Global Jurassic tetrapod biochronology

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ABSTRACT: Jurassic tetrapod fossils are known from all of the continents, and their distribution documents a critical paleobiogeographic juncture in tetrapod evolution – the change from cosmopolitan Pangean tetrapod faunas to the provincialized faunas that characterize the late Mesozoic and Cenozoic. Two global tetrapod biochronological units (faunachrons) have been named for the Early Jurassic – Wassonian and Dawan – and reflect some Early Jurassic tetrapod cosmopolitanism. However, after the Dawan, a scattered and poorly-dated Middle Jurassic tetrapod record and a much better understood Upper Jurassic tetrapod record indicate that significant provincialization of the global tetrapod fauna had begun. Middle Jurassic tetrapod assemblages include distinct local genera of sauropod dinosaurs, which are large, mobile terrestrial tetrapods, and this suggests marked provinciality by Bajocian time. The obvious provincialism of well known Chinese Middle-Upper Jurassic dinosaur faunas also documents the end of tetrapod cosmopolitanism. The distribution of some Late Jurassic dinosaur taxa defines a province that extended from the western USA through Europe into eastern Africa. Provincial tetrapod biochronologies have already been proposed for this province and for the separate eastern Asian Late Jurassic province. Tetrapod footprints only identify two global assemblage zones, one of Early Jurassic and the other of Middle-Late Jurassic age. The incomplete state of Jurassic tetrapod biochronology reflects both an inadequate record with poor temporal constraints and a relative lack of study of the biostratigraphy of Jurassic fossil vertebrates.

INTRODUCTION

Much effort has been expended on developing regional and global tetrapod biochronologies for the Triassic and Cretaceous (see reviews by Lucas 1997, 1998). However, not as much work has been devoted to Jurassic tetrapod biochronology. Here, I review the status of Jurassic tetrapod biochronology and suggest some patterns that are evident and merit further investigation.

EARLY JURASSIC

Late Triassic tetrapod assemblages show a fair degree of cosmopolitanism across Pangea (*e.g.*, Shubin and Sues 1991). Thus, for example, phytosaurs and aetosaurs, two conspicuous groups of Late Triassic crurotarsans, are known from fossils found in North America, South America, Europe, India, North Africa and Madagascar. Indeed, some Late Triassic genera, such as the aetosaur *Stagonolepis*, are known from three or more continents (Lucas 1998). A high degree of cosmopolitanism of some tetrapod taxa continued into the Early Jurassic (Shubin and Sues 1991; Upchurch *et al.* 2002), with broadly similar tetrapod assemblages known from various parts of Pangea (Fig. 1).

Early Jurassic tetrapod assemblages have been assigned to two time intervals (land-vertebrate faunachrons, LVFs), the Wassonian and the Dawan (Fig. 2). The Wassonian is the time between the FAD (first appearance datum) of the crocodylomorph

Protosuchus and the beginning of the Dawan LVF (Lucas and Huber 2003; Lucas *et al.* 2005; Lucas and Tanner 2007). *Protosuchus* (known from Arizona, Nova Scotia and South Africa) is the principal index fossil of the Wassonian LVF.

Tetrapod assemblages of Wassonian age include those of the upper part of the Moenave Formation in Arizona-Utah, USA (Lucas *et al.* 2005), the McCoy Brook Formation in Nova Scotia, Canada (Shubin *et al.* 1994) and the middle to upper Elliot Formation and lower Clarens Formation in South Africa (Kitching and Raath 1984). Some of the Jurassic fissure-fill assemblages in Great Britain (Evans and Kermack 1994) may be of Wassonian age, but this is not certain.

Lucas (1996a) introduced the Dawan LVF as the time equivalent to the vertebrate fossil assemblage of the Lufeng Formation in southern China. The beginning of the Dawan is the FAD of the theropod dinosaur *Megapnosaurus* ("*Syntarsus*") (known from Arizona and southern Africa with certainty, and less certainly from China and Europe) (Lucas and Tanner 2007). The end of the

Dawan LVF is the beginning of the next LVF introduced by Lucas (1996a), the Dashanpuan. The beginning of the Dasahanpuan is the FAD of the sauropod dinosaur *Shunosaurus*.

Index taxa of the Dawan include *Megapnosaurus*, *Dilophosaurus*, *Massospondylus* and *Oligokyphus*. The principal tetrapod assemblages of Dawan age are from the Lufeng Formation in Yunnan, China (Luo and Wu 1994), Kayenta Formation in Arizona, USA (Curtis and Padian 1999) and the Fallan Formation in Antarctica (Hammer and Hickerson 1996). Some of the British fissure-fill assemblages are of Dawan age (they include *Oligokyphus*), and it is likely that the tetrapod assemblages of the La Boca Formation in Mexico (Fastovsky *et al.* 1995) and the Kota Formation of India (Bandyopadhyay and RoyChowdhury 1996) are of Dawan age. However, the possibility that these latter two assemblages are younger than Dawan needs to be considered.

Palynostratigraphy, magnetostratigraphy and radio-isotopic ages from North America indicate the Wassonian is at least in part of Hettangian age
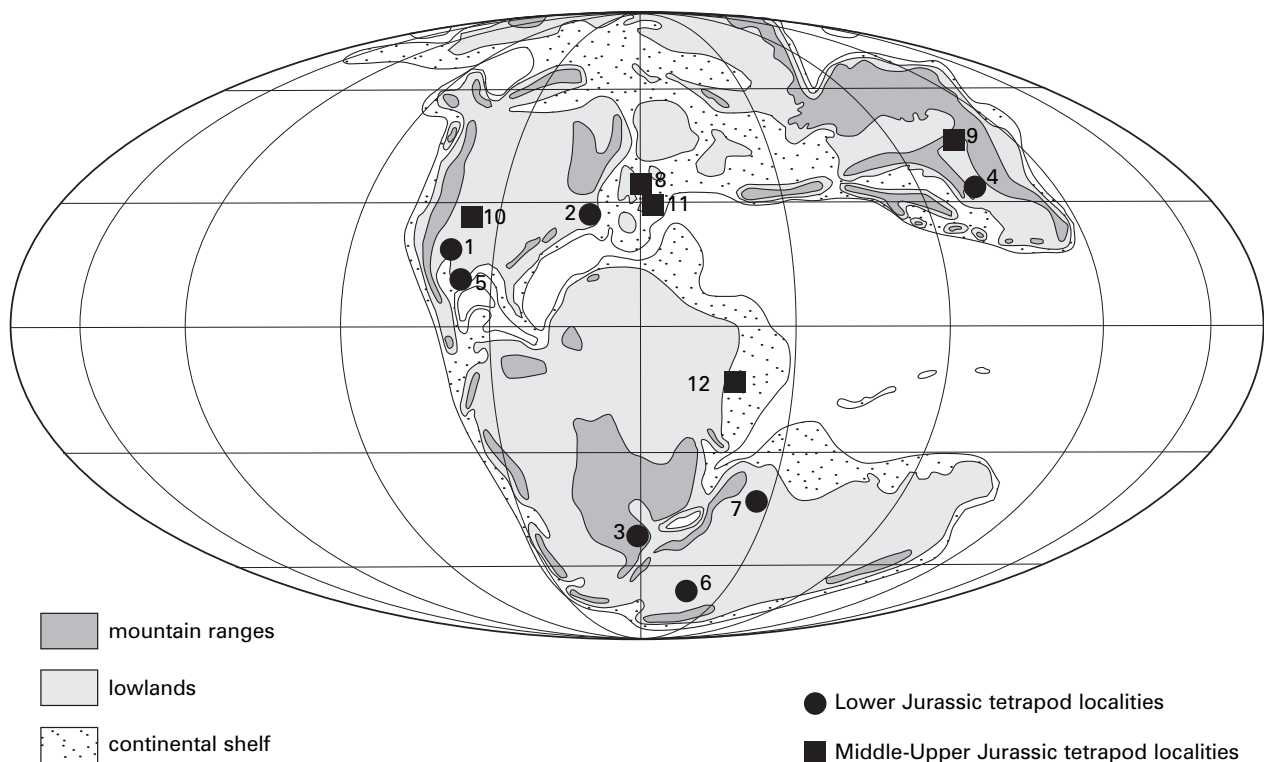

Fig. 1. Map of Late Jurassic continental configuration showing principal Jurassic tetrapod fossil assemblages: 1 – Moenave-Kayenta formations, Arizona-Utah, USA; 2 – McCoy Brook Formation, Nova Scotia; 3 – Elliott-Clarens formations, South Africa; 4 – Lufeng Formation, Yunnan, China; 5 – La Boca Formation, Tamaulipas, Mexico; 6 – Fallan Formation, Antarctica; 7 – Kota Formation, India; 8 – various Middle Jurassic units, United Kingdom – France; 9 – Sichuan basin, China; 10 – Morrison Formation, western USA; 11 – various Upper Jurassic formations, United Kingdom – Spain – Portugal; 12 – Tendaguru Beds, Tanzania.

(Fig. 2) (*e.g.*, Olsen *et al.* 2002; Molina-Garza *et al.* 2003; Lucas *et al.* 2005; Lucas and Tanner 2007). It has been argued that the Dawan is as old as Sinemurian because the Dawan dinosaur *Scelidosaurus* is known from Sinemurian marine strata in the United Kingdom (Padian 1989; Lucas 1996b). However, the possibility that the Dawan is as old as Hettangian based on footprint biostratigraphy (G. Pieńkowski, written commun., 2007) needs to be considered, though at present it is not possible to discriminate distinct footprint assemblages of Wassonian and Dawan age. Dawan time thus equates to part of the Sinemurian, and all of the Pliensbachian, Toarcian and possibly the Aalenian, as the base of the Dashanpuan appears to be Bajocian in age. The Dawan thus represents about 25 million years of geologic time (Fig. 2).

MIDDLE JURASSIC

Middle Jurassic tetrapod assemblages are best known from Europe and southern China, though scattered records are also present in North America, South America, Africa and Australia (Fig. 1). No low level taxa (genera or species) are shared between any of the continents, and it is striking that genera of sauropod dinosaurs, the largest (and presumably most mobile) terrestrial tetrapods, are endemic to the different continents; for example, *Cetiosaurus* in Europe, *Shunosaurus* in China, *Rhoetosaurus* in Australia and *Patagosaurus* in South America. This indicates substantial provincialization of the global terrestrial tetrapod fauna by Middle Jurassic time (*e.g.*, Russell 1993; Upchurch *et al.* 2002).

Most of the Middle Jurassic tetrapod record comprises low diversity assemblages dominated by fragmentary remains of large dinosaurs. Thus, North American Middle Jurassic records include a crocodylomorph and a sauropod, Australian records encompass theropod (*Ozraptor*) and sauropod (*Rhoetosaurus*) dinosaurs, and Middle Jurassic records from North Africa and Madagascar are primarily of sauropod dinosaurs (*Atlasaurus*, *Lapparentasaurus*). These are isolated records whose correlation to each other and to the marine timescale is problematic. In Argentina, the Cañodon Asfalto Formation yields a dinosaur-dominated assemblage of theropods (*Piatnitzkysaurus*) and sauropods (*Patagosaurus*, *Volkheimeria*, *etc.*) that is also endemic and of little biochronological utility.

Ma	SGCS		LVF
—150	LATE	Tithonian	Comobluffian/ Ningjiagouan
		Kimmeridgian	
—160		Oxfordian	
	MIDDLE	Callovian	Tuojiangian
		Bathonian	
—170		Bajocian	Dashanpuan
		Aalenian	
—180	EARLY	Toarcian	Dawan
		Pliensbachian	
—190		Sinemurian	
		Hettangian	Wassonian

Fig. 2. Jurassic timescale (after Ogg, 2004) showing currently named Jurassic land-vertebrate faunachrons (LVFs).

The European Middle Jurassic record is more extensive and diverse; it includes amphibians, turtles, crocodylomorphs, lepidosauromorphs, pterosaurs, dinosaurs and mammals (*e.g.*, Benton and Spencer 1995; Weishampel *et al.* 2004). Much of this record is in marginal marine or marine rocks that can be correlated to the marine timescale (the standard global chronostratigraphic scale), and such correlation suggests there may be two temporally distinct tetrapod assemblages differentiated by their dinosaurs, one of Aalenian-Bathonian age, and the other of Callovian age.

The older assemblage is best known from the United Kingdom (*e.g.*, Inferior Oolite, Chipping Norton Formation, Cotswold Slate, Forest Marble, Stonesfield Slate, Great Oolite) and France, and includes stegosaurs, the theropod *Megalosaurus* and the sauropod *Cetiosaurus*. In the United Kingdom, younger units such as the lower and middle Oxford Clay, yield different stegosaurs (*Lexovisaurus*), the ankylosaur *Sarcolestes* and *Megalosaurus* plus different theropods, and may represent a distinct vertebrate fauna of Callovian age. Similar Callovian assemblages are also known in France and Germany. Further investigation of the European Middle Jurassic tetrapod record is needed to determine if it provides the basis for recognizing two LVFs.

However, even if two LVFs can be recognized in the European Middle Jurassic record, they will only be of provincial use within Europe. Lucas (1996a) proposed two LVFs for the Middle Jurassic of China, and these are of value to correlation in eastern Asia only (Fig. 2). Note also that the two Jurassic "Mongolian land-vertebrate ages" named by Jerzykiewicz and Russell (1991) lack vertebrate characterization, so they have been abandoned (Lucas and Estep 1998; Lucas 2001, 2006).

The Dashanpuan LVF may encompass part of Bajocian time based on correlations of charophytes, ostracods, conchostracans and nonmarine bivalves (Chen *et al.* 1982). It is characterized by a diverse assemblage that includes an amphibian, turtle, pterosaur and dinosaurs, notably the very primitive stegosaur *Huayangosaurus* and the sauropods *Datousaurus* and *Shunosaurus*. The younger Tuojianguian LVF has been assigned a Bathonian-Callovian age based on conchostracans (Chen *et al.* 1982) and is characterized by a diverse assemblage of turtles, crocodiles and dinosaurs, most notably the stegosaur *Tuojiangosaurus*, the theropods *Szechuanosaurus* and *Yangchuanosaurus* and the sauropods *Omeisaurus* and *Mamenchisaurus*. Some workers (*e.g.*, Dong *et al.* 1983) have correlated the Tuojiangian to the Upper Jurassic Morrison Formation in the western USA, but there are no shared low-level vertebrate taxa to support this correlation. Nevertheless, precise correlation of the Tuojiangian (and the Dashan-puan) to the standard global chronostratigraphic is tenuous.

LATE JURASSIC

Late Jurassic tetrapod assemblages (Fig. 1) are better understood in terms of their age relationships than are Middle Jurassic assemblages. Thus, the classic Late Jurassic assemblage in western North America, from the Morrison Formation, is the characteristic assemblage of the Comobluffian LVF of Lucas (1993). It has long been correlated to the Tendaguru Beds of Tanzania and to Upper Jurassic strata in the United Kingdom, Spain and Portugal based largely on shared dinosaur genera, such as *Allosaurus*, *Ceratosaurus* and/or *Brachiosaurus* (Lucas 1993; Mateus 2006). The broad geographic distribution of these genera suggests a single paleobiogeographic province that extended from western North America through western Europe into eastern Africa during the Late Jurassic (*e.g.*, Upchurch *et al.* 2002).

In contrast, the well known Chinese Upper Jurassic tetrapod assemblages are essentially endemic at the generic level, most notably the sauropod dinosaurs. These are tetrapods of the Ningjiagouan LVF of Lucas (1996a) and include uniquely Chinese taxa, such as the turtle *Sinemys* and the sauropod dinosaur *Euhelopus*. Late Jurassic tetrapod records, from South America and other regions, are very poorly known.

JURASSIC TETRAPOD FOOTPRINT BIOSTRATIGRAPHY

Dinosaur tracks dominate the global Jurassic tetrapod footprint record, and it is a truly global footprint record, with tracksites on all of the continents except Antarctica. Nevertheless, at the level of a global footprint biostratigraphy, I can only recognize two assemblages (Lucas 2007).

Early Jurassic tetrapod footprint assemblages are dinosaur dominated. The absence of some characteristic Late Triassic footprint ichnogenera (especially *Brachychirotherium*), and the appearance of a few characteristic Early Jurassic ichnogenera (such as *Otozoum*), distinguish the Jurassic record from the earlier Triassic record.

The classic Early Jurassic tetrapod footprint assemblages are from the Newark Supergroup of eastern North America. In the western United States (especially Arizona and Utah), strata of much of the Glen Canyon Group (upper Moenave,

Kayenta and Navajo formations) in Arizona and Utah yield extensive Early Jurassic tetrapod footprint assemblages (*e.g.*, Lockley and Hunt 1995). In the European Lower Jurassic, the principal tetrapod footprint sites are in France, Sweden, Hungary and Poland (*e.g.*, Gierliński 1991, 1997; Gierliński and Ahlberg 1994; Gierliński and Pieńkowski 1999; Lockley and Meyer 2000; Avanzini *et al*. 2001; Gierliński *et al*. 2001, 2004). Like the North American Lower Jurassic, many of these sites are theropod-footprint dominated (ichnogenera *Eubrontes* and *Grallator*), but include other ichnogenera such as *Anomoepus* and *Moyenosauripus* attributed to ornithopods and thyreophorans. In the North American and European Lower Jurassic, sauropod tracks are conspicuous in their virtual absence except in northern Italy (Avanzini *et al*. 1997, 2003).

Sauropod tracks are also known from the Lower Jurassic of Morocco and Afghanistan (Ishigaki 1988; Farlow 1992). Lower Jurassic tracks are abundant in China, and the assemblages are theropod dominated. Major tracksites are in the Fengjiahe Formation of Yunnan Province (Zhen *et al*. 1986, 1989), and include *Eubrontes* and other widely distributed forms (Lockley *et al*. 2003).

In southern Brazil, the Botucatú Formation, probably of Early Jurassic age (though an age as young as Early Cretaceous has been suggested), yields theropod and therapsid tracks (Leonardi 1981; Leonardi and Sarjeant 1986). In Australia, Lower Jurassic tracks from Carnarvon Gorge in Queensland are of large theropods, small theropods, ornithopods and thyreophorans (Bartholomai 1966; Hill *et al*. 1966; Molnar 1980, 1991).

Ellenberger (1970, 1972, 1974, 1975) described Late Triassic-Early Jurassic footprint assemblages from southern Africa, introducing 69 new ichnogenera and 174 new ichnospecies, many as *nomina nuda*. Olsen and Galton (1984) reviewed the literature and published a sweeping revision of the Early Jurassic footprint assemblages described by Ellenberger from the upper part of the Stormberg Group (upper Elliott and Clarens formations and equivalents). They thus revised the upper Stormberg footprint fauna to include *Batrachopus* (crocodylomorph), theropod tracks referable to *Grallator* (*Anchisauripus*) and *Grallator* (*Eubrontes*), *Anomoepus* sp. (Ornithischia), *Ameghinichnus* sp. (mammal or therapsid) and the enigmatic *Episcopopus ventrosus*.

I suspect that more of Ellenberger's ichnotaxa are valid than Olsen and Galton concede (also see Lockley and Meyer 2000), but the important point is that the Lower Jurassic footprint assemblages from southern Africa are theropod dominated and include numerous synapsid/mammal tracks.

Lockley (1993; Lockley and Hunt 1994, 1995) identified two temporally successive footprint Early Jurassic assemblages in the Glen Canyon Group of the western United States, an older, *Anomoepus-Eubrontes* zone (with *Batrachopus*) in the upper Wingate-Moenave-lower Kayenta (Hettangian-Sinemurian) and a younger, *Otozoum-Brasilichnium* zone in the upper Kayenta-Navajo (Pliensbachian-Toarcian). However, according to Rainforth (2003), *Otozoum* is present in Hettangian strata of the Newark Supergroup, the Navajo Sandstone in the western United States and the Clarens Formation in South Africa. Lockley *et al*. (2004) recently documented an occurrence in the Wingate Sandstone of probable Hettangian age. This means that *Otozoum* has a temporal range of Hettangian through Toarcian. *Batrachopus* is known from the Upper Triassic of the Newark Supergroup (Szajna and Silvestri 1996), and, in addition to its Hettangian records, *Eubrontes* occurs in the Navajo Sandstone (Rainforth and Lockley 1996). Thus, currently understood stratigraphic ranges of tetrapod footprints do not support recognition of two Lower Jurassic footprint zones, though there are trends in footprint size and diversity in the Lower Jurassic strata that may enable future biostratigraphic subdivision (Lucas *et al*. 2006). Indeed, the global stratigraphic ranges of tetrapod footprints do not support recognition of more than one Lower Jurassic footprint zone (Lucas 2007).

The widespread tetrapod footprint record of the Middle Jurassic is more sparse than those of the Early Jurassic and the Upper Jurassic. However, during the Middle Jurassic, the footprint record includes larger theropod tracks (up to 77 cm long) than did earlier records, and sauropod tracks first become abundant and widespread (Lockley *et al*. 1994). The Middle and Late Jurassic footprint record thus is a global record dominated by large theropod and sauropod tracks. It may be possible, with a more extensive Middle Jurassic footprint record, to separate the Middle and Late Jurassic into separate assemblages, but for now I combine them into a single global assemblage.

Significant Middle Jurassic footprint records are in the San Rafael Group of the western United States, where tracksites are theropod dominated (Lockley and Hunt 1995; Lockley *et al.* 1996). Particularly noteworthy is the Moab megatracksite in the Entrada Sandstone (Callovian) of southeastern Utah, which preserves many thousands of theropod (and rare sauropod) tracks (Lockley 1991).

In contrast, Middle Jurassic tracksites in Portugal (Fatima) are sauropod dominated (Santos *et al.* 1994). Sauropod and theropod tracksites, and probable thyreophoran tracks (ichnogenus *Deltapodus*), are known from the Middle Jurassic of England (Whyte and Romano 1994). In China, a few theropod-dominated tracksites have been reported to be Middle Jurassic (Zhen *et al.* 1989) but may be older (Early Jurassic; Lockley *et al.* 2003). Middle Jurassic sauropod tracks are known from Morocco (Ishigaki 1989), and theropod-dominated tracksites are present in Santa Cruz Province, Argentina (Leonardi 1994). Middle Jurassic mammal tracks are very rare, and include *Ameghinichnus* from Argentina (Casamiquela 1964) and *Pooleyichnus* (doubtfully a mammal track) from England (Sarjeant 1975).

Large theropod ("megalosaur") and sauropod tracks also dominate the Late Jurassic tetrapod footprint record (Farlow 1992; Lockley *et al.* 1994, 1996). Sauropod-dominated Late Jurassic tracksites are found in the western United States (Lockley and Hunt 1995), Chile (Dingman and Galli 1965), Tadjikistan (Lockley *et al.* 1994), Spain (Mensink and Mertmann 1984), Germany (Kaever and Lapparent 1974), Switzerland (Meyer 1993), Portugal (Santos *et al.* 1994) and Niger (Ginsburg *et al.* 1966). Large theropod tracks of Late Jurassic age are well known from Australia, Utah, Arizona, New Mexico, Oklahoma, Croatia, England, Spain, Brazil and Uzbekistan (*e.g.*, Haubold 1971; Lockley *et al.* 1996; Lucas 2007).

The lowest occurrence of pterosaur tracks is in Upper Jurassic rocks in the western United States and France (Lockley and Rainforth 2002). This could be used to distinguish between Middle and Late Jurassic tetrapod footprint assemblages. However, the body fossil record of pterosaurs extends back to the Late Triassic, so it is likely that pterosaur tracks older than Late Jurassic will be discovered.

Lockley (1998; Lockley *et al.* 1996; Lockley and Meyer 2000) has advocated some relatively precise footprint-based Jurassic correlations. These use the theropod ichnogenus *Carmelopodus* (correlates Bajocian/Bathonian strata in the United States and Europe), the theropod ichnogenus *Megalosauripus* (correlates Oxfordian/Kimmeridgian strata in the United States, Europe and Middle Asia), the ornithopod ichnogenus *Dinehichnus* (correlates Kimmeridgian strata in the United States and Europe) and the enigmatic ichnogenus *Ravatichnus* (correlates Bajocian strata in Europe and Middle Asia). The correlation based on *Megalosauripus* is impressive because it is widespread and abundant. The other ichnogenera are rare, so their stratigraphic ranges may not be well established. Furthermore, recent discoveries in Spain suggest that some of these characteristic Jurassic ichnotaxa may occur in the lowermost Cretaceous (Barco *et al.* 2004). Clearly, if these correlations withstand further testing, they will be some of the most precise correlations based on the Jurassic tetrapod footprint record.

CONCLUSIONS

Current tetrapod biochronology of the Jurassic provides very poor temporal resolution. The two globally correlateable Early Jurassic LVFs represent about 24 million years; one is about 4 million years long, whereas the other is about 20 million years long. Only provincial biochronological units can be recognized in the Middle and Late Jurassic, and at most three have been identified to encompass about 27 million years. Thus, the Jurassic LVFs are resolving Jurassic time less than half as well as do the Jurassic marine stages: 11 stages vs. at most five LVFs. Footprint biostratigraphy identifies only two intervals of Jurassic time, Early and Middle-Late Jurassic. Correlation of Jurassic tetrapod assemblages to the SGCS is also imprecise and in many cases tenuous.

Several factors contribute to the poor state of Jurassic tetrapod biochronology: (1) a poor record of low diversity assemblages widely scattered geographically, especially in the Middle Jurassic; (2) poor temporal constraints on the Jurassic vertebrate fossil record from other means of age determination, such as magnetostratigraphy, radioisotopic dates and other biostratigraphic methods (palynostratigraphy, conchostracans); and (3) relatively little effort has been expended on developing a Jurassic tetrapod biostratigraphy and biochronology. Further collecting, discovery

and biostratigraphic research are thus needed to improve our understanding of Jurassic tetrapod biochronology.

Acknowledgments

REFERENCES

Avanzini M., van den Dreissche K. and Keppens E. 1997. A dinosaur tracksite in an early Liassic tidal flat in northern Italy: Paleoenvironmental reconstruction from the sedimentology and geochemistry. *Palaios,* **12**: 538-51.

Avanzini M., Gierliński G. and Leonardi G. 2001. First report of sitting *Anomoepus* tracks in European Lower Jurassic (Lavini di Marco site-northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia,* **107**: 131-136.

Avanzini M., Leonardi G. and Mietto P. 2003. *Lavinipes cheminii* ichnogen., ichnosp. nov., a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. *Ichnos*, **10**: 179-193.

Bandyopadhyay S. and RoyChowdhury T. K. 1996. Beginning of the continental Jurassic in India: A paleontological approach. *Museum of Northern Arizona Bulletin*, **60**: 371-378.

Barco J. L., Canudo J. L. and Ruiz-Omeñaca J. I. 2004. Presencia de la icnoasociación *Megalosauripus-Therangospodus* en el Berrianense (Cretácico inferior) de la Península Ibérica (Cuenca de Cameros, Soria): Implicaciones paleobiogegráficas. *Geo-Temas*, **6**: 15-18.

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

Benton M. J. and Spencer P. S. 1995. Fossil reptiles of Great Britain, 1-386. Chapman & Hall, London.

Casamiquela R. M. 1964. Estudios Icnológicos; Problemas y métodos de la icnología con aplicación al estudio de pisadas mesozóicas (Reptilia, Mammalia) de la Patagonia, 1-125. Ministério do Asundos Sociales, Buenos Aires.

Chen P., Li W., Chen J., Ye C., Wang Z., Shen Y. and Sun S. 1982. Stratigraphical classification of Jurassic and Cretaceous in China. *Scientia Sinica Series B*, **25**: 1227-1248.

Curtis K. and Padian K. 1999. An Early Jurassic microvertebrate fauna from the Kayenta of northeastern Arizona: Microfaunal change across the Triassic-Jurassic boundary. *Paleobios,* **19**: 19-37.

Dingman R. J. and Galli C. O. 1965. Geology and ground water resources of the Oica area, Tarapaca Province, Chile. *U.S. Geological Survey Bulletin*, **1189**: 1-113.

Dong Z., Zhou S. and Zhang Y. 1983. The dinosaurian remains from Sichuan Basin, China. *Palaeontologia Sinica Series C*, **23**: 1-147.

Ellenberger P. 1970. Les niveaux paléontologiques de premiere apparition des mammiferes primordiaux en Afrique du Sud et leur ichno-logie: Establissement de zones stratigraphiques detaillées dans le Stormberg du Lesotho, (Afrique du Sud) (Triassique supérieur à Jurassique. *In*: S. H. Haughton (*Ed*.), *International Union of Geological Sciences, Second Symposium on Gondwana Stratigraphy and Paleontology*, 347-370. Council for Scientific and Industrial Research, Pretoria.

Ellenberger P. 1972. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stromberg d'Afrique du Sud (I). *Palaeovertebrata, Mémoire Extraordinaire*: 1-152.

Ellenberger P. 1974. Contribution à la classification des pistes de vertébrés du Trias: Les types du Stromberg d'Afrique du Sud (II partie: Le Stromberg supérieur – I. Le biome de la zone B/1 ou niveau de Moyeni: ses biocenoses). *Palaeovertebrata, Mémoire Extraordinaire*: 1-142.

Ellenberger P. 1975. L'explosion démographique des petits quadrupeds à allure de mammiféres dans le Stormberg supérieur (Trias) d'Afrique du Sud: Aperćus sur leur origine au Permien (France et Karroo). *Colloque Internationale du Centre National de la Recherche Scientifique,* **218**: 409-432.

Evans S. E. and Kermack K. A. 1994. Assemblages of small tetrapods from the early Jurassic of Britain. *In*: N. C. Fraser and H-D. Sues (*Eds*), In the shadow of the dinosaurs early Mesozoic tetrapods, 271-294. Cambridge University Press.

Farlow J. O. 1992. Sauropod tracks and trackmakers: Integrating the ichnological and skeletal records. *Zubia,* **10**: 89-138.

Fastovsky D. E., Clark J. M., Strater N. H., Montellano M., Hernandez R. and Hopson J. A. 1995. Depositional environments of a Middle Jurassic terrestrial vertebrate assemblage, Huizachal Canyon, Mexico. *Journal of Vertebrate Paleontology*, **15**: 561-575.

Gierliński G. 1991. New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeclimatology, Palaeoecology*, **85**: 137-148.

Gierliński G. 1997. Sauropod tracks in the Early Jurassic strata of Poland. *Acta Palaeontologica Polonica*, **42**: 533-538.

Gierliński G. and Ahlberg A. 1994. Late Triassic and Early Jurassic dinosaur footprints in the Hoganas Formation of southern Sweden. *Ichnos*, **3**: 99-105.

Gierliński G., Niedźwiedzki G. and Pieńkowski G. 2001. Gigantic footprint of a theropod dinosaur in the Early Jurassic of Poland. *Acta Palaeontologica Polonica*, **46**: 441-446.

Gierliński G., Niedźwiedzki G. and Pieńkowski G. 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its palaeoenvironmental background. *Ichnos*, **11**: 195-213

Gierliński G. and Pieńkowski G. 1999. Dinozaur track assemblage from Hettangian of Poland. *Geological Quarterly*, **43**: 329-346.

Ginsburg L., Lapparent A. F. de Loiret B. and Taquet P. 1966. Empreintes de pas de vertebres tetrapodes dans les séries continentals a l'Ouest d'Agades (Republique du Niger). *Compte Rendus Academie Science Paris,* **263**: 28-31.

Hammer W. R. and Hickerson W. J. 1996. Implications of an Early Jurassic vertebrate fauna from Antarctica. *Museum of Northern Arizona Bulletin*, **60**: 215-218.

Haubold H. 1971. Ichnia amphibiorum et reptiliorum fossilium. *Encyclopedia of Paleoherpetology,* **18**: 1-124.

Hill D., Playford G. and Woods J. T. 1966. Jurassic fossils of Queensland. 1-38. Queensland Palaeontological Society, Brisbane.

Ishigaki S. 1988. Les empreites de dinosaurs du Jurassique inférieur du Haut Atlas central marocain. *Notes Service Geologique Maroc,* **44**: 79-86.

Ishigaki S. 1989. Footprints of swimming sauropods from Morocco. *In*: D. D. Gillette and M. G. Lockley (*Eds*), Dinosaur Tracks and Traces, Cambridge University Press, Cambridge: 83-86.

Jerzykiewicz T. and Russell D. A. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi basin. *Cretaceous Research*, **12**: 345-377.

Kaever M. and de Lapparent A. F. 1974. Dinosaur footprints of Jurassic age from Barkhausen. *Bulletin de la Société Géologique de France,* **16**: 516-25.

Kitching J. W. and Raath M. A. 1984. Fossils from the Elliott and Clarens formations (Karoo Sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia Africana*, **25**: 111-125.

Leonardi G. 1981. As localidades com rastros fósseis de tetrápodes na América Latina. *Anais 2° Congreso Latinoamericano de Paleontologia Porto Alegre,* **2**: 929-40.

Leonardi G. 1994. Annotated atlas of South American tetrapod footprints (Devonian to Holocene). 1-212. Ministério de Minas e Energia, Brasilia.

Leonardi G. and Sarjeant W. A. S. 1986. Footprints representing a new Mesozoic vertebrate fauna from Brazil. *Modern Geology,* **10**: 73-84.

Lockley M. G. 1991. The Moab megatracksite: A preliminary description and discussion of millions of middle Jurassic tracks in eastern Utah. *In*: W. R. Averitt (*Ed*.), Guidebook for dinosaur quarries and tracksites tour, Western Colorado and Eastern Utah, 59-65. Grand Junction Geological Society, Grand Junction.

Lockley M. G. 1993. Auf der Spuren der Dino-Saürier. 1-212. Birkhaüser, Basel.

Lockley M. G., 1998. The vertebrate track record. *Nature,* **396**: 429-432.

Lockley M. G. and Hunt A. P. 1994. A review of Mesozoic vertebrate ichnofaunas of the Western Interior Unites States: Evidence and implications of a superior track record. *In*: M. V. Caputo, J. A. Peterson and K. J. Franczyk (*Eds*), Mesozoic Systems of the Rocky Mountain Region, USA, 95-108. RMS-SEPM, Denver.

Lockley M. G. and Hunt A. P. 1995. Dinosaur tracks and other fossil footprints of the Western United States. 1-338. Columbia University Press, New York.

Lockley M. G. and Meyer C. 2000. Dinosaur tracks and other fossil footprints of Europe. 1-323. Columbia University Press, New York.

Lockley M. G. and Rainforth E. C. 2002. The track record of Mesozoic birds and pterosaurs: An ichnological and paleoecological perspective. *In*: L. M. Chiappe and L. M. Witmer (*Eds*). Mesozoic birds above the heads of dinosaurs, 405-418. University of California Press, Berkeley.

Lockley M. G., Meyer C. A., Hunt A. P. and Lucas S. G. 1994. The distribution of sauropod tracks and trackmakers. *Gaia*, **10**: 233-48.

Lockley M. G., Hunt A. P. and Lucas S. G. 1996. Vertebrate track assemblages from the Jurassic Summerville Formation and correlative deposits. *Museum of Northern Arizona Bulletin,* **60**: 249-254.

Lockley M. G., Lucas S. G., Hunt A. P. and Gaston R. 2004. Ichnofaunas from the Triassic-Jurassic boundary sequences of the Gateway area, Western Colorado: Implications for faunal composition and correlation with other areas. *Ichnos,* **11**: 89-102.

Lockley M. G., Matsukawa M. and Li J. 2003. Crouching theropods in taxonomic jungles: Ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos,* **10**: 169-177.

Lucas S. G. 1993. Vertebrate biochronology of the Jurassic-Cretaceous boundary, North American Western Interior. *Modern Geology,* **18**: 371-390.

Lucas S. G. 1996a. Vertebrate biochronology of the Jurassic of China. *Museum of Northern Arizona Bulletin,* **60**: 23-33.

Lucas S. G. 1996b. The thyreophoran dinosaur *Scelidosaurus* from the Lower Jurassic Lufeng Formation, Yunnan, China: *Museum of Northern Arizona Bulletin,* **60**: 81-85.

Lucas S. G. 1997. Land-mammal ages. *In*: P. J. Currie and K. Padian (*Eds*), Encyclopedia of dinosaurs, 395-398. Academic Press, San Diego.

Lucas S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **143**: 347-384.

Lucas S. G. 2001. Chinese fossil vertebrates, 1-375. Columbia University Press, New York.

Lucas S. G. 2006. The *Psittacosaurus* biochron, Early Cretaceous of Asia. *Cretaceous Research*, 27: 189-198.

Lucas S. G. 2007. Tetrapod footprint biostratigraphy and biochronology. *Ichnos*, **14**: 5-38.

Lucas S. G. and Estep. J. W. 1998. Vertebrate biostratigraphy and biochronology of the Cretaceous of China. *New Mexico Museum of Natural History and Science Bulletin*, **14**: 1-20.

Lucas S. G. and Huber P. 2003. Vertebrate biostratigraphy and biochronology of the non-marine Late Triassic. *In*: P. M. LeTourneau and P. E. Olsen (*Eds*), The great rift valleys of Pangea in eastern North America. Volume 2. Sedimentology, stratigraphy, and paleontology, 143-191. Columbia University Press, New York.

Lucas S. G. and Tanner L. H. 2007. Tetrapod biostratigraphy and biochronology of the Triassic-Jurassic transition on the southern Colorado Plateau, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **244**: 242-256.

Lucas S. G., Tanner L. H. and Heckert A. B. 2005. Tetrapod biostratigraphy and biochronology across the Triassic-Jurassic boundary in north-eastern Arizona: *New Mexico Museum of Natural History and Science Bulletin*, **29**: 84-94.

Lucas S. G., Lockley M. G., Hunt A. P., Milner A. R. C. and Tanner L. H. 2006. Tetrapod footprint biostratigraphy of the Triassic-Jurassic transition in the American Southwest: *New Mexico Museum of Natural History and Science Bulletin*, **37**: 105-108.

Luo Z. and Wu X. 1994. The small tetrapods of the lower Lufeng Formation, Yunnan, China. *In*: N. C. Fraser and H-D. Sues (*Eds*), In the shadow of the dinosaurs: Early Mesozoic tetrapods, 251-270. Cambridge University Press, Cambridge.

Mateus O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinh and Alcobaća formations (Portugal), and the Tendaguru beds (Tanzania): a comparison. *New Mexico Museum of Natural History and Science Bulletin*, **36**: 223-231.

Mensink H. and Mertmann D. 1984. Dinosauries-Fährten (*Gigantosauropus asturiensis* n.g. n.sp.; *Hispanosauropus hauboldi* n.g. n.sp.) im Jura Asturiens bei La Griega und Ribadesella (Spanien). *Neues Jahrbuch für Geologie und Paläontologie*: 405-415.

Meyer C. A. 1993. A sauropod dinosaur megatrack-site from the Late Jurassic of northern Switzerland. *Ichnos,* **3**: 29-38.

Molina-Garza R. S., Geissman J. W. and Lucas S. G. 2003. Paleomagnetism and magnetostratigraphy of the lower Glen Canyon and upper Chinle groups, Triassic-Jurassic of northern Arizona and northeast Utah. *Journal of Geophysical Research,* **108**, B4: 1-24.

Molnar R. 1980. Australian late Mesozoic terrestrial tetrapods, some implications. *Memoire Société Géologique de France*, **139**: 131-143.

Molnar R. E. 1991. Fossil reptiles in Australia. *In*: P. Vickers-Rich, J. M. Monaghan, R. F. Baird and T. H. Rich (*Eds*), Vertebrate palaeontology of Australasia, 605-702. Pioneer Design Studio, Melbourne.

Ogg J. G. 2004. The Jurassic Period. *In*: F. M. Gradstein, J. G. Ogg and A. G. Smith (*Eds*),

A geological time scale 2004, 307-343. Cambridge University Press.

Olsen P. E. and Galton P. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Paleontologia Africana,* **25**: 87-110.

Olsen P. E., Koeberl C., Huber H., Montanari A., Fowell S. J., Et-Touhani M. and Kent D. V. 2002. 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.

Padian K. 1989. Presence of the dinosaur *Scelidosaurus* indicates Jurassic age for the Kayenta Formation (Glen Canyon Group, northern Arizona). *Geology*, **17**: 438-441.

Rainforth E. C. 2003. Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus *Otozoum*. *Palaeontology*, **46**: 803-838.

Rainforth E. C. and Lockley M. G. 1996. Tracking life in a Lower Jurassic desert: Vertebrate tracks and other traces from the Navajo Sandstone. *Museum of Northern Arizona Bulletin,* **60**: 285-289.

Russell D. A. 1993. The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences,* **30**: 2002-2012.

Santos V. F., Lockley M. G., Meyer C. A., Carvalho J., Galopim de Carvalho A. M. and Moratalla J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia,* **10**: 5-13.

Sarjeant W. A. S. 1975. A vertebrate footprint from the Stonesfield Slate (Middle Jurassic) of Oxfordshire. *Mercian Geologist,* **5**: 273-277.

Shubin N. J. and Sues H. -D. 1991. Biogeography of early Mesozoic continental tetrapods. Patterns and implications. *Paleobiology* **17**: 214-230.

Shubin N. H., Olsen P. E. and Sues H. -D. 1994. Early Jurassic small tetrapods from the Mccoy Brook Formation of Nova Scotia, Canada. *In*: N. C. Fraser and H. D. Sues (*Eds*), In the shadow of dinosaurs: Early Mesozoic tetrapods, 242-250. Cambridge University Press, Cambridge.

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.

Upchurch P., Hunn C. A. and Norman D. B. 2002. An analysis of dinosaurian biogeography: Evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings Royal Society London B*, **269**: 613-621.

Weishampel D. B., Barrett P. M., Coria R. A., LeLoeuff J., Xu X., Zhao X., Sahni A., Gomani E. and Noto C. R. 2004. Dinosaur distribution. *In*: D. B. Weishampel, P. Dodson and H. Osmólska (*Eds*), The Dinosauria Second Edition, 517-606. University of California Press, Berkeley.

Whyte M. A. and Romano M. 1994. Probable sauropod footprints from the Middle Jurassic of Yorkshire, England. *Gaia,* **10**: 15-26.

Zhen S., Zhen B. and Rao C. 1986. Dinosaur footprints of Jinning, Yunnan. *Memoirs Beijing Museum of Natural History,* **33**: 1-18.

Zhen S., Li R., Rao C., Mateer N., and Lockley M. G. 1989. A review of dinosaur footprints in China. *In*: D. D. Gillette and M. G. Lockley (*Eds*), Dinosaur tracks and traces, 187-198. Cambridge University Press, Cambridge.