, U. S. A.): *Journal of Vertebrate Paleontology*, 18: 586-601.
- Olsen, P.E., Kent, D.V., Sues, H.D., Koeberl, C., Huber, H., Montanari, A., Rainforth, E.C., Powell, S.J., Szajna, M.J. and Hartline, B.W., 2002a. Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary. *Science*, 296: 1305-1307.
- Olsen, P.E., Kent, D.V., Sues, H.D., Koeberl, C., Huber, H., Montanari, A.,
- Rainforth, E.C., Powell, S.J., Szajna, M.J. and Hartline, B.W., 2003. Response to comment on "Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary." *Science*, 301: 169c.
- Olsen, P.E., Koeberl, C., Huber, H., Montanari, A., Fowell, S.J., Et-Touhani, M., and Kent, D.V., 2002b. The continental Triassic-Jurassic boundary in central Pangea: recent progress and preliminary report of an Ir anomaly. *Geological Society of America Special Paper*, 356: 505-522.
- Orbell, G., 1973. Palynology of the British Rhaeto-Liasic. *Bulletin Geological Society Great Britain*, 44: 1-44.
- Orchard, M. J., 1991. Upper Triassic conodont biochronology and new index species from the Canadian Cordillera. *Geological Survey Canada, Bulletin*, 417: 299-335.
- Orchard, M. J., 2003. Changes in conodont faunas through the Upper Triassic and implications for boundary definitions. *Geological Association of Canada, Vancouver 2003 Meeting, Abstracts Volume*, 28: CD-ROM.
- Pálfy, J., 2003. Volcanism of the central Atlantic magmatic province as a potential driving force in the end-Triassic mass extinction. *AGU Geophysical Monograph*, 136: 255-267.
- Pedersen, K.R. and Lund, J.J., 1980. Palynology of the plant-bearing Rhaetian to Hettangian Kap Stewart Formation, Scoresby Sund, East Greenland. *Review of Palaeobotany and Palynology*, 31: 1-69.
- Racki, G., 2003. Silica-secreting biota and mass extinctions: survival patterns and processes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 154: 107-132.
- Schuurman, W. M. L., 1979. Aspects of Late Triassic palynology. 3. Palynology of latest Triassic and earliest Jurassic deposits of the northern limestone Alps in Austria and southern Germany, with special reference to a palynological characterization of the Rhaetian stage in Europe. *Review of Palaeobotany and Palynology*, 27: 53-75.
- Sepkoski, J. J., Jr., 1982. Mass extinctions in the Phanerozoic oceans: A review. *Geological Society of America Special Paper*, 190: 283-289.
- Signor, P.W. III and Lipps, J.H., 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. *Geological Society of America Special Paper*, 190: 291-296.
- Simms, M.J. and Ruffell, A.H., 1990. Climatic and biotic change in the Late Triassic. *Journal Geological Society (London)*, 147: 321-327.
- Skelton, P.W. and Benton, M.J., 1993. Mollusca: Rostroconchia, Scaphopoda and Bivalvia. In: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 237-263.
- Staines, H.R.E. and Woods, J.T., 1964. Recent discovery of Triassic dinosaur footprints in Queensland. *Australian Journal of Science*, 27: 55.
- Stanley, G. D., Jr., 1988. The history of early Mesozoic reef communities: a three-step process. *Palaios*, 3: 170-183.
- Sweet, W.C., 1988. *The Conodonta*. Clarendon Press, New York, 212 pp.
- Szajna, M. J. and Silvestri, S. M., 1996. A new occurrence of the ichnogenus *Brachychirotherium*: Implications for the Triassic-Jurassic mass extinction event. *Museum of Northern Arizona Bulletin*, 60: 275-283.
- Tanner, L. H., Lucas, S. G. and Chapman, M. G., 2004. Assessing the record and causes of late triassic extinctions. *Earth-Science Reviews*, 65: 103-139.

- Taylor, D.G., Boelling, K. and Guex, J., 2000. The Triassic/Jurassic System boundary in the Gabbs Formation, Nevada. In: Hall, R.L., Smith, P.L. (Eds.), *Advances in Jurassic Research 2000*. Tran Tech Publications LTD, Zurich, pp. 225-236.
- Taylor, D.G., Guex, J. and Rakus, M., 2001. Hettangian and Sinemurian ammonoid zonation for the western Cordillera of North America. *Bulletin de Géologie de l'Université de Lausanne*, 350: 381-421.
- Teichert, C., 1988. Crises in cephalopod evolution. In: Marois, M. (Ed.), *L'évolution dans sa Réalité et ses Diverses Modalités*. Fondation Singer-Polignac, Paris, pp. 7-64.
- Thulborn, T. 1998. Australia's earliest theropods: footprint evidence in the Ipswich Coal Measures (Upper Triassic) of Queensland. *Gaia*, 15: 301-311.
- Thulborn, T., 2003. Comment on "Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary." *Science*, 301: 169b.
- Tipper, H.W., Carter, E.S., Orchard, M.J. and Tozer, E.T., 1994. The Triassic-Jurassic (T-J) boundary in Queen Charlotte Islands, British Columbia defined by ammonites, conodonts, and radiolarians. *Geobios Mémoire Special*, 17: 485-492.
- Traverse, A., 1988. Plant evolution dances to a different beat. *Historical Biology*, 1: 277-301.
- Ulrichs, M., 1972. Ostracoden aus den Kössener Schichten und ihre Abhängigkeit von der Ökologie. *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten in Österreich*, 21: 661-710.
- Vishnevskaya, V., 1997. Development of Palaeozoic-Mesozoic Radiolaria in the northwestern Pacific rim. *Marine Micropalaeontology*, 30: 79-95.
- Ward, P.D., Haggart, J.W., Carter, E.S., Wilbur, D., Tipper, H.W. and Evans, T., 2001. Sudden productivity collapse associated with the Triassic-Jurassic boundary mass extinction. *Science*, 292: 1148-1151.
- Welles, S.P., 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda) osteology and comparisons. *Palaeontographica A*, 185: 85-180.