

# THE RHYNCHOSAUR *HYPERODAPEDON* FROM THE UPPER TRIASSIC OF WYOMING AND ITS GLOBAL BIOCHRONOLOGICAL SIGNIFICANCE

SPENCER G. LUCAS<sup>1</sup>, ANDREW B. HECKERT<sup>1</sup> and NICHOLAS HOTTON III<sup>2†</sup>

<sup>1</sup>New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104-1375;

<sup>2</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (†deceased)

**Abstract**—Fragmentary fossils collected by one of us (NH) from the Upper Triassic Popo Agie Formation represent the first occurrence of the rhynchosaur *Hyperodapedon* in the Chinle Group. The Wyoming record is of Otischalkian (Late Triassic: late Carnian) age. Globally, *Hyperodapedon* occurrences define a *Hyperodapedon* biochron of late to latest Carnian (Otischalkian-Adamanian) age for strata in North America, Scotland, India, Tanzania, Zimbabwe, Madagascar, Argentina, and Brazil. This resolution is coarser than that achieved using other taxa, principally phytosaurs and aetosaurs, but helps to correlate strata in which these taxa are rare or absent.

**Keywords:** rhynchosaur, *Hyperodapedon*, Wyoming, biochronology, Late Triassic, Popo Agie.

## INTRODUCTION

Rhynchosaurs are an order of primitive archosauromorph reptiles with an Upper Triassic fossil record from all modern continents except Antarctica and Australia. Hunt and Lucas (1991a) last reviewed the global record of Late Triassic rhynchosaurs and placed them in a biochronological framework. However, in the decade that has passed since their article, new discoveries and taxonomic revisions have greatly altered our understanding of Late Triassic rhynchosaur distribution and taxonomy. Particularly important is recognition of the wide distribution of *Hyperodapedon* Huxley, based on a revision of some South American and Malagasy rhynchosaurs (Contreras, 1999; Langer and Schultz, 2000; Langer et al., 2000a,b). Furthermore, a rhynchosaur discovered by one of us (NH) in the Popo Agie Formation of Wyoming can also be assigned to *Hyperodapedon* (Figs. 1,2). Here, we document this first Chinle Group record of *Hyperodapedon* and define a Pangean *Hyperodapedon* biochron of Otischalkian-Adamanian age. USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

## POPO AGIE HYPERODAPEDON

### Description

USNM 494329 (Fig. 2) is a left maxilla, premaxilla and other cranial fragments of a rhynchosaur collected by N. Hotton III near Willow Creek, Wyoming in the SW1/4 SW1/4 SW1/4 sec. 10, T41N, R83W, Natrona County. The locality is in a conglomerate bed in the lower part of the Popo Agie Formation of the Chinle Group (Fig. 1).

The most significant element of USNM 494329 is the incomplete left maxilla (Fig. 2D-G). Seen ventrally (occlusally), the maxilla is a posteriorly widening, triangular wedge of bone that is curved, so that it is concave medially and convex laterally. The ventral surface has a single, central groove flanked by tooth rows on each side. On USNM 494329, much of the lateral tooth field is preserved and shows two rows of teeth with oval cross sections. The posterior portion of the preserved central groove contains the broken tips of part of the single row of dentary teeth (Fig. 2F-G). Comparison to illustrations of Benton (1984, figs. 6, 15, 53) indicate that USNM 494329 only preserves the anterior half, at most, of a left maxilla.

Other significant elements preserved include an incomplete left premaxilla and dentary. Part of the left premaxilla is present, and it is an edentulous, blade-like bone that is laterally compressed

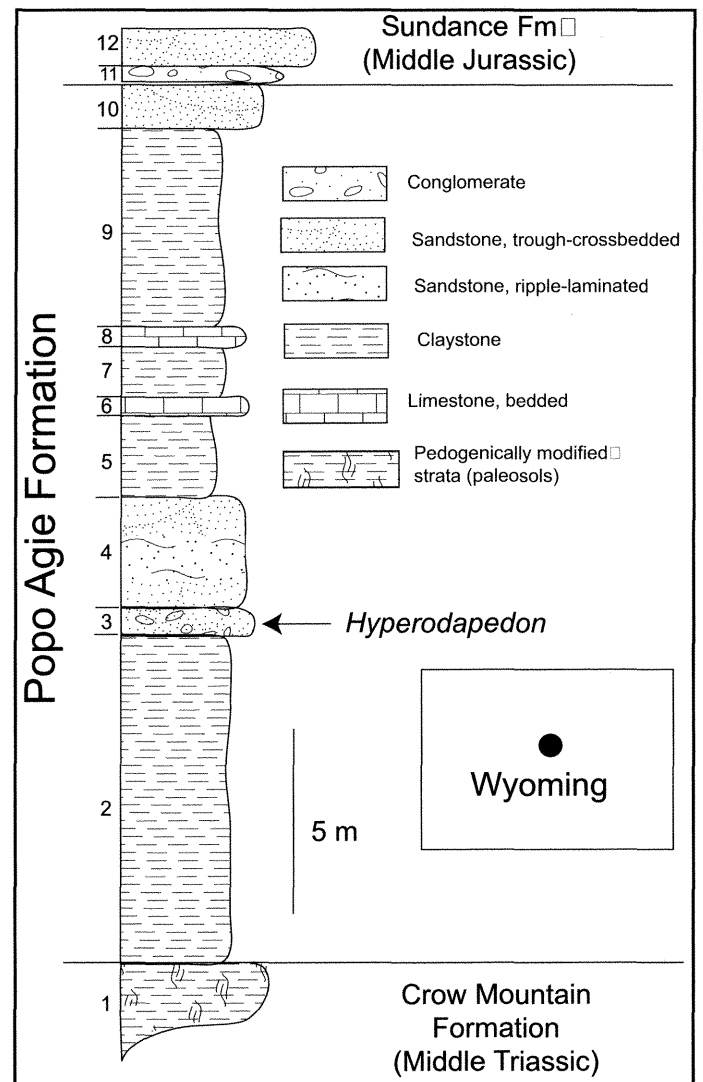


FIGURE 1. Map of Wyoming (inset) and measured stratigraphic section at Willow Creek showing the *Hyperodapedon* locality in the Popo Agie Formation of the Chinle Group.

and tapers distally (Fig. 2A-C). A piece of the left dentary has the bases of a single row of teeth on the occlusal surface (Fig. 2H-J). It

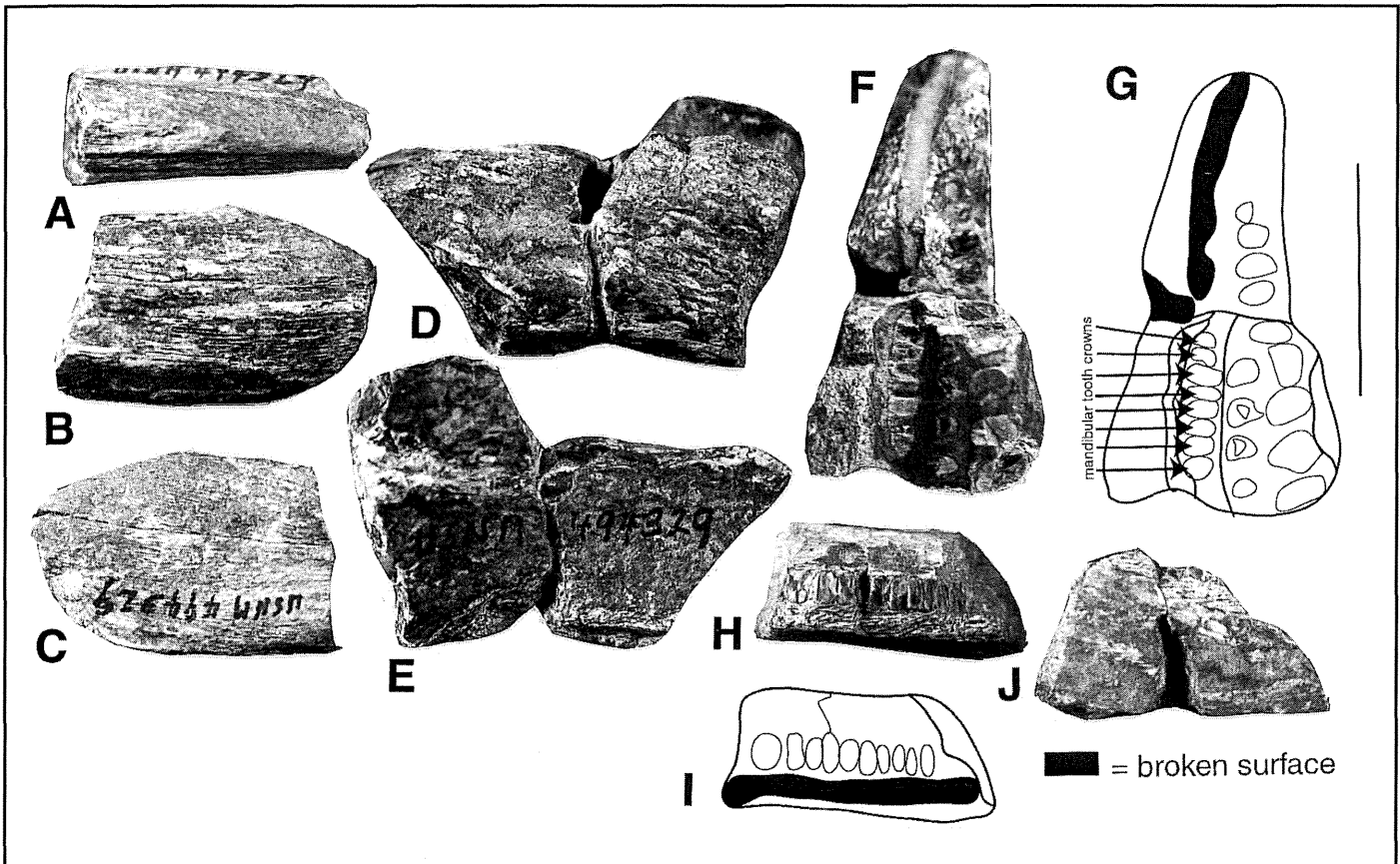


FIGURE 2. USNM 494329, *Hyperodapedon* cf. *H. sanjuanensis* from the Popo Agie Formation of the Chinle Group in Wyoming. A-C, Left? premaxilla in A, ventral, B, medial, and C, lateral views. D-G, Left maxilla in D, lateral, E, medial and G, occlusal views. H-J, Left dentary fragment in H-I, occlusal, and J, lateral views. Scale bar = 2 cm.

fits into (occludes with) the left maxilla, so the tooth crowns embedded in the central groove on the maxilla are from this dentary fragment.

USNM 494329 closely resembles specimens of *Hyperodapedon* illustrated by Benton (1984, figs. 6, 13, 15, 53), Langer and Schultz (2000, text-figs. 4-5) and Langer et al. (2000a, fig. 2). Key features that justify assignment to *Hyperodapedon* are the single maxillary central groove, lack of lingual teeth and single row of dentary teeth.

Three features of the specimen suggest it should be assigned to *Hyperodapedon sanjuanensis*: a single ventral groove on the maxillary, medial tooth bearing area of maxillary much narrower than lateral and dentary without medial (lingual) teeth (M. Langer, written commun., 2002). The specimen, nevertheless, is very fragmentary, so we identify it as *Hyperodapedon* cf. *H. sanjuanensis*.

#### Age

The Popo Agie Formation is the stratigraphically lowest Upper Triassic unit throughout its outcrop belt in Wyoming, Idaho, Colorado, and Utah (Branson, 1927; Lucas, 1993, 1994). The most age-diagnostic fossils from the Popo Agie Formation are the tetrapod assemblage collected near Lander, Wyoming by E.B. Branson and M.G. Mehl (e.g., Mehl, 1913, 1915a,b, 1928; Branson, 1915; Branson and Mehl, 1928, 1929). This assemblage includes the phytosaurs *Paleorhinus* and *Angistorhinus* and the metoposaur *Buettneria* (taxonomy follows Hunt, 1993, 1994; Long and Murry, 1995) as well as rarer rauisuchians, including *Poposaurus gracilis* Mehl and *Heptasuchus clarkei* Dawley et al. (Mehl, 1915, Dawley et al, 1979; Lucas, 1993, 1994, 1997; Long and Murry, 1995). *Paleorhinus* is an index taxon of the Otischalkian (late Carnian)

land-vertebrate faunachron (lvf) and thus demonstrates that the Popo Agie Formation, and this occurrence of *Hyperodapedon*, are of late Carnian (Otischalkian) age (e.g., Hunt and Lucas, 1991b; Lucas, 1993, 1998).

#### Regional Significance

The record we document here is one of only two rhynchosaurs from the Upper Triassic of western North America. The other record, the type of *Otischalkia elderae* Hunt and Lucas, 1991a, is from the lowermost Chinle Group in West Texas (Hunt and Lucas, 1991a). Thus, despite more than 120 years of fossil collecting in the Chinle basin, rhynchosaur fossils remain exceedingly rare. This may in part reflect facies differences, as phytosaurs and metopososaurs are more common in the Chinle than in basins with abundant rhynchosaurs. It is also possible that, in the Chinle, the ecological niche occupied by rhynchosaurs elsewhere is instead occupied by the aberrant archosauromorph *Trilophosaurus*, which is locally common in Chinle strata of late Carnian age (Gregory, 1945; Murry, 1987; Long and Murry, 1995).

#### THE HYPERODAPEDON BIOCHRON

When Hunt and Lucas (1991a) reviewed the distribution of Late Triassic rhynchosaurs, they only recognized two records of *Hyperodapedon*—the type locality in the Lossiemouth Sandstone Formation of Scotland and the Maleri Formation of India. The Popo Agie Formation record of *Hyperodapedon* reported here, a record from Zimbabwe (Raath et al., 1992), and taxonomic revisions (Langer and Schultz, 2000; Langer et al., 2000a, b) have resulted in a much broader paleogeographic distribution of *Hypero-*

dapedon (Fig. 3). The stratigraphic distribution of *Hyperodapedon* is restricted to rocks of Otischalkian and Adamanian age, and this establishes a *Hyperodapedon* biochron of that age (Fig. 4). Here, we review the geographic and temporal distribution of *Hyperodapedon*.

### Nova Scotia

In the Fundy basin of Nova Scotia, the middle part of the Wolfville Formation yields a tetrapod assemblage that was summarized by Baird and Olsen (1983) and Olsen (1988, 1989). Baird (1964), Hopson (1984), Sues (1992) and Hunt (1993) have described some elements of this assemblage, which includes the temnospondyl amphibian *Metoposaurus*, an index taxon of the Otischalkian lfv. The rhynchosaur from this assemblage has been assigned to *Scaphonyx* (Hunt and Lucas, 1991a), and *Hyperodapedon* (Langer et al., 2000a; M. Langer, written commun., 2002). The Nova Scotia *Hyperodapedon* is thus part of a tetrapod assemblage of well-established Otischalkian age (Huber et al., 1993).

### Scotland

The tetrapod assemblage of the Lossiemouth Sandstone Formation of Grampian (Elgin) Scotland comes from small quarry workings and the coastal section at Lossiemouth. Benton and Spencer (1995, p. 62-72) provided a detailed summary and indicate that all sites come from a narrow stratigraphic range, so we treat the vertebrates as a single biostratigraphic assemblage. This assemblage includes: the procolophonid *Leptopleuron lacertinum*, the sphenodont *Brachyrhinodon taylori*, the rhynchosaur *Hyperodapedon gordonii*, the aetosaur *Stagonolepis robertsoni*, the ornithosuchid *Ornithosuchus longidens* (= *O. woodwardi*; Walker, 1964), the ornithodirans *Erpetosuchus granti* and *Scleromochlus taylori* and the dinosaur *Saltopus elginensis* (Benton and Spencer, 1995 and references cited therein). The presence of *Stagonolepis* supports correlation of this assemblage to the Chinle Group Adamanian, and therefore it is of late Carnian age.

### India

In the Pranhita-Godavari Valley of south-central India, the Maleri Formation is up to 330 m thick and consists mostly of red-bed mudstones, siltstones and sandstones. We recognize two vertebrate assemblages—lower and upper—in the Maleri Formation (e.g., Kutty et al., 1987; Kutty and Sengupta, 1989).

The lower assemblage we recognize is from the basal Maleri and includes the lungfish *Ceratodus hislopianus* and *C. virapa*, the elasmobranch *Xenacanthus indicus*, a “holostean” fish, the temnospondyl *Buettneria perfecta*, the rhynchosaur *Hyperodapedon huxleyi*, the phytosaur *Paleorhinus* (= *Parasuchus*) *hislopi*, the protosaurus *Malerisaurus*, an aetosaur, the theropod dinosaur *Alwalkeria maleriensis*, a prosauropod (“cf. *Massospondylus*” of Kutty and Sengupta, 1987), a large dicynodont, and the cynodont *Exeraetodon statisticae* (e.g., Miall, 1878; Huene, 1940; Roy-Chowdhury, 1965; Chatterjee, 1967, 1974, 1978, 1980b, 1982, 1987; Chatterjee and Roy-Chowdhury, 1974; Jain, 1980, 1990; Chatterjee and Majumdar, 1987; Jain and Roy-Chowdhury, 1987). This is the only well-described assemblage from the Pranhita-Godavari Valley. It includes *Paleorhinus*, an index taxon of late Carnian strata (especially Otischalkian age strata of the Chinle Group), and is securely assigned a late Carnian age.

The upper Maleri assemblage is from an interval stratigraphically higher than the lower assemblage, but its precise stratigraphic range is not clear (Fig. 4). It also includes *Ceratodus hislopianus*, *Xenacanthus indicus*, an aetosaur, prosauropods and a large dicynodont. Chigutisaurid amphibians (*Compsoceros cosgriffi* and *Kuttycephalus triangularis*; Sengupta, 1995) and a “*Rutiodon*-like” phytosaur are also present. Therefore, this assemblage also appears to be late Carnian, with much of the

formation clearly Otischalkian and perhaps some of it as young as Adamanian.

### Zimbabwe

Raath et al. (1992) documented specimens of *Hyperodapedon* from the “Pebbly Arkose Formation” at Dande in the western Cabora Bass basin of the Lower Zambezi Valley. These specimens were associated with fragmentary dinosaur bones and a *Dicroidium* paleoflora, which led Raath et al. (1992) to assign them a Late Triassic age. Raath (1996) considered the Pebbly Arkose Formation a distal facies of, and thus stratigraphically equivalent to, the Molteno Formation in South Africa. Although many workers interpret the age of the Molteno Formation differently (see Anderson et al., 1998), most lithologic and biostratigraphic evidence supports a late Carnian age for the Molteno Formation (Hancox, 1998; Lucas and Hancox, 2001). Based on the temporal range of *Hyperodapedon* elsewhere, we would assign the Zimbabwe *Hyperodapedon* occurrence a late Carnian (Otischalkian-Adamanian) age (Fig. 4).

### Tanzania

Boonstra (1953) named two new species of rhynchosaur, *Scaphonyx stockleyi* and *S. africanus*, from un-named Triassic strata in the Tunduru district of what is now Tanzania. Chatterjee (1980a) erected the genus *Supradapedon* for *S. stockleyi*. However, as Benton (1983) and Hunt and Lucas (1991a) concluded, *Supradapedon* is most likely a large *Hyperodapedon*, though they only referred it to *Hyperodapedontinae* indeterminate. Langer et al. (2000b), however, assign it to *Hyperodapedon*. *S. africanus*, based on a femur fragment, is best regarded as a *nomen dubium* (Hunt and Lucas, 1991b). The Tanzanian *Hyperodapedon* record is evidently of Otischalkian or Adamanian age, but no stratigraphic data or other vertebrate fossil association is known for this record. Consequently, we omit it from Figure 4.

### Madagascar

In western Madagascar, Besarie (1930; also see Besarie and Collignon, 1960, 1971) coined the term Isalo Group (“Groupe d’Isalo”) and divided it into informal units with numerical designations (Isalo I, Isalo II, Isalo III) based on perceived age. The

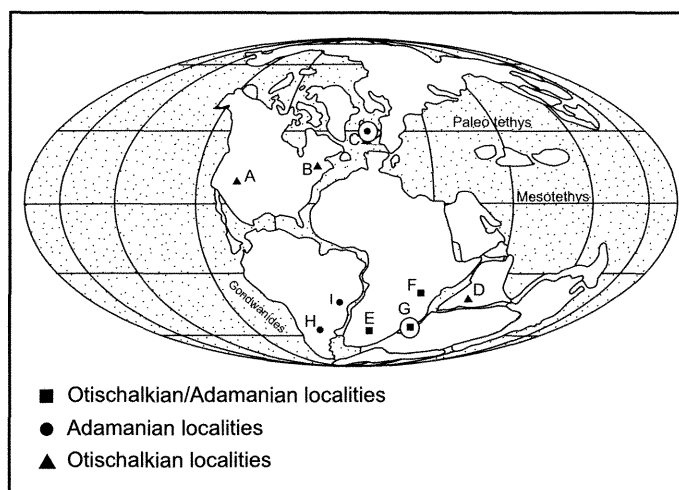


FIGURE 3. Map of Late Triassic Pangea showing *Hyperodapedon* localities. A = Popo Agie Formation, Wyoming, U.S.A.; B = Wolfville Formation, Nova Scotia, Canada; C = Lossiemouth Sandstone, Scotland; D = Maleri Formation, India; E = Pebbly Arkose Formation, Zimbabwe; F = unnamed strata, Tanzania; G = “Isalo II beds,” Madagascar; H = Ischigualasto Formation, Argentina; I = Santa Maria and Caturrita formations, Brazil.

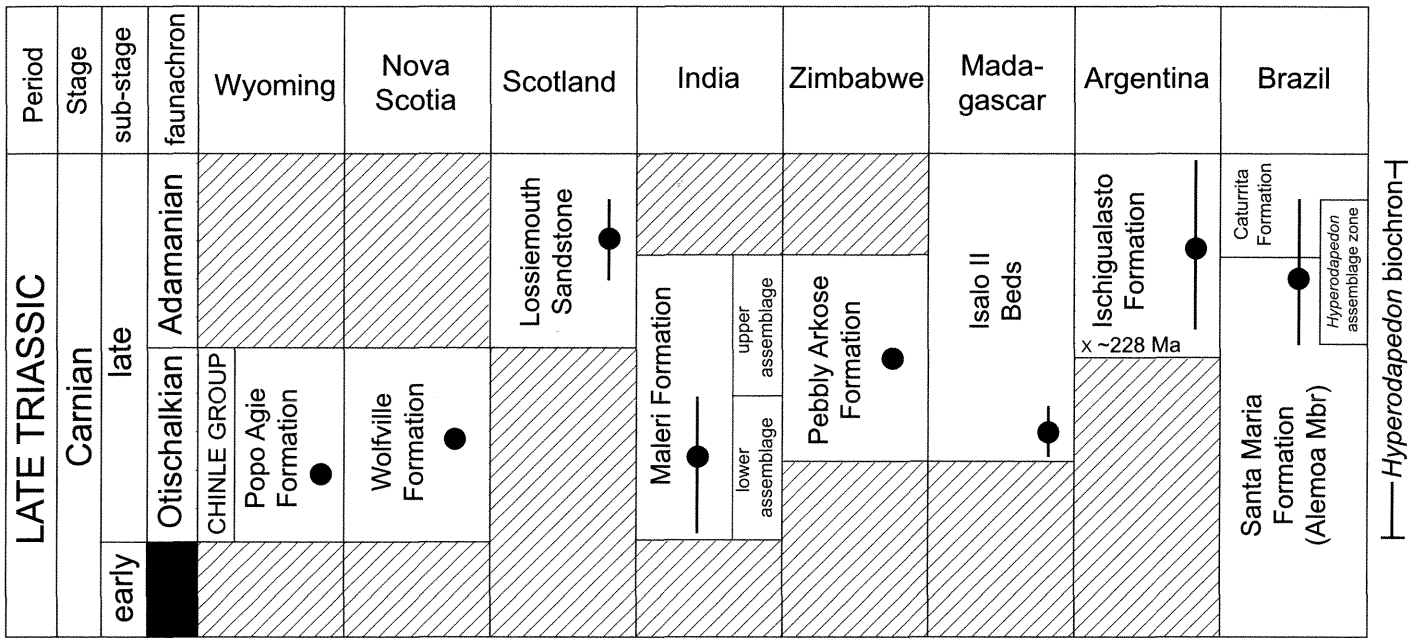


FIGURE 4. Global correlation of *Hyperodapedon* localities. The occurrence in Tanzania is not included for lack of stratigraphic data. Circles mark *Hyperodapedon* occurrences, lines through the circles indicate inferred ranges.

Isalo II strata are as much as 2000 m thick and dominantly red-bed sandstones of fluvial origin (e.g., Besarie and Collignon, 1971; Wescott and Diggins, 1998; Piqué et al., 1999)

“Early” collections from the nonmarine portion of the Isalo II beds produced Late Triassic vertebrate fossils: osteoderms of phytosaurs (Guth, 1963; Westphal, 1970), metoposaur fragments (Dutuit, 1978), and lungfish toothplates assigned to *Ceratodus acutus* and *C. hislopianus* (Martin, 1981). As noted above, *C. hislopianus* also is known in the upper Carnian Maleri Formation of India (Martin, 1981).

The rhynchosaur *Isalorhynchus genovefae* Buffetaut (Buffetaut, 1983; Hunt and Lucas, 1991a), reassigned to *Hyperodapedon* by Langer et al. (2000a), comes from the base of the Isalo II along the Malio River in the Morondava basin of west-central Madagascar. Subsequently collected Madagascan specimens of *Hyperodapedon* apparently are from the same stratigraphic level along the Malio River (Langer et al., 2000a). These *Hyperodapedon* records thus suggest the Isalo II base is no older than Otischalkian (Carnian), which is consistent with palynological age determinations of the unit (Razafimbelo, 1987). Furthermore, it has long been recognized that the Isalo Group is correlative to the Stormberg Group of South Africa: both represent pericratonic deposits that postdate a significant tectonic pulse in the rifting of eastern and southern Africa (e.g., Boast and Nairn, 1982; Wopfner, 1994). The oldest age of the Stormberg Group is late Carnian (e.g., Lucas and Hancox, 2001), so a consistent correlation of tectonic, palynostratigraphic and vertebrate biochronologic data indicates a late Carnian age for the Isalo Group base.

Indeed, Burmeister (2000) has recently described a vertebrate fossil assemblage from stratigraphically high in the Isalo II west of Malaimbandy in the central Morondava basin that includes acrodontid, semionotid and colobodontid fish, the characteristically Otischalkian-Adamanian aetosaur *Desmatosuchus haplocerus*, phytosaur, poposaur, postosuchid and theropod fossils. Although Burmeister (2000) suggested a possible Norian age for this assemblage, the *Desmatosuchus* fossils indicate it is Carnian.

Flynn et al. (1999, 2000) have reported a vertebrate fossil

assemblage from near Sakaraha in the Morondava basin that includes sphenodontids, rhynchosaurs, cynodonts, dicynodonts and prosauropod dinosaurs. This assemblage is near the base of the Isalo II (it is estimated to be about 1200 m lower than the assemblage described by Burmeister) but is evidently either at the same approximate stratigraphic level or stratigraphically above the *Hyperodapedon* records documented by Buffetaut (1983) and Langer et al. (2000a). Despite this, Flynn et al. (1999, 2000) suggest this assemblage may be as old as Ladinian, though they base this on their ideas about the evolutionary grade of some of the fossils, not on index fossils. Instead, we assign all of the Isalo II tetrapod assemblages a late Carnian (Otischalkian-Adamanian) age and consider that *Hyperodapedon* records in Madagascar place a maximum age of Otischalkian on the Isalo II beds.

#### Argentina

In the Ischigualasto-Villa Unión basin, the Ischigualasto Formation is 500 to 900 m thick and consists of drab mudstones, tuffs and sandstones that produce an extensive tetrapod assemblage including: the temnospondyl *Promastodontosaurus*; the chiniquodontid cynodont *Chiniquodon*, the gomphodont cynodonts *Exaraetodon*, *Proexaraetodon*, and *Ischignathus*; the dicynodont *Ischigualastia*, the pseudosuchia *Proterochampsa*, the aetosaur *Stagonolepis* (= *Aetosauroides*), the rauisuchian *Saurosuchus*, the rhynchosaur *Hyperodapedon* (formerly *Scaphonyx*); the poposaurid *Sillosuchus* and the dinosaurs *Herrerasaurus* (= *Ischisaurus*, = *Frenquellisaurus*), *Eoraptor*, and *Pisanosaurus* (e.g., Cabrera, 1944; Reig, 1959, 1961, 1963; Casamiquela, 1960, 1961; Cox, 1965; Bonaparte, 1976; Rogers et al., 1993; Sereno et al., 1993; Alcober and Parrish, 1997). The assemblage slightly and mostly overlies the Herr Toba bentonite that yielded an  $^{40}\text{Ar}/^{39}\text{Ar}$  age of  $227.8 \pm 0.3$  Ma (Rogers et al., 1993).

Romer (1960, 1962a, b) and Reig (1961, 1963) assigned the Ischigualasto tetrapods a Middle Triassic (Ladinian) age. This fits well the concept—developed and best articulated by Romer—that Middle Triassic tetrapod assemblages had numerous gomphodont cynodonts and an “explosive development” of rhynchosaurs. However, Bonaparte (1966, 1967), noting that rhynchosaurs co-

occur with phytosaurs and aetosaurs in the Upper Triassic of Europe and India, assigned a Carnian age to the Ischigualasto vertebrate assemblage.

Subsequent workers have accepted the Carnian age assignment but have correlated the Ischigualasto tetrapods as early or "middle" Carnian, arguing that they predate late Carnian assemblages such as the basal Chinle or lower Maleri. Therefore, according to common practice, the dinosaur fossils from the Ischigualasto Formation are often considered to be the oldest known (e.g., Benton, 1990; Rogers et al., 1993; Novas, 1996).

Hunt and Lucas (1991a, b), Lucas et al. (1992) and Lucas and Hunt (1993) challenged this practice, arguing that the Ischigualasto Formation is of late Carnian age based on: (1) postcrania identified as cf. *Ischigualastia* sp. from Adamanian-aged strata of the Chinle Group, suggesting an Adamanian-Ischigualastian correlation; (2) the presence of *Staurikosaurus*-like dinosaurs in the Adamanian interval of the Chinle Group; and (3) presence of rhynchosaurs in late Carnian strata of the Chinle Group, Newark Supergroup, Lössiemouth Sandstone Formation and Maleri Formation. Although rhynchosaurs are not usually abundant in these strata, their presence refutes Romer's assertion that rhynchosaurs indicate a Middle Triassic age.

None of these arguments are incontrovertible evidence for a late Carnian age of the Ischigualasto tetrapods. However, recent revision of the South American aetosaurs by Heckert and Lucas (1996, 2002) indicates that *Aetosauroides* from Argentina and Brazil is a subjective junior synonym of the Adamanian index fossil *Stagonolepis*. Recognition of *Hyperodapedon* in the Ischigualasto Formation (Contreras, 1999) supports this correlation as well. This secures an Adamanian correlation of the Ischigualasto tetrapods, which are thus clearly of latest Carnian age. We note also that ongoing refinement of the Triassic timescale also suggests that 227.8 Ma is a late Carnian age (e.g., Kent et al., 1995), not the early or "middle" Carnian age suggested by the less precise Triassic timescales utilized by Rogers et al. (1993) and others.

### Brazil

The Upper Triassic vertebrate assemblage from the upper part of the Alemoa Member of the Santa Maria Formation is mostly from the vicinity of Santa Maria City in Rio Grande do Sul, southern Brazil (Huene, 1935-1942). This is the Rhynchocephalia Assemblage Zone of Barberena (1977) or the *Scaphonyx* Zone of Barberena et al. (1985). As the rhynchosaurs in this assemblage are dominantly *Hyperodapedon*, not *Scaphonyx* (Langer and Schultz, 2000), Lucas (2001) renamed the zone the *Hyperodapedon* Assemblage Zone.

The *Hyperodapedon* Assemblage Zone in the Alemoa Member includes abundant fossils of the rhynchosaur *Hyperodapedon* (formerly *Scaphonyx*); a few specimens of the aetosaur *Stagonolepis* (formerly *Aetosauroides*); traversodontids and other cynodonts, including *Charrudon*, *Therioherpeton* and *Gomphodontosuchus*; the proterochampsids *Cerritosaurus binsfeldi*, *Rhadinosuchus gracilis*, and *Hoplitosuchus rauti*; and the archetypal rauisuchian *Rauisuchus tiradentes*. Alemoa Member dinosaurs are the theropod *Staurikosaurus pricei* Colbert, 1970, the prosauropod *Saturnalia tupiniquim* Langer et al. 1999 (also see Kellner and Campos, 2000), and the theropod *Teyuwasu barberenai* Kischlat, 1999.

In this assemblage zone most, if not all, of the rhynchosaurs, long referred to *Scaphonyx*, are now assigned to *Hyperodapedon* (Hunt and Lucas, 1991a; Langer and Schultz, 2000; Langer et al., 2000b). The aetosaur *Stagonolepis*, present in the Alemoa Member, is also of well documented Adamanian age in the USA and Europe and is abundant in the Ischigualasto Formation in Argentina (Lucas and Heckert, 2001; Heckert and Lucas, 2002). Clearly,

the presence of *Hyperodapedon* and *Stagonolepis* supports correlation of the *Hyperodapedon* Assemblage Zone of the Santa Maria Formation with the vertebrates of the Ischigualasto Formation in Argentina, and therefore an Ischigualastian (Adamanian) age assignment (Lucas, 1998; Lucas and Heckert, 2001).

The tetrapod assemblage from the Caturrita Formation, which overlies the Santa Maria Formation, includes a sphenodont skull and postcrania, the proterochampsid *Proterochampsia nodosa*, archosaur teeth, phytosaur teeth and jaw fragments, the cynodonts *Exaeretodon* and *Riograndia*, the rhynchosaur *Hyperodapedon*, the dicynodont *Ischigualastia* (= *Jachaleria candelieriensis* Araújo and Gonzaga) and a supposed *Erythrotherium*-like mammalian mandible fragment (Araújo and Gonzaga, 1980; Barberena et al., 1985; Dornelles, 1990; Ferigolo, 1999; Bonaparte et al., 1999, 2001; Faccini et al., 2000). Caturrita Formation dinosaurs are the theropod? *Guaibasaurus candelarai* Bonaparte et al. 1999 and a new, undescribed prosauropod (Azevedo et al., 1990, 1999; Azevedo, 1993). Lucas and Wild (1995) suggested that the skull assigned to *Jachaleria* belongs to *Ischigualastia*, and we maintain this conclusion, having now studied the Brazilian material firsthand.

The Caturrita assemblage thus shares index taxa with the Ischigualasto Formation of Argentina (*Ischigualastia*, *Exaeretodon* and *Hyperodapedon*), so we also assign it an Ischigualastian (Adamanian) age. We therefore reject correlations, such as Bonaparte (1982), Barberena et al. (1985) and Schultz et al. (2000), that indicate that at least part of the Caturrita Formation is younger than the Ischigualastian. All Late Triassic tetrapods known from Brazil are of Ischigualastian (Adamanian) age (Fig. 4).

Certainly the Caturrita Formation tetrapods are stratigraphically above those from the upper part of the Alemoa Member of the Santa Maria Formation. However, the two assemblages are not, at present, biochronologically separable. Thus, both are of Ischigualastian age, and we include both in the *Hyperodapedon* Assemblage Zone (Fig. 4). More collecting and study of Caturrita Formation tetrapods are needed to provide a basis for recognizing them as a biochronologically distinct assemblage. Using the correlations and biochronology documented here, then, all Brazilian, and indeed all South American occurrences of *Hyperodapedon* are of latest Carnian (Adamanian) age.

### CONCLUSIONS

Clearly, ongoing work has greatly increased our knowledge of Upper Triassic rhynchosaurs since Hunt and Lucas (1991a) last reviewed their distribution. Particularly significant are new occurrences from North America (documented here), South Africa (Raath et al., 1992) and the taxonomic revisions of Langer and Schultz (2000) and Langer et al. (2000a, b). The result is a much more unified understanding of the distribution of Upper Triassic rhynchosaurs in general and *Hyperodapedon* in particular. Presently, the *Hyperodapedon* biochron delineates a substantial interval of time (Otischalkian-Adamanian), as opposed to the finer resolution achieved with, for example, genera of phytosaurs or aetosaurs, many of which are restricted to a single l.v.f. Still, the *Hyperodapedon* biochron is exceptionally useful, as *Hyperodapedon* appears to be one of the most widely distributed (Pangean) Upper Triassic tetrapods, and thus facilitates correlations in places where other index taxa, particularly phytosaurs, are absent.

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