

A DREPANOSAURID PECTORAL GIRDLE FROM THE GHOST RANCH (WHITAKER) COELOPHYSIS QUARRY (CHINLE GROUP, ROCK POINT FORMATION, RHAETIAN), NEW MEXICO

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ABSTRACT—An isolated but three-dimensionally preserved pectoral girdle from the Rock Point Formation (Rhaetian) of New Mexico represents the youngest known drepanosaurid. The specimen preserves, in articulation, both scapulae, coracoids, clavicles, and sternal plates; clavicles and sternal plates were previously poorly documented or unknown in the Drepanosauridae. The elongate, thin, dorsally-oriented scapular blades are distinctive autapomorphies of the clade and strongly support the drepanosaurid origin of the specimen. The paired clavicles resemble the furculae of some theropod dinosaurs and basal birds, but the morphology of the remainder of the girdle demonstrates that it cannot belong to either group. The specimen's three dimensional preservation provides new information concerning the pectoral morphology of drepanosaurids.

INTRODUCTION

Much attention has been focused on Upper Triassic sediments because they contain fossils representing the earliest known representatives of many of the tetrapod clades that would later dominate terrestrial environments, including turtles, lepidosaurs, crocodylomorphs, dinosaurs, and mammals. Historically, sediments of the Chinle Group of southwestern North America have been among the most important for this understanding. Of numerous Chinle Group quarries, the Ghost Ranch (also called Whitaker) *Coelophysis* Quarry near Abiquiu, New Mexico, has been one of the most productive and historically active (Colbert, 1989). In particular, the quarry has been most famous for its ubiquitous fossils of the primitive theropod *Coelophysis* (Colbert, 1989; Sullivan et al., 1996). However, *Coelophysis* is not the only taxon represented in the quarry: other taxa recovered include palaeonisciform and actinistian osteichthyans (Schaeffer, 1967), phytosaurs (Colbert, 1989; Hunt and Lucas, 1993), a possible rauisuchian (attributed to *Postosuchus* by Long and Murry [1995]), the sphenosuchian *Hesperosuchus* (Clark et al., 2000) and a peculiar, new, armored taxon (Downs and Davidge, 1997).

Recently, while preparing a block from the Ghost Ranch (Whitaker) *Coelophysis* Quarry containing numerous specimens of *Coelophysis* as well as the aforementioned armored taxon, one of us (AD) discovered a small (42.6 mm dorsoventrally), articulated pectoral girdle of uncertain affinities. The specimen, GR 1113, consists of two articulated scapulae, coracoids, clavicles, and sternal plates. The elements are complete except for a small amount of bone along the midline, presumably where the coracoids would meet. Based on morphology, it is clearly not referable to *Coelophysis* and represents a taxon previously unknown from the Ghost Ranch (Whitaker) *Coelophysis* Quarry. Here we show that the specimen possesses distinctive characteristics of the Drepanosauridae and provides additional information about the anatomy of the clade.

Abbreviations—**CCSR**, Collezione del Centro Studi e Ricerche, Perugia, Italy; **GR**, Ruth Hall Museum of Paleontology, Ghost Ranch Conference Center, Abiquiu, NM, USA; **MCSN**,

Museo Civico di Storia Naturale 'E. Caffi', Bergamo, Italy; **MFSN**, Museo Friulano di Storia Naturale, Udine, Friuli, Italy; **MPUM**, Museo di Paleontologia Università di Milano, Milano, Italy.

Locality and Stratigraphy

The Ghost Ranch (Whitaker) *Coelophysis* Quarry occurs in the Rock Point Formation of the Chinle Group (Hunt and Lucas, 1993). The quarry is located on the property of the Ghost Ranch Conference Center, 20 km north of Abiquiu, New Mexico, at 36° 20' N, 106° 27' 30" E. A specimen of the phytosaur *Redondasaurus bermani*, an index taxon of the Apachean faunal stage, denoting a latest Triassic (Rhaetian) age (Lucas, 1998), was recovered just above the main quarry level (Sullivan et al., 1996).

Taphonomy

Taphonomic studies of avians (Schäfer, 1972; Davis and Briggs, 1998) and mammals (Hill, 1979; Hill and Behrensmeyer, 1984) demonstrate that, owing to its lack of direct articulation to the rest of the skeleton, the higher tetrapod pectoral girdle is relatively easily separated from a decaying body, so pectoral elements are easily lost early in the taphonomic history of an individual. Once dissociated, the girdle as a whole, however, can remain articulated for some time. GR 1113 was thus probably disarticulated from the rest of the body but buried by, or suspended in, sediment before further decay of the girdle and disarticulation of its elements could occur. This is consistent with the preservation of articulated series of skeletal elements, apart from whole skeletons, of *Coelophysis* and other animals in the Ghost Ranch (Whitaker) *Coelophysis* Quarry.

DESCRIPTION

The precise morphology of the proximal scapulae cannot be fully described because the suture between the scapula and the coracoid cannot be discerned on either side, indicating complete fusion and possibly the fully adult status of the individual. In all tetrapods which retain both scapulae and coracoids, the suture divides the glenoid more or less in half (Zug, 1979); measurements used here assume this position of the suture, although we acknowledge that, dorsal to the glenoid, the suture could

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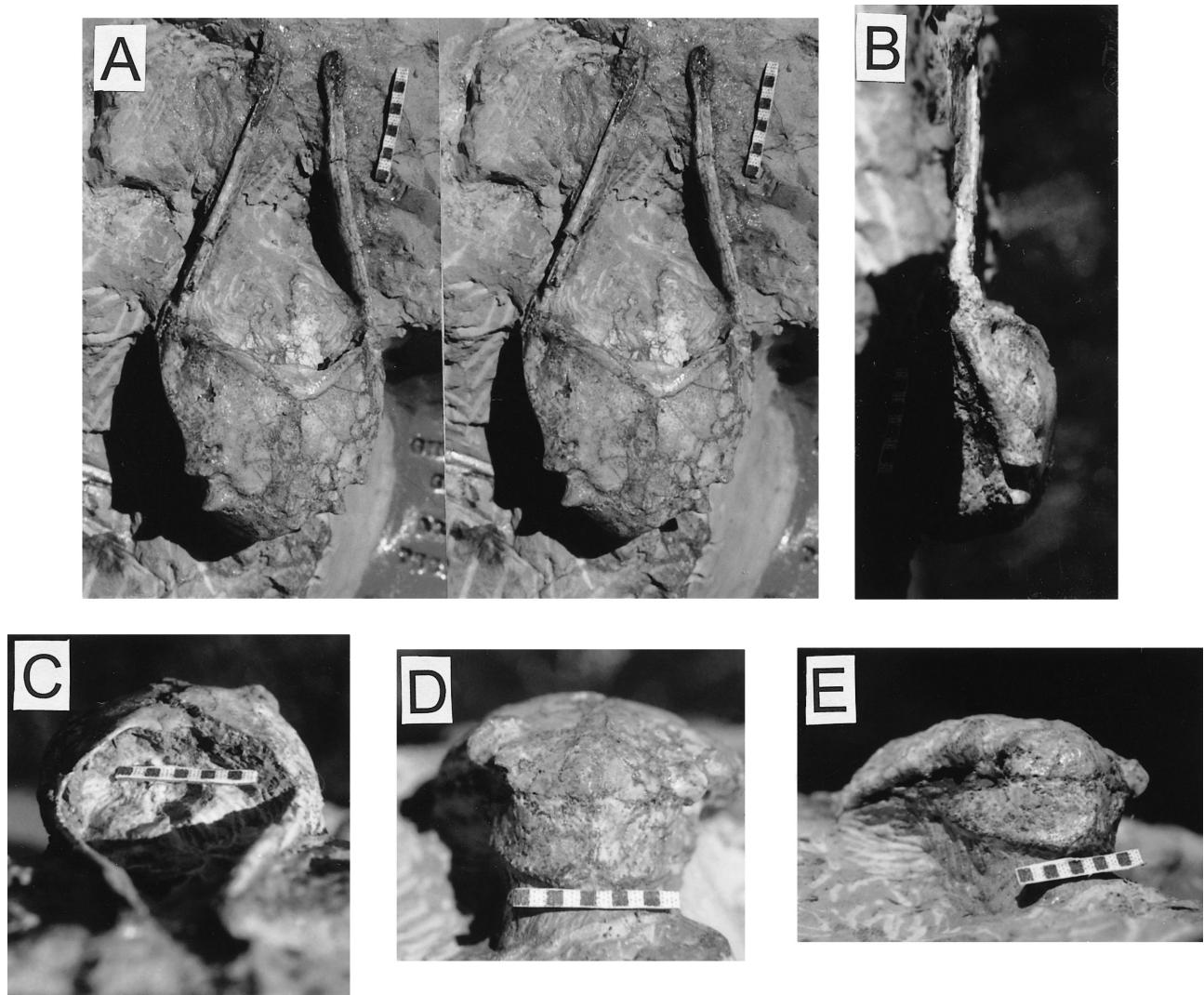


FIGURE 1. GR 1113, drepanosaurid pectoral girdle from Rock Point Formation (Chinle Group, Rhaetian) of Ghost Ranch, New Mexico, in (A) cranial view (stereo photograph pair), (B) right lateral view, (C) dorsal view, (D) ventral view, and (E) oblique right ventrolateral view (showing fullest view of sternal plate). Scale bars equal 1 cm.

conceivably bear in many directions, rendering its precise morphology unclear. The scapulae are long (40 mm from the distal end of the scapular blade to the midpoint of the glenoid, as measured along the outer curvature). The scapular blade is proximodistally long (24 mm), craniocaudally low (3.1 mm), and mediolaterally thin (just over 1 mm; Figs. 1A, B, 2A, B). The distal end is slightly expanded mediolaterally, but not craniocaudally (Figs. 1A, B, 2A, B). In cranial view, the blades angle toward each other (Figs. 1A, 2A), though how much of this is due to diagenetic distortion is unclear. The acromial portion expands suddenly from the narrow blade; it is deep, measuring 9.7 mm just caudal to the glenoid. In lateral view, there is a pronounced angle (120° on the right side; 132° on the left) between the scapular blade and acromial region; the scapular blade angles dorsally from the acromion (Figs. 1B, 2B).

As above, the lack of an identifiable scapula-coracoid suture renders the precise morphology of the coracoid ambiguous. With the same assumption regarding the location of the scapula-coracoid suture, the coracoid measures 8 mm along its outer margin. There is no apparent coracoid foramen, but each half of the girdle bears two small foramina: one is located along the dorsal margin, just cranial to the angle between the blade and

acromion, and a second just caudal to the glenoid, close to the ventral margin (Figs. 1A, 2A). These probably represent nutrient foramina and do not display pneumatic characteristics (per Britt, 1993).

The glenoid fossae are craniocaudally compressed and are bounded dorsally and ventrally by pronounced ridges that project beyond the lateral margin of the rest of the girdle (Figs. 1A, 2A). The fossae are selliform (saddle-shaped) and oriented primarily laterally with a moderate ventral component (Figs. 1B, 2B). Compared to the overall size of the girdle, the fossae are small and indicate a proportionately diminutive forelimb.

The clavicles are closely appressed to the dorsal margin of the girdle (Figs. 1A–C, 2A–C) and are separated from it, and each other, by shallow but visible sutures. Each clavicle is broadest at the midline suture, where they measure 3.3 mm in height. The expanded medial portion is distinctly set off from the tapered lateral process, this is particularly visible on the left clavicle (Fig. 1A, 2A). Together, they form a broadly parabolic element that resembles in shape the purported furcula of *Longisquama* (Sharov, 1970) and the true furculae of some theropods and birds (Beer, 1954; Burnham and Zhou, 1999). The clavicles in GR 1113 are closely appressed to the remainder of

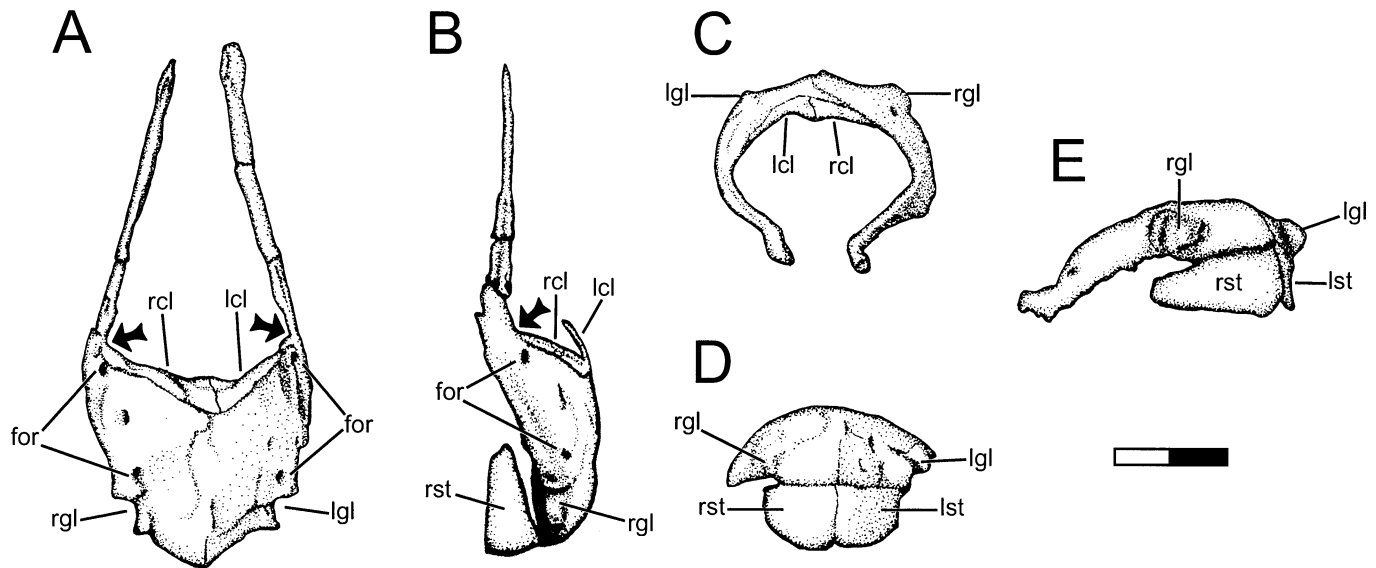


FIGURE 2. Schematic drawings of GR 1113, drepanosaurid pectoral girdle from Rock Point Formation (Chinle Group, Rhaetian) of Ghost Ranch, New Mexico, in (A) cranial view, (B) right lateral view, (C) dorsal view, (D) ventral view, and (E) oblique right ventrolateral view (showing fullest view of sternal plate). **Abbreviations:** for, foramen; lcl, left clavicle; lgl, left glenoid fossa; lsl, left sternal plate; rcl, right clavicle; rgl, right glenoid fossa; rst, right sternal plate. Arrow points to pronounced angle between scapular blade and acromion. Scale bar equals 1 cm.

the girdle along its entirety. Each clavicle bears a low ridge along the dorsal margin that extends from the distal end to a point just short of the median suture.

The paired sternal plates have a long, rounded triangular morphology, broadest medially and tapering laterally (Figs. 1B, D, E, 2B, D, E). The left plate measures 12.9 mm mediolaterally; the right 12.4 mm. At their broadest (cranio-caudally) points, just lateral to the midline, they each measure 5.9 mm cranio-caudally. Both contact the rest of the girdle (presumably the coracoids) medially, but there is no contact caudal to the cranial

margin of the glenoid on either side (Figs. 1E, 2E). There is no medial carina.

DISCUSSION

Phylogenetic Relationships

GR 1113 displays a combination of primitive and derived features that obfuscates its identity. In overall morphology, the specimen is quite unlike the pectoral girdle of contemporaneous anapsids or therapsids, and is thus not likely to belong to either group. Within the Diapsida, few pectoral characters have been cited as useful apomorphies. GR 1113 lacks a cleithrum; this absence is considered an archosauromorph synapomorphy by Benton (1985).

GR 1113 lacks any evidence of suprascapular cartilage. The ossified scapular blade is very long proximodistally, with a width/length ratio $< \frac{1}{4}$, a synapomorphy of the Archosauria per Benton (1985) and Benton and Clark (1988); this condition supports an archosaurian affinity for GR 1113. A proximodistally long, narrow, "strap-like" (presumably meaning one in which the blade is parallel-sided and of narrow dimension along the entire length) scapular blade lacking a distal expansion is considered a dinosaurian synapomorphy by Benton and Clark (1988); an expansion is absent in *Herrerasaurus* (Sereno, 1993) but coelophysoid theropods, including *Coelophysis* (Colbert, 1989), possess marked distal expansions (Fig. 3C). This may represent a reversal, and the permanent loss of a distal expansion may be synapomorphic at a deeper node within the Theropoda (Tetanurae or Neotetanurae).

A "strap-like" scapula was considered an avian autapomorphy by Tarsitano (1991) and Feduccia (1993). However, a "strap-like" scapula is also characteristic of the peculiar Drepanosauridae (probable basal archosauromorphs per Dilkes, 1998), including *Megalancosaurus* (Feduccia, 1993; Renesto, 1994a, 2000; Fig. 4), *Drepanosaurus* (Fig. 3E; Renesto, 1994b; contra Pinna, 1984), and the *Hypuronector* (Olsen, 1980; Colbert and Olsen, 2001) from the Lockatong Formation of New Jersey; the latter taxa share with GR 1113 a vertical orientation of the scapular blade (Figs. 3A, E, 4), unlike the horizontal avian condition (Fig. 3G, H). The vertical orientation contrasts

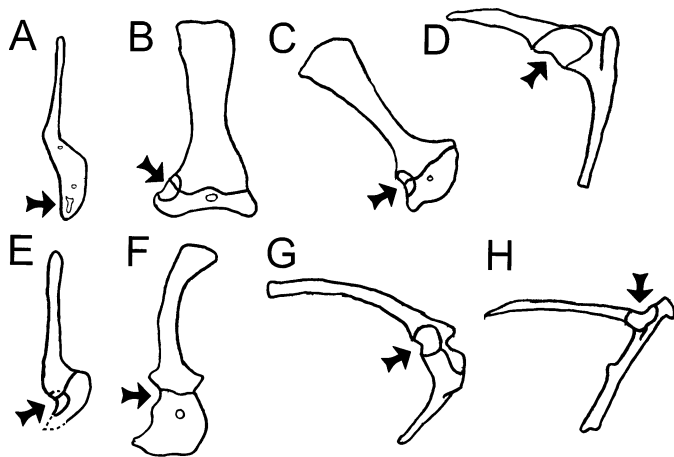


FIGURE 3. Schematic drawings of select diapsid pectoral girdles in right lateral view. Drawings are scaled to the same distance between the glenoid fossa and the distal end of the scapular blade, and are oriented in approximate life position. A, GR 1113; B, the generalized, primitive, terrestrial archosaur *Euparkeria* (reversed from Ewer, 1965). C, the primitive theropod *Coelophysis* (from Colbert, 1989). D, the pterosaur *Rhamphorhynchus* (reversed from Wellnhofer, 1991). E, the drepanosaurid *Drepanosaurus* (from Renesto, 1994b). F, the modern, arboreal lacertilian *Chamaeleo* (reversed from Parker, 1867). G, the basal bird *Archaeopteryx* (from Ostrom, 1976). H, the modern bird *Sturnus* (from Jenkins, 1993). Arrows indicate glenoid fossae. See text for discussion of the orientation of the glenoids.

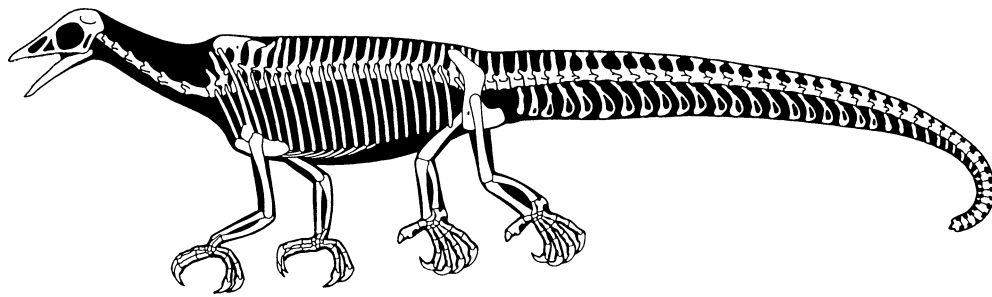


FIGURE 4. Skeletal reconstruction of *Megalancosaurus* by Gregory S. Paul. Note the vertical orientation of the scapular blade.

with the angled condition seen in dinosaurs and advanced, non-dinosaurian archosaurs and is probably a retention of the plesiomorphic archosaurian state (e.g., Ewer, 1965). Feduccia (1993) interpreted the orientation of the disarticulated scapula of the holotype of *Megalancosaurus* (MFSN 1769) to reflect an avian-like position parallel to the apparent axis of the postcranial skeleton (which is not preserved), but new specimens of *Megalancosaurus* demonstrate that this orientation is a taphonomic artifact (Renesto, 2000). The long, strap- or rod-like morphology of vertically-oriented scapular blades is synapomorphic of drepanosaurids (Dilkes, 1998; Renesto, 2000; Colbert and Olsen, 2001); it is also present, though to a lesser extent, in the kuehneosaur *Icarosaurus* (Colbert, 1970) and the peculiar reptile of uncertain affinities *Longisquama* (Sharov, 1970; Renesto, 1994b). Although not noted as a synapomorphy in previous analyses, the pronounced bend between the scapular blade and the acromion in GR 1113 is present in *Megalancosaurus* (Renesto, 1994a, 2000), *Drepanosaurus* (Renesto, 1994b), and the *Hypuronector* (Colbert and Olsen, 2001); this feature is also present in *Icarosaurus* (Colbert, 1970). However, the scapular blade of both *Icarosaurus* and *Longisquama* are much shorter than in the drepanosaurids or GR 1113. In overall morphology, GR 1113 is much more similar to drepanosaurids than other archosaurs.

Unfused clavicles are plesiomorphic for the Diapsida, and the retention of unfused clavicles in GR 1113, despite complete scapular-coracoid fusion, indicates that the lack of fusion in the taxon is an adult, not ontogenetic, feature. Paired clavicles are retained throughout the Lepidosauromorpha except in highly derived taxa (e.g., the lizard *Chamaeleo* [Parker, 1867; Peterson, 1973]). Reduction or absence (presumably in ossified form and not necessarily entailing complete absence) of clavicles was considered a synapomorphy of the Ornithodira by Sereno (1991), implying that its reappearance in later dinosaurs was a reversal. However, because of the sporadic preservation of clavicles and furculae, even in taxa known to possess them, the utility of clavicular morphology, or even presence, as useful phylogenetic characters are dubious. Lacking complete medial fusion, GR 1113 cannot be said to possess a true furcula (although a medial suture is retained in many birds). The appearance of a true furcula was initially considered an avian (avialae) autapomorphy (Heilmann, 1927), but furculae have subsequently been discovered in various non-avian theropod dinosaurs, including the coelophysoid *Syntarsus kayentakatae* (Tykoski, 1998). The presence of a true furcula appears to be autapomorphic for the Neotheropoda (per Sereno, 1998; see also Padian et al., 1999); it may even be diagnostic for the Theropoda as a whole. GR 1113 thus does not appear referable to the Theropoda. Unfused clavicles remain plesiomorphic for the Dinosauria, however, and have been identified in some prosauropods, sauropods and ornithischians (Bryant and Russell, 1993; Padian, 1997), and some theropods retain unfused clavicles, as in the ceratosaurian *Segisaurus* (Camp, 1936; Bryant and Russell, 1993). The latter may be an ontogenetic feature

for the taxon or indicate the variability of clavicular fusion in primitive theropods. A possible furcula was also reported in *Longisquama* (Sharov, 1970), but the interpretation of this element remains controversial, and we here caution that articulated clavicles with a shallow midline suture, such as that in GR 1113, if disarticulated from the remainder of the girdle, could be mistaken for an isolated furcula.

The abrupt and pronounced medial expansion of the clavicles in GR 1113 is absent in probable *Coelophysus* furculae from the same quarry (Downs, 2000:fig. 2E) and other reported theropod furculae (Chure and Madsen, 1996; Makovicky and Currie, 1998). The extremely close appression of the clavicles to the remainder of the pectoral girdle in GR 1113 is quite unlike the looser articulation of the furcula in non-avian theropods (e.g., Makovicky and Currie, 1998). A possible clavicular fragment in the *Hypuronector* is similarly appressed, although the fragment has a greater dorsal extent than in GR 1113 (Colbert and Olsen, 2001). Renesto (2000) reports unambiguous clavicles in a new specimen of *Megalancosaurus* (CCSR 63115); his reconstruction places the clavicles in virtually identical position to that in GR 1113. Possible clavicles in the holotype of *Megalancosaurus* were reidentified as dorsal ribs by Feduccia (1993) and, given the much greater length and narrower divarication angle of the questioned element in the latter than in GR 1113, we agree with Feduccia's interpretation. Despite the similarity in morphology of the joint clavicles in GR 1113 to the furculae of theropods and birds, the complete appression of the elements in GR 1113 is more similar to that of drepanosaurids (Renesto, 2000) and obviates a theropod origin for the specimen.

Evans (1988) and Gauthier et al. (1988) found the retention of paired sternal plates in an adult individual a synapomorphy of the Lepidosauromorpha. However, paired sternal plates are also primitive for the Archosauromorpha, and are retained in numerous taxa, including many dinosaurs (Padian, 1997), rendering the utility of this trait in placing GR 1113 dubious. Within the Theropoda, both paired (e.g., Norell and Makovicky, 1997) and fused, unpaired (e.g., Currie and Zhao, 1993) sternal plates are known. An unpaired sternum occurs in *Archaeopteryx* (Wellnhofer, 1993). The fusion of paired sternal plates into a single element may be an ontogenetic, phylogenetically uninformative, feature. The partially disarticulated pectoral and forelimb elements of the most complete and articulated specimen of *Drepanosaurus* (MCSN 5728) have been interpreted differently by different authors (Pinna, 1984; Renesto, 1994b), but neither interpretation identifies sternal plates. Similarly, although suspected, sternal plates have not been confirmed in *Megalancosaurus* (Renesto, 2000). Ultimately, however, this is negative evidence, and cannot be used to prove the actual lack of these elements in these taxa. Historically, an apparent absence of many features, particularly pectoral girdle elements, has led to conflicting, and often erroneous, systematic and phylogenetic interpretations in many taxa: in a particularly relevant example, the lack of a sternum in *Archaeopteryx*, represented

by several virtually complete and articulated specimens, was considered by many (e.g., Beer, 1954) as indicative that early birds lacked this feature. New discoveries (Wellnhofer, 1993; Hou et al., 1995), however, confirm that the earliest and most primitive known birds do indeed possess sterna. Similarly, the absence of clavicles or furculae in dinosaurian taxa prevented Heilmann (1927) from identifying dinosaurs as avian ancestors, but clavicles and furculae were subsequently discovered in many dinosaurs (Bryant and Russell, 1993; Padian, 1997; Tykoski, 1998). This, coupled with the only recent discovery of clavicles in other drepanosaurids, implies that the lack of these elements is often a taphonomic artifact and not necessarily a useful phylogenetic character.

In summary, GR 1113 displays the drepanosaurid autapomorphic morphology and orientation of the scapular blades (Dilkes, 1998; Renesto, 2000; Colbert and Olsen, 2001). Furthermore, it is more similar to drepanosaurids in other features, such as the marked angulation between the scapular blade and the acromion and in the morphology and articulation of the clavicles. GR 1113 is thus most parsimoniously referred to the Drepanosauridae, and presents new information about the pectoral region in this clade. With the exception of *Dolabrosaurus* (see below), all other specimens of drepanosaurids are, as is typical for lithographic limestones, heavily compacted into two dimensions. This renders their three-dimensional reconstructions somewhat problematic. Combining data from multiple specimens (e.g., Renesto, 1994b, 2000) has alleviated this problem somewhat, and demonstrates that these animals possess exceptionally long and narrow scapular blades and broad, expansive acromial and coracoidal regions. The reconstruction of the pectoral girdle of *Drepanosaurus* (Renesto, 1994b) is very similar to GR 1113; the pectoral region of *Megalancosaurus* is even more similar (Renesto, 2000), although in that taxon, the broad coracoidal region appears to face much more ventrally than demonstrated by GR 1113. Much of this reconstruction, however, may incorporate unrecognized sternal plates (Renesto, 2000), and may also mistakenly incorporate compactional rotation of the coracoids. The best-preserved *Megalancosaurus* pectoral girdle (MPUM 608; Renesto, 2000:pl. 3B) depicts a scapula very similar to GR 1113 and it is easy to imagine GR 1113 mediolaterally compacted to produce the orientation of the broad coracoids of the Italian specimen. Alternatively, this may be a generic difference between *Drepanosaurus* and *Megalancosaurus*. GR 1113 also documents the presence of paired sternal plates in these animals.

Biostratigraphy

Drepanosaurids are currently known only from Upper Triassic rocks. The oldest, and most primitive, member of the clade is the *Hypuronector* (Olsen 1980); q.v. Colbert and Olsen (2001), recovered from the latest Carnian (Adamanian faunachron [Lucas, 1998]) Locketong Formation (Newark Supergroup) of New Jersey. *Megalancosaurus* and *Drepanosaurus* are both only known from Lagerstätten of northern Italy; these sediments are considered early Norian (Revueletian faunachron [Lucas, 1998]). GR 1113 represents the second confirmed occurrence of the Drepanosauridae in the Chinle Group (see below), and the first with preserved pectoral elements.

The presence of a drepanosaurid in the Chinle Group is not unprecedented: Berman and Reisz (1992) described the partial skeleton, lacking any pectoral elements, of *Dolabrosaurus aquatilis* from the Petrified Forest Formation very near Ghost Ranch. *Dolabrosaurus* is from the Petrified Forest Formation that produces Reueletian index taxa. Renesto (2000) notes that the cervical vertebrae of *Megalancosaurus* are extremely similar to those of *Protoavis* (Chatterjee, 1995) and proposes that the cervicals attributed to that taxon may in fact be drepanosaurid. Thus, drepanosaurids may also be present in the Reueletian fauna from the Dockum Formation of Texas. Coming from the Rhaetian (Apachean faunachron) Rock Point Forma-

tion, GR 1113 is, biostratigraphically, the youngest known representative of the Drepanosauridae. Whether GR 1113 represents *Dolabrosaurus*, another drepanosaurid, or a new taxon, cannot be assessed with present material.

Functional Morphology

The behavior of drepanosaurids has been the subject of much debate, and Renesto (2000) provides a thorough summary and discussion. Most workers reject the fossorial habit proposed initially for *Drepanosaurus* by Pinna (1986). An arboreal lifestyle is supported by the morphology of the manus in *Megalancosaurus* (Renesto, 1994a, 2000), whereas a natatory habit is supported by the deep tail of *Megalancosaurus*, *Drepanosaurus*, and, especially, the *Hypuronector*. While it is difficult to ascertain the function of an animal based solely on the pectoral girdle morphology, it is worthwhile to note that a long, vertically-oriented scapular blade, as in GR 1113 and other drepanosaurids, is characteristic of some extant, arboreal lizards, including *Anolis* and *Chamaeleo* (Lécureu, 1968; Peterson, 1984), although the latter autapomorphically lacks clavicles to allow the pectoral girdle to rotate as part of the locomotory step.

ACKNOWLEDGMENTS

The authors benefited greatly from conversations and access to unpublished material about *Drepanosaurus* and *Megalancosaurus* from Dr. Silvio Renesto (Università degli Studi, Milano) and about *Hypuronector* from Dr. Paul Olsen (Columbia University). Conversations with Gregory S. Paul (Baltimore) and Drs. Dan Chure (Dinosaur National Monument), Susan Evans (University College of London), Nick Fraser (Virginia Museum of Natural History), Jacques Gauthier (Yale University), Terry Jones (Oregon State University), John Merck (University of Maryland), and Hans-Dieter Sues (Royal Ontario Museum) were likewise invaluable. John Hutchinson (University of California at Berkeley) provided unpublished photographs of the pectoral girdle of *Segisaurus* for analysis and comparison. Andrew Heckert (University of New Mexico at Albuquerque) clarified Chinle Group stratigraphy and correlation; Drs. Heckert and Cathy Forster (State University of New York at Stony Brook), Spencer Lucas (New Mexico Museum of Natural History), Michael Parrish (Northern Illinois University), Silvio Renesto, and two anonymous reviewers made helpful comments on early versions of this paper. Maureen Kearney (George Washington University) provided some references, and Greg Paul kindly provided Figure 4.

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