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The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian *Placerias* Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae

Silvio C. Renesto, Varese, **Justin A. Spielmann** and **Spencer G. Lucas,** Albuquerque

With 3 figures

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Abstract: Previous detailed descriptions of relatively complete drepanosaurid material make it possible to recognize isolated drepanosaurid elements from other localities. The identification of isolated elements from the USA and Great Britain extended the geographical distribution of the group and encouraged a review of Triassic collections for characteristic elements of this family. In this paper, isolated vertebrae previously described as problematic reptiles from the famous *Placerias* Quarry, near St. Johns, Arizona, USA are re-identified as drepanosaurids. These specimens represent the oldest occurrence of this family, which is earliest Adamanian.

Key words: Drepanosauridae (Reptilia, Diapsida), Chinle Group, isolated vertebrae, biostratigraphy.

1. Introduction

Originally erected by Olsen & Sues (1986) and first diagnosed by Berman & Reisz (1992), the Drepanosauridae are a family of diapsid reptiles with highly modified postcrania and are interpreted as arboreal (Renesto 1994a, b, 2000; Renesto & Binelli 2006; though see Colbert & Olsen 2001 and Berman & Reisz 1992 for differing interpretations). *Drepanosaurus* (Pinna, 1980) and *Megalancosaurus* (Calzavara et al., 1980) from the Calcare di Zorzino (Zorzino Limestone, Norian, Late Triassic) of Northern Italy were the first taxa of this family to be described. *Dolabrosaurus* from the Petrified Forest Formation, Chinle Group, New Mexico (Berman & Reisz 1992), and *Hypuronector*, from the Newark Supergroup (Colbert & Olsen 2001) ("deep-tailed swimmer" of Olsen 1980), were for many years the only two named drepanosaurid taxa from North America. Recently, *Vallesaurus*, also from the Italian Calcare di Zorzino, was described (Renesto & Binelli 2006). Although these forms exhibit different sizes and slightly diverse body form, all share characteristic features that unequivocally demonstrate their close relationships (Renesto 1994a, b, 2000; Renesto & Fraser 2003). Nevertheless, there is some uncertainty about the relationships of the Drepanosauridae with other diapsids. Berman & Reisz (1992) considered drepanosaurids to be lepidosauromorphs, whereas Renesto (1994a, b, 2000) suggested archosauromorph affinities. Analyses by Benton & Allen (1997) and Dilkes (1998) lent further support to the hypothesis that drepanosaurids are archosauromorphs, specifically closely related to Prolacertiformes, a hypothesis also proposed in the recent revision of Prolacertiformes (Protorosauria) by

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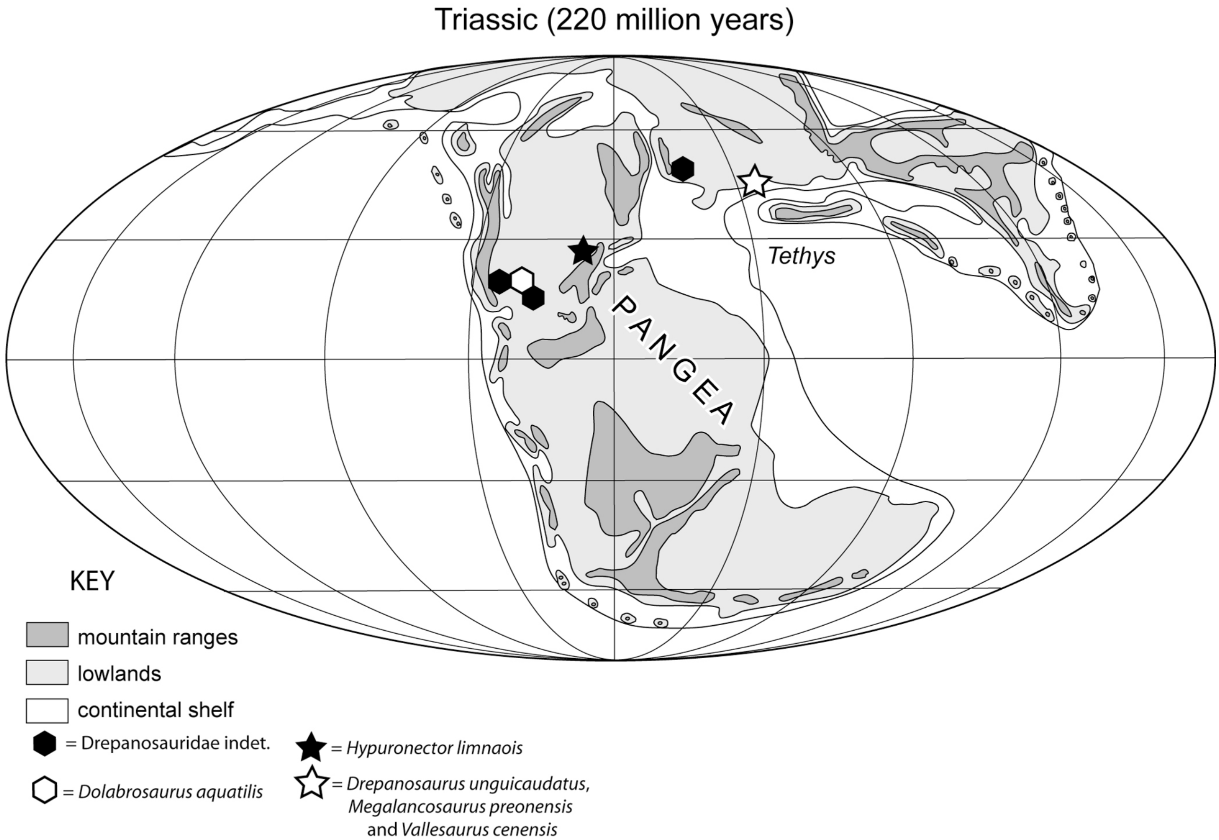

Fig. 1. Paleogeographic map of the Late Triassic (~220 Ma) with drepanosaurid localities highlighted. Base map after Wing & Sues (1992)

Rieppel et al. (2003). The phylogeny of Senter (2004) suggested that the Drepanosauridae are closely related to the Permian Coelurosauravidae. However, Renesto & Binelli (2006) demonstrated that Senter's analysis reflected much confusion about drepanosaurid anatomy, rather than helping to resolve relationships. Renesto & Binelli (2006), on the basis of more complete material, proposed a new analysis, which placed the Drepanosauridae within Archosauromorpha, close to Protorosauria and basal archosaurs.

Based on detailed descriptions (Renesto 1994 a, b, 2000; Colbert & Olsen 2001; Renesto & Binelli 2006) of various drepanosaurs, known from relatively complete material, it is now possible to recognize isolated drepanosaurid elements. Indeed, Harris & Downs (2002) identified a characteristic drepanosaurid shoulder girdle from the famed Ghost Ranch *Coelophysis* Quarry, and, more recently, Renesto & Fraser (2003) and Fraser & Renesto (2005) recognized isolated drepanosaurid cervical vertebrae among the disassociated vertebrate assemblages of the Upper Triassic fissure deposits at Cromhall Quarry, England. The addition of the isolated elements from the USA and Great Britain extended the geographical distribution of the group and encouraged a review of Triassic collections for characteristic elements of this distinct family. Here we report some isolated vertebrae, previously described as "Reptilia Problematica" (Kaye & Padian 1994), from the large microvertebrate collection of the famous *Placerias* Quarry, near St. Johns, Arizona, USA, and redescribe and identify them as drepanosaurid specimen.

These newly recognized drepanosaurid specimens from the *Placerias* Quarry represent the oldest occurrence of this family of archosauromorphs. Here, we also review the geographic and biostratigraphic range of the Drepanosauridae and discuss the age of the various drepanosaurid occurrences (Fig. 1).

Institutional abbreviations: AUP, Aberdeen University Palaeontology Collection, Aberdeen, Scotland; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; MPUM, Museo Paleontologico Università di Milano, Dipartimento di Scienze della Terra dell'Università degli Studi di Milano, Milan, Italy.

2. Drepanosauridae from the *Placerias* Quarry

2.1. Geological setting

Near St. Johns in east-central Arizona, USA, the *Placerias* Quarry ranks among the richest fossiliferous localities for Triassic continental vertebrates (Camp & Welles 1956; Jacobs & Murry 1980; Murry & Long, 1989; Kaye & Padian 1994; Lucas et al. 1997). Discovered in the 1930s, the quarry takes its name from the abundance of bones of one of the last Triassic dicynodonts, *Placerias*, monographed by Camp & Welles (1956). The stratigraphically equivalent Downs Quarry is very close to the *Placerias* Quarry (Murry & Jacobs 1988). In the 1970s and 1980s, screenwashing yielded a diverse microvertebrate fauna from the *Placerias* Quarry (Murry & Jacobs 1988; Tannenbaum 1983; Kaye & Padian 1994; Heckert 2004), and other elements of its macrovertebrate assemblage were described in the 1990s, including aetosaurs, phytosaurs and dinosaurs (Lucas et al. 1992, 1997; Long & Murry 1995; Nesbitt et al. 2007).

The quarry is located in the Bluewater Creek Formation, near the base of the Upper Triassic Chinle Group (Lucas et al. 1997). It is of earliest Adamanian age, based on the co-occurrence of *Stagonolepis, Parasuchus* (= *Paleorhinus*) and *Rutiodon*-grade phytosaurs (Lucas et al. 1997, 2007).

2.2. Material examined

MNA V3637, originally identified by Kaye & Padian (1994: 184, fig. 9.76) as a "procoelous posterior caudal centrum" of a reptile. We interpret it as a posterior caudal vertebra of a drepanosaurid (Fig. 2R-V).

MNA V3652 (Fig. 2A-Q) consists of three elements, one originally described and figured by Kaye & Padian (1994: 185, fig. 9.88) as a reptilian "procoelous centrum with flaring transverse processes." We interpret it as the posteriormost cervical vertebra of a drepanosaurid, very similar to *Megalancosaurus*. The other two elements were not illustrated or described by Kaye & Padian (1994); they are a centrum missing its neural arch and a neural arch with a mediolaterally-compressed, semicircular neural spine. We interpret these elements to be the centrum of a drepanosaurid and a cf. drepanosaurid neural arch.

2.3. Description and identification

MNA V3637 was originally described as a "posterior caudal centrum with a thin ridge on the ventral surface" by Kaye & Padian (1994: 186). It consists of an almost complete small vertebra, about 10 mm long (Fig. 2R-V). The centrum is low and elongate, extending caudally well beyond the walls of the neural arch, it is wider than high and also slightly constricted in the middle, so that its ventral margin has a concave outline. The cranial articular surface is concave, whereas the posterior surface is convex; thus the vertebra is procoelous. Because of the caudal extension of the centrum, the zygapophyseal articulation between pre- and postzygapophyses lies well forward of the intercentral articulation. The prezygapophyses lie very close to the midline, and their articular facets are oriented close to vertical, allowing good mobility on the vertical plane, while hindering lateral mobility. The neural arch is partially broken at the caudal end, revealing a wide neural canal. The neural spine is almost missing, but judging from the outline of the preserved portion, it had to be low. Neither articular areas for ribs, nor can transverse processes be detected.

MNA V3637 shows a combination of characters such as procoelous centra with large neural canal and end of the centrum protruding beyond postzigapophyses, praezygapophyses forward protruding and with subvertical articular facets, that correspond to that of the caudal vertebrae of the drepanosaurids especially of *Vallesaurus* in which, the haemal arches are intercentral in position and not fused with the posteroventral end of the centrum as it occurs in *Drepanosaurus* and *Megalancosaurus*. Thus, we interpret MNA V3637 as a posterior caudal vertebra of a drepanosaurid.

Specimen MNA V3652 consists of three elements – a vertebra, a centrum and a neural arch. The vertebra (Fig. 2A-E) was described as "a relatively large, non-nothocordal, procoelous centrum" which "has a well developed posterior condyle and is roughly triangular in outline. Transverse processes are present anterolaterally, and a small neural spine dorsally" (Kaye & Padian 1994: 186). Indeed, the morphology

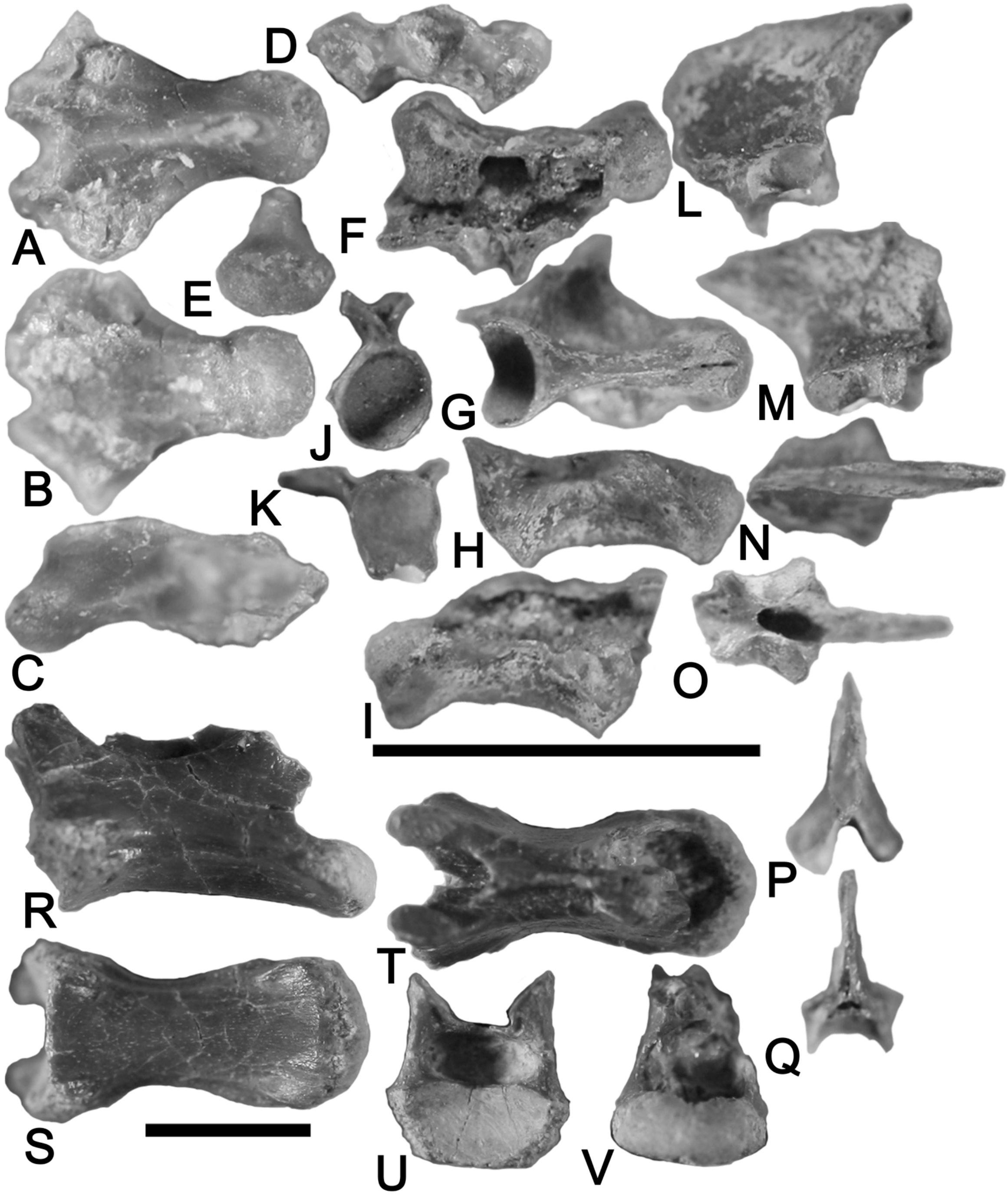

Fig. 2. A-E, MNA V3652 (in partim), drepanosaurid cervical vertebra in **A,** dorsal, **B,** ventral, **C,** right lateral, **D,** anterior and **E,** posterior views. **F-K,** MNA V3652 (in partim), drepanosaurid cervical vertebra in **F,** dorsal, **G,** ventral, **H,** left lateral, **I,** right lateral, **J,** anterior and **K,** posterior views. **L-Q,** MNA V3652 (in partim), drepanosaurid neural spine of dorsal vertebra in **L,** left lateral, **M,** right lateral, **N,** dorsal, **O,** articular, **P,** anterior and **Q,** posterior views. **R-V,** MNA V3637, drepanosaurid dorsal vertebra in **R,** right lateral, **S,** ventral, **T,** dorsal, **U,** anterior and **V,** posterior views. **A-Q** are to the same scale, as are **R-V.** Scale bars equal 5 mm.

of this vertebra in dorsal view matches that of the last cervical vertebra of *Megalancosaurus* specimen MPUM 6008 (Renesto 1994, 2000), the only specimen in which cervical vertebrae are exposed in dorsal and ventral view. Both this vertebra and the last cervical vertebra of MPUM 6008 are procoelous, bearing laterally-flaring parapophyses anteriorly. The cotyle, which is the concave articular surface, has a kidney-shaped outline, and the neural spine is low, features also present in a drepanosaurid cervical vertebra, AUP 11362, from Cromhall (Renesto & Fraser 2003). The main difference, as noted by Kaye & Padian (1994), is that the ventral surface of the *Placerias* Quarry centrum is smooth, and this may contradict the attribution of the centrum to drepanosaurids, because most drepanosaurid cervical vertebrae bear a well-developed hypapophysis. However, the last cervical vertebra of *Megalancosaurus* specimen MPUM 6008 lacks a hypapophysis (Renesto 1994, 2000) and, as noted above, matches the morphology of the *Placerias* Quarry centrum. Thus, we identify it as a posterior cervical vertebra of a drepanosaurid.

The centrum of MNA V3652 (Fig. 2F-K) is heterocoelous with a distinctly concave ventral margin that gives it an hourglass-shaped outline in lateral viev. Also, the ventral margin is keeled, and its caudal end bears a broken surface, suggesting that it may have continued to form a small hypapophysis. On the dorsal margin close to the cranial end, fragments of a laterally flaring process similar to a wide parapophysis are visible. A forked dorsal structure represents the base of the neural arch, which is not preserved. The overall morphology is similar to a mid or cranial cervical vertebra of a drepanosaurid.

The neural arch of MNA V3652 has a mediolaterally compressed, triangular neural spine, with the point of the neural spine directed posteriorly. This neural spine morphology is most similar to the dorsal vertebrae of *Megalancosaurus*. However, there are some differences. *Megalancosaurus* has a tall neural spine that terminates dorsally with triangular expansions that generally have rounded anterior margins (Renesto 1994, fig. 5). The relatively short height and the pointed anterior margin of the MNA V3652 neural spine would seem to argue against it pertaining to *Megalancosaurus*. However, some specimens illustrated by Renesto (1994, fig. 5c) are relatively shorter than other specimens and have a more pointed anterior margin. Thus, the neural arch of MNA V3652 cannot be definitively assigned to the Drepanosauridae, so we assign it to cf. Drepanosauridae.

MNA V3671 (not illustrated) was described as "Procoelous, non notochordal anterior caudal vertebra" showing "a high, rectangular neural arch directly fused to the centrum, with a thin high neural spine bearing distinct midlateral ridge that culminates in an anteriorly projecting nub. The narrow but rounded surface has posteroventral chevron facets" (Kaye & Padian 1994: 187). Although most drepanosaurid specimens are preserved as a heavily-flattened skeleton in which bones became nearly two-dimensional, it is possible to recognize that the overall structure of the drepanosaurid proximal caudal vertebrae matches that of MNA V3671, not only in the features described by previous authors, but also in other aspects. They show, in fact, high and wide neural arches with very high and narrow neural spines and well developed zygapophyses with a nearly vertical articular surface (Renesto 1994, 2000; Fraser & Renesto 2005), which are also present in MNA V3671. In addition, a mediolateral ridge is also present in the proximal caudals of *Megalancosaurus*. This evidence supports the attribution of MNA V3671 to a drepanosaurid; it should be added that caudal neural of drepanosaurids show a consistent morphology across taxa, but the morphology of the centrum may vary. In fact, it is procoelous in *Megalancosaurus* (Renesto, 1994), but amphicoelous in *Drepanosaurus* (Pinna, 1984) and possibly *Vallesaurus* (Renesto & Binelli, 2006), as well as in the Cromhall specimens (Fraser & Renesto 2005). Thus, the procoelous structure does not contradict the attribution of MNA V3671 to the Drepanosauridae.

3. Stratigraphic range of the Drepanosauridae

As noted above, only four general areas have yielded drepanosaurid fossils: the limestone deposits of northern Italy; the fissure fills of central England; the Newark Supergroup of the eastern United States; and the Chinle Group in the southwestern United States (Fig. 1). Here, we discuss the age of these records of drepanosaurids and place them in their stratigraphic context (Fig. 3).

3.1. Bluewater Creek Formation, Chinle Group

The five specimens described above demonstrate the presence of drepanosaurid material in the *Placerias* Quarry fauna. Traditionally, the *Placerias* Quarry was thought to lie in the Blue Mesa Member of the Petri-

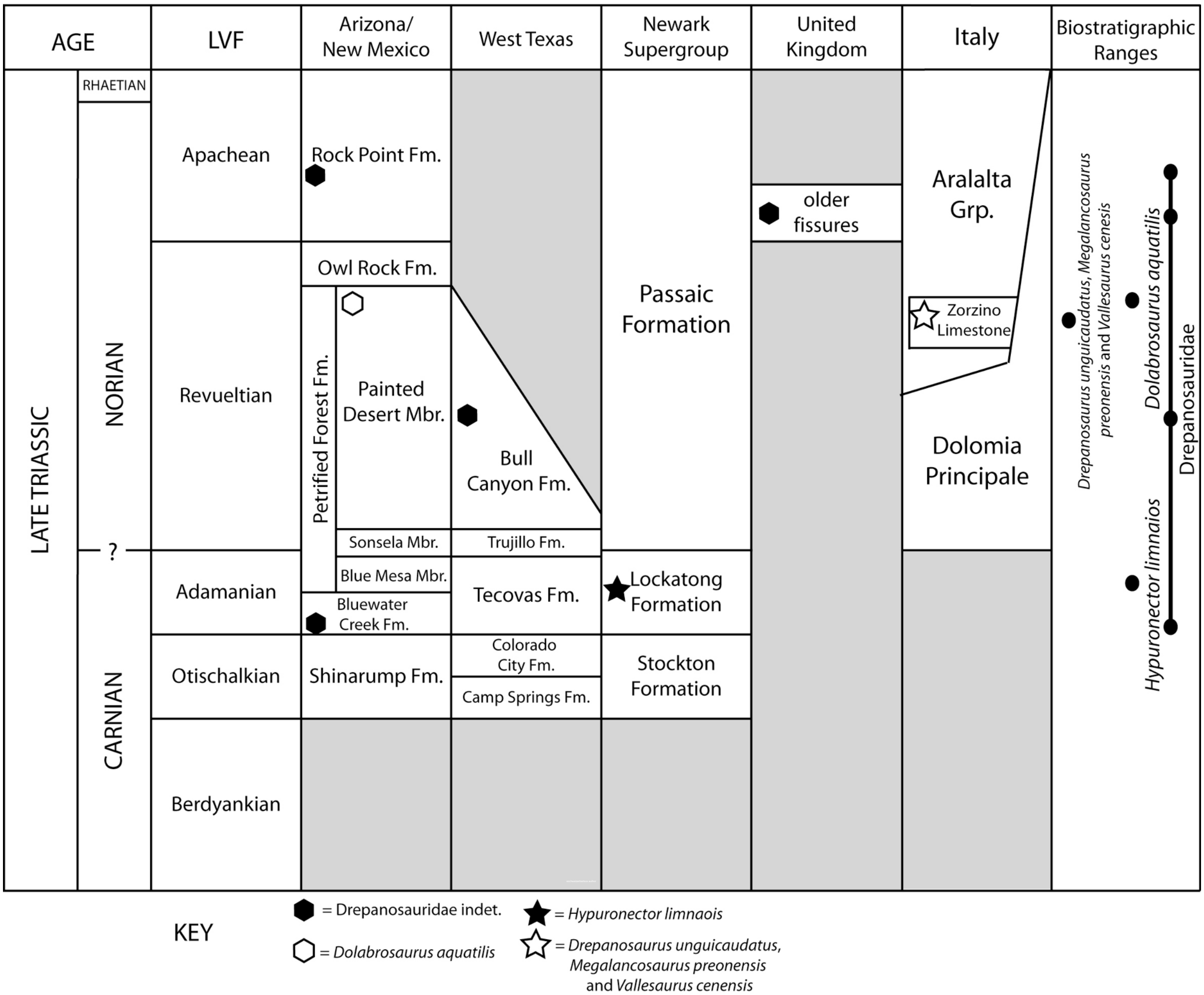

Fig. 3. Correlation chart of drepanosaurid-bearing strata and biostratigraphic ranges of the Drepanosauridae. Correlation based principally on LUCAS & HUBER (2003); biochronology based on LUCAS et al. (2007); see text for individual locality references.

fied Forest Formation, however, LUCAS et al. (1997) demonstrated that this exceptionally rich quarry is actually near the base of the Chinle Group, in the Bluewater Creek Formation. The Bluewater Creek Formation is interpreted as earliest Adamanian in age (LUCAS et al. 1997, 2007; HECKERT 2004). Most significantly, it includes a record of the phytosaur *Parasuchus*, which is generally regarded as an index fossil of the older Otischalkian lvf (LUCAS et al. 1997). This indicates that the *Placerias* quarry sits right at the Otischalkian-Adamanian boundary and thus is older than all other known Adamanian localities (LUCAS et al. 2007). Thus, this site is older than the younger Adamanian drepanosaurid record in the Lockatong Formation (see below) and represents the oldest occurrence of drepanosaurids.

3.2. Lockatong Formation, Newark Supergroup

COLBERT & OLSEN (2001) described *Hypuronector limnaios* from the Lockatong Formation, Newark Supergroup, specifically the Granton Quarry, North Bergen, New Jersey and the Weehawken Quarry at Kings Bluff, Weehawken, New Jersey. The material they described was originally collected in the 1950s and 1960s ("some 40 years or more ago" and "about a half century ago" are both used to describe the time frame of the excavation by COLBERT & OLSEN 2001: 1 f.). Consisting of articulated, associated and isolated postcrania and an isolated lower jaw, the material collected from the two quarries provides representative elements from the entire skeleton, with the exception of the skull and cervical vertebral series. The Granton Quarry has "not been definitively correlated," but, COLBERT & OLSEN (2001: 5) noted that the "best match" is to the Ewing Creek Member. The Weehawken Quarry occurs in the Nursery Member of the Lockatong Formation.

The Lockatong Formation is interpreted as Conewagian in age, following the vertebrate biostratigraphy of LUCAS & HUBER (2003), based on the presence of the lepidosauromorph *Icarosaurus siefkeri* and the protorosaur *Tanytrachelos anhyis* and *Rutiodon*-grade phytosaurs. The presence of *Rutiodon*-grade phytosaurs broadly correlates the Conewagian with the Adamanian lvf of LUCAS (1998) and LUCAS et al. (2007). It is important to stress that no record of the Otischalkian phytosaur *Parasuchus* is known from the Conewagian, and this suggests that the Conewagian is younger than the *Placerias* Quarry, which is at the beginning of Adamanian time.

The Conewagian lvf (and the Adamanian lvf) has been considered late Carnian (late Tuvalian) in age (e.g., LUCAS 1998). This is congruent with the age of the quarries as interpreted by COLBERT & OLSEN (2001), which they assigned to the late Carnian (between 221 and 222 Ma, based on fig. 2). However, recent magnetostratigraphic data suggest it may be early Norian in age and therefore much or all of the Adamanian is of early Norian age (MUTTONI et al. 2004), although this correlation is a topic of much debate (e.g., KOZUR & WEEMS 2007 and references cited therein). Both the Nursery and Ewing Creek members are near the middle of the Lockatong Formation (COLBERT & OLSEN 2001, fig. 2), so we interpret the age of the two occurrences of *Hypuronector limnaios* as Adamanian, and younger than the *Placerias* Quarry.

3.3. Bull Canyon Formation, Chinle Group

The Post Quarry is located south of Post in Garza County, Texas in the Bull Canyon Formation (also referred to as the Cooper Canyon Formation by some Texas workers) of the Chinle Group. The Post Quarry has produced a large tetrapod fauna including temnospondyl amphibians, large archosauromorphs (CHATTERJEE 1985; LONG & MURRY 1995) and a putative bird, *Protoavis texensis*. *P. texensis* has been described and figured by CHATTERJEE (1991, 1995, 1998, 1999), though doubt has been cast on the association of the specimen and whether it even represents a single taxon (e.g., OSTROM 1991, 1996; CHIAPPE 1995). RENESTO (2000) noted similarities between the cervical vertebrae of *Megalancosaurus* and the cervical vertebrae of the *P. texensis* material (CHATTERJEE 1991, 1995, 1998, 1999), and concluded that the cervical vertebrae of *P. texensis* likely represent a *Megalancosaurus*-like drepanosaurid. The occurrence of *Typothorax coccinarum* in the Bull Canyon Formation indicates a Revueltian age for the formation (HUNT 2001; LUCAS et al. 2007 and references cited therein).

3.4. Painted Desert Member, Petrified Forest Formation, Chinle Group

BERMAN & REISZ (1992) described the holotype, and only known specimen, of *Dolabrosaurus aquatilis*, which is an incomplete vertebral skeleton, with a nearly complete articulated caudal series, portions of the right manus, right and left hindlimbs and right pes. BERMAN & REISZ (1992: 1002) listed the type horizon and locality as:

"Middle of the Upper Petrified Forest Member, Chinle Formation, Early Norian, Late Triassic; NE1/4, NE1/4, sec. 30, T24N, R3E, near the base of Mesa Prieta, west side of entrance of Chama River into Abiquiu Resevoir, Rio Arriba County, north-central New Mexico."

It should be noted that following LUCAS' (1993) raising of the Chinle to group status the Petrified Forest is now a formation rank unit within the Chinle Group (HECKERT & LUCAS 2002). In addition, the two junior authors field checked the published locality data with Berman in the spring of 2007 and found that it was erroneous. The site is in the lower Painted Desert Member (~20 m above the base of the unit) at UTM zone 13, 358587E, 4016830N, NAD 27 which is ~10 km east of the coordinates reported by BERMAN & REISZ (1992). The fauna of the Painted Desert Member is Reveultian in age, based on the presence of *Pseudopalatus*-grade phytosaurs (HECKERT et al. 2005). Thus, the holotype of *D. aquatilis* is late Norian in age, an age assignment consistent with palynostratigraphy (LITWIN et al. 1991).

3.5. Calcare di Zorzino, Italy

The Calcare di Zorzino was deposited in basins surrounded by the Dolomia Principale platform. These basins were periodically enclosed by small islands formed from emergent portions of the platform or by patch reefs and organic mounds (Renesto 2006: 445, fig. 1B). The Calcare di Zorzino has yielded a rich vertebrate fauna (Renesto 2006), including three drepanosaurids, *Drepanosaurus unguicaudatus, Megalancosaurus preonensis* and *Vallesaurus cenensis. D. unguicaudatus* is known from the holotype specimen, originally described by Pinna (1980, 1984), consisting of a nearly complete, articulated skeleton, missing the head. Calzavara et al. (1980) originally described *Megalancosaurus preonensis* from the Dolomia di Forni Formation, coeval with the Calcare di Zorzino, based on a single specimen, the holotype, consisting of a skull, forelimb, cervical vertebrae and various postcrania. Subsequently, Renesto (1994, 2000, 2006) has described numerous other examples of *M. preonensis*, including articulated postcrania, thus allowing for a complete skeletal reconstruction of this taxon. *Vallesaurus cenesis*, though originally named by Wild (1991), was described by Renesto & Binelli (2006) from the holotype and only known specimen, a complete, articulated skeleton.

Lucas & Huber (2003: 163) concluded that the Calcare di Zorzino is very close in age to the Alaunian-Sevatian boundary and can be correlated with the younger part of the *Himavatites columbianus* Ammonite Zone. This correlation makes the Calcare di Zorzino upper Middle Norian in age (Fig. 3; Lucas & Huber 2003, fig. 11.13). Thus, we place the Calcare di Zorzino as middle to upper Revueltian in age.

3.6. Cromhall Quarry, United Kingdom

Renesto & Fraser (2003) and Fraser & Renesto (2005) reported six isolated vertebrae from the Late Triassic fissure infilling from the Cromhall quarry, Avon, United Kingdom. They identified them as drepanosaurid, based on features of the cotyle, neural spine and zygapophyses. However, they noted that the Cromhall drepanosaurid has "larger prezygapophyses with a more arcuate cranial [anterior] margin" than those of *Megalancosaurus* or *Drepanosaurus* (Renesto & Fraser 2003: 704).

As documented by Fraser (1985, 1986), the age of the fissure fills of southwestern Britain is unclear. In regard to these fissure fills, Lucas & Hunt (1994: 340) noted, "Like all cave deposits, the fissure fills have complicated stratigraphic sequences, with evidence of mixing of strata. It is clear that parts of some fissures must be Late Triassic in age, as they contain aetosaurs and rauisuchians." Indeed, both Late Triassic and early Jurassic vertebrates are recovered from these fissure fills. Following Robinson (1957, 1973), Lucas & Hunt (1994, fig. 20.4) identified two assemblages, the older assemblage ranging from late Norian to mid Rhaetian in age and the younger ranging from late Rhaetian to mid Sinemurian. This division is based on the older fissures containing Late Triassic tetrapods, as noted above, while the younger fissures contain *Hirmeriella* pollen, indicating a Rhaetian to Sinemurian age (Kermack et al. 1973). We follow Renesto & Fraser (2003) and Fraser & Renesto (2005) and conclude that the drepanosaurid record from the Cromhall quarry is Late Triassic in age. This is the more parsimonious interpretation, given that all other drepanosaurid records are Late Triassic in age. Furthermore, the fissure fills are most likely late Norian or Rhaetian in age, as this is the age of apparently contemporaneous deposition of stratified deposits of the Mercia Mudstone Group (cf. Whiteside & Marshall 2008).

3.7. *Coelophysis* Quarry, northern New Mexico

Harris & Downs (2002) reported an isolated, three-dimensionally preserved pectoral girdle of a drepanosaurid from the *Coelophysis* Quarry, also known as the Ghost Ranch Quarry or Whitaker Quarry, 20 km north of Abiquiu, north-central New Mexico. The specimen was identified as drepanosaurid based on the thin, dorsally-oriented scapular blade. Additional comments by the authors suggested it was more similar to *Megalancosaurus* than *Drepanosaurus*, although they could not assign the material to a more inclusive taxon with confidence; however, a detailed comparison between the cast of the shoulder girdle from the *Coelophysis* Quarry and that of *Drepanosaurus unguicaudatus* holotype suggests that the two elements are nearly identical both in shape and size (Renesto pers. obs.).

The *Coelophysis* quarry occurs in the Rock Point Formation, Chinle Group (Hunt & Lucas 1993). As noted by Harris & Downs (2002), a specimen of the phytosaur *Redondasaurus bermani*, an index taxon of the Apachean land-vertebrate faunachron (Lucas 1998; Lucas et al. 2007), was recovered from just above the level of the *Coelophysis* quarry. Thus, the quarry is interpreted as Apachean (late Norian) in age (LUCAS & TANNER 2007).

4. Conclusions

The drepanosaurid material we report here is the oldest occurrence of this highly specialized family of archosauromorphs. When examining the stratigraphic range of this family it is significant that both its oldest and youngest occurrences are in the Chinle Group in the western United States, suggesting that drepanosaurids were a rare, but longstanding, component of Chinle faunas. The *Placerias* Quarry specimens exemplify this; only five elements among the thousands collected from the quarry pertain to drepanosaurids.

The Drepanosauridae has a stratigraphic range that encompasses much of Late Triassic time (Fig. 3), though they are known from relatively few records either based on single specimens (*Dolabrosaurus, Drepanosaurus* and *Vallesaurus*), numerous specimens found exclusively in a single area (*Hypuronector* and *Megalancosaurus*) or material undiagnostic below the family level (specimens from the *Placerias* and Cromhall quarries). Further discovery and recognition of drepanosaurid material will test the apparent endemism of the individual taxa in this family. It would appear that drepanosaurids originated in western North America in the earliest Adamanian, before radiating eastward into the rest of Laurasia by the Revueltian. Currently, there are no Gondwanan records of drepanosaurids. This is curious given the interchange of other taxa between the two landmasses during the same time, most notably dinosaurs/dinosauromorphs, which originate in Gondwanan South America during the Adamanian (late Carnian) and appear in the fossil record of Laurasian western North America shortly thereafter (COLBERT & OLSEN 2001).

Given the wide paleogeographic and long stratigraphic range of drepanosaurids, their fossil record is woefully incomplete. Further collecting and recognition of new specimens, especially in microvertebrate assemblages like the *Placerias* Quarry, will further refine our knowledge of this rare and unique family of archosauromorphs.

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Addresses of the authors:

Silvio C. Renesto, Dipartimento di Biologia Struttale e Funzionale, Università degli Studi dell'Insubria, via Dunant 3, I 21100 Varese, Italy;
e-mail: silvio.renesto@uninsubria.it;

Justin A. Spielmann, Spencer G. Lucas, New Mexico Museum of Natural History and Science, Albuquerque, NM 87104-1375, USA.