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ABSTRACT

The Drepanosauridae is a group of enigmatic tetrapods represented primarily by articulated material from the Late Triassic of northern Italy and eastern North America. The principal taxa are *Drepanosaurus* and *Megalancosaurus* from Italy and *Hypuronector* from New Jersey. In addition, *Dolabrosaurus* was erected on the basis of somewhat less complete material from the Chinle Formation of New Mexico. Recently, isolated cervical vertebrae from Norian fissure sediments of the Cromhall Quarry, Avon, England, were referred to the Drepanosauridae. Here we report on additional elements from the same fissure infills that can also be assigned to the Drepanosauridae. These include several caudal vertebrae and possibly also the claw-like, terminal element of a drepanosaur tail.

INTRODUCTION

The family Drepanosauridae was erected by Olsen & Sues (1986) and first diagnosed by Berman & Reisz (1992). Of the taxa now included within the family, *Drepanosaurus* (Pinna, 1980) and *Megalancosaurus* (Calzavara et al., 1980), from the Late Triassic of northern Italy, were the first to be described. Later, *Dolabrosaurus*, from the Petrified Forest Formation, Chinle Group, New Mexico (Berman & Reisz, 1992) and, most recently, *Hypuronektor* (informally known for many years as the “deep-tailed swimmer” [Olsen, 1980]) from the Newark Supergroup (Colbert and Olsen, 2001), were described. In addition, an unnamed, small reptile from the Late Triassic Calcare di Zorzino (northern Italy), MCSNB 4751 (Renesto, 2000: fig. 11), can unquestionably be regarded as a drepanosaurid distinct from *Drepanosaurus* and *Megalancosaurus*.

While these taxa exhibit a rather diverse array of body forms, all share some very characteristic features that unequivocally demonstrate their close relationships. In particular, diagnostic features include a very slender, rod-like scapula, dorsal vertebrae with high neural spines sometimes expanded craniocaudally at their distal ends, and exceptionally tall neural and haemal spines on the caudal vertebrae together with prezygopophyses that lie very close to the midline and considerably overlap the centrum of the previous vertebra. Additional shared characteristics include: a barrel shaped trunk; ribs mostly holocephalous, slender, and triangular in section; gastralia absent; coracoid flat, somewhat expanded caudally; pelvic girdle with a high iliac blade, a rather narrow pubis and an ischium that is elongate caudally; femoral shaft lacking sigmoid curvature; tarsus and carpus modified to allow high mobility of both manus and pes (Renesto 1994a, b, 2000); fifth metatarsal straight; very long and narrow ungual phalanges with well developed flexor processes. Furthermore, *Drepanosaurus* and *Megalancosaurus* both possess a curious, claw-like, terminal element on the tail. Such a feature has also been inferred for *Dolabrosaurus* (Renesto, 2000).

With the detailed descriptions of a variety of relatively complete drepanosaur specimens, it became possible to recognize isolated drepanosaur elements. Thus Harris & Downs (2002) identified a characteristic drepanosaur shoulder girdle from the famed Ghost Ranch *Coelophysis* Quarry.

Most recently, on the basis of a detailed study of the cervical vertebrae of *Megalancosaurus* from the Calcare di Zorzino (Zorzino Limestone) and Dolomia di Forni (Forni Dolostone) formations, isolated drepanosaur cervical vertebrae were recognized amid the disassociated vertebrate assemblages of the Upper Triassic fissure deposits at Cromhall Quarry, England (Renesto & Fraser, 2003). Although the preservation of the material from the two regions is very different – the former consisting of compressed, articulated material, and the latter three-dimensional, isolated elements – the unique shape of the cervical vertebrae is so compellingly similar as to allow for the unquestioned recognition of drepanosaurs within the fissure infill fauna.

Further bulk preparation of matrix from the fissure fills at Cromhall Quarry, along with sorting of previously processed vertebrate elements, was undertaken in an attempt to determine whether more drepanosaur material could be identified. This was rewarded with a number of new finds that are described here.

Abbreviations used to identify the institutional collections cited here are

CCSR – Collezione del Centro Studi e Ricerche Villa Anita, Sigillo

Umbro (Perugia, Italy);

MCSNB – Museo Civico Scienze Naturali “Caffi” Bergamo

(Bergamo, Italy);

MFSN – Museo Friulano di Storia Naturale (Udine, Friuli, Italy);

UMZC – University Museum of Zoology, Cambridge (Cambridge,

U.K.)

MATERIAL

The new material derives from four separate fissure fills at Cromhall Quarry, Avon, England. These fissures were numbered S3, S4, 4/5 and S7 by Walkden & Fraser (1993:514), and the reader is referred to that paper for details of the geology of Cromhall Quarry.

The drepanosaur cervicals described by Renesto & Fraser (2003) originated from fissures S7 and 4/5, and these two sites have now yielded a number of very distinctive, small caudal vertebrae, five of which are illustrated here (Figs. 1, 2), together with three dorsal vertebrae (Fig. 3).

Figure 1. UMZC 2004.4, drepanosaur caudal vertebra in left lateral view. Scale bar represents 1.0 mm.



These notochordally amphicoelous vertebrae are characterized by short but high neural arches. None of the specimens have complete neural spines, but they were apparently very tall and exceptionally slender. In UMZC 2004.17 (Fig. 2D), for example, the preserved portion of the neural spine is as long as the centrum. It is impossible to determine whether any had expanded distal ends. In an articulated tail, the prezygapophyses would

have extended over at least half the length of the centrum of the preceding vertebra. This gives the vertebrae the appearance of being strongly “inclined” anteriorly. The centrum is slightly constricted towards the middle. The zygapophyses are positioned very close to the midline, and the

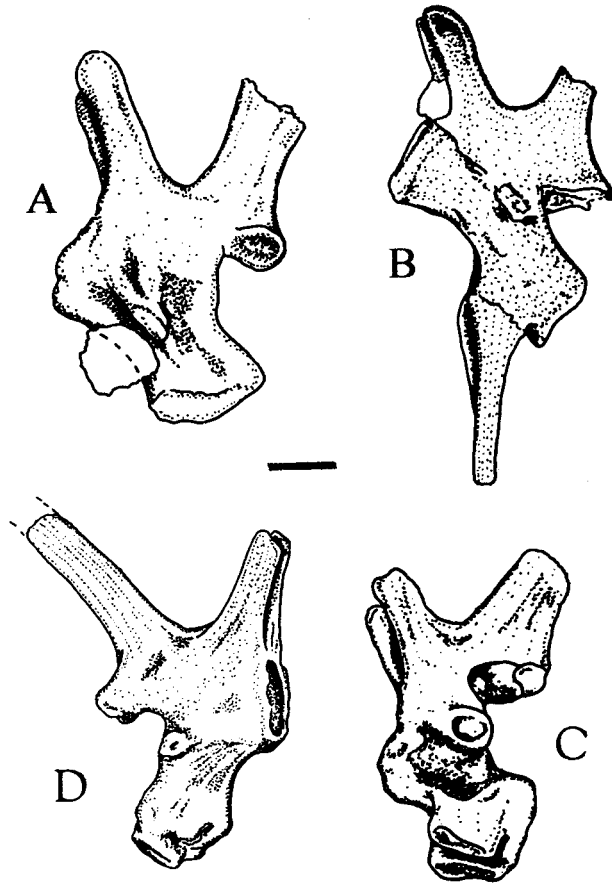


Figure 2. Drepanosaur anterior caudal vertebrae in left lateral views. A) UMZC 2004.2, B) UMZC 2004.5, C) UMZC 2004.6, and D) UMZC 2004.17. Scale bar represents 1.0 mm.

articular surfaces are oriented close to vertical. Two of the specimens have preserved chevron bones (haemal spines) still fused with the posterior edge of the centrum. The chevrons are deflected backward which further enhances the angled appearance of the vertebrae.

Three specimens are here regarded as dorsal vertebrae (Fig. 3). In UMZC 2004.15 (Fig. 3A) the neural arch is tall, but shorter than those of vertebrae referred to the caudal series. It is distinguished by the preservation of ribs fused low down on the neural arch and onto the centrum. On one side, the suture between the neural arch and the rib head is preserved.

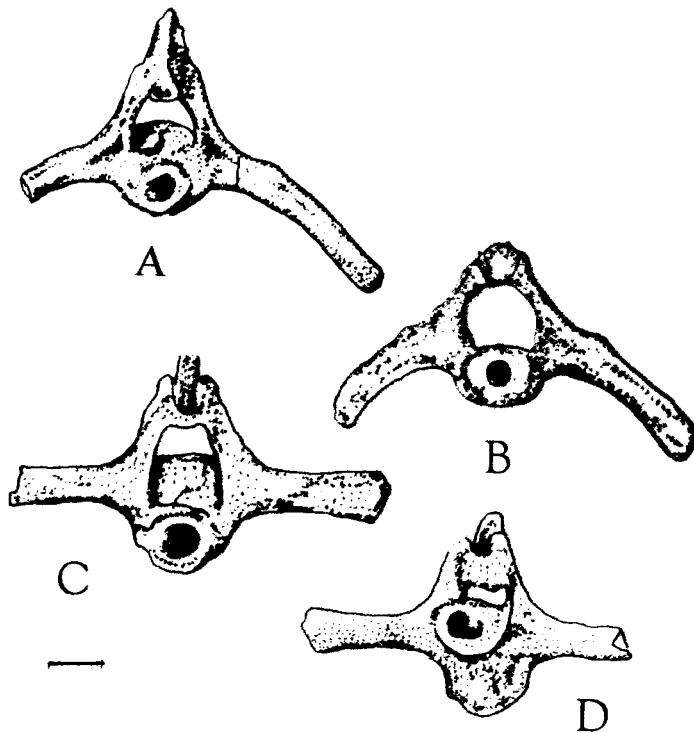


Figure 3. Drepanosaur dorsal vertebrae. A) UMZC 2004.15 in anterior view, B) UMZC 2004.7, in posterior view, and UMZC 2004.16 in C) anterior and D) posterior views. Scale bar represents 1.0 mm.

Neither rib is complete, but each arches downwards, and, when restored, they would provide a structure consistent with the barrel-shaped trunk described by Renesto (2000) as a drepanosaur characteristic.

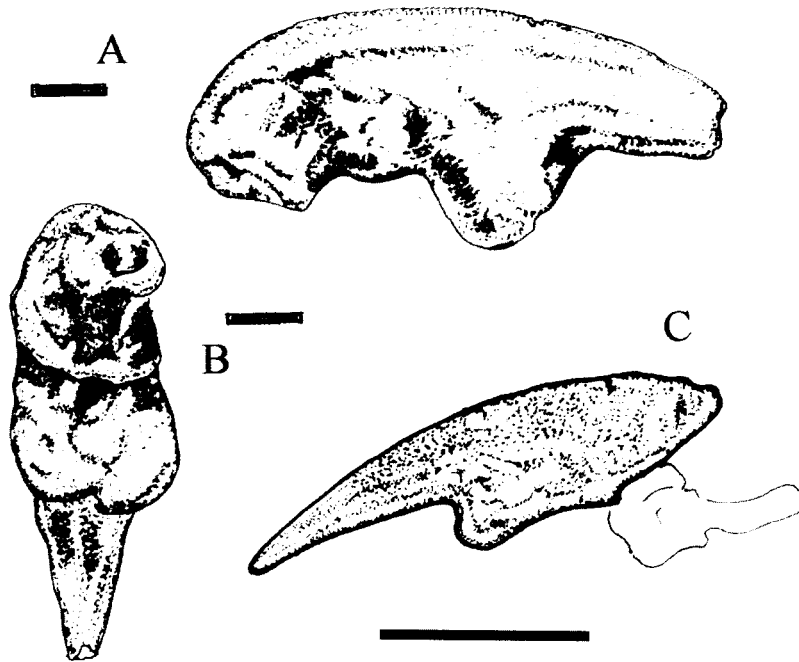


Figure 4. UMZC 2004.8, possible drepanosaur terminal caudal element in A) lateral view and B) proximal view. Scale bar represents 1.0 mm. C) Terminal caudal element in *Drepanosaurus*, MCSNB 5728.

A single, curious, claw-like bone was recovered from S4 (Fig. 4). While distally it resembles an ungual phalanx, the structure of the proximal end departs significantly from the typical, concave, articular surface for the reception of the penultimate phalanx. Instead, it is bulbous and displays a clear opening in the end so that it looks like the end of a notochordal

amphicoelous centrum. It bears a close resemblance to the terminal elements that characterizes the tail of *Megalancosaurus* (Fig. 5) and *Drepanosaurus* (Fig. 6). The long, low profile in lateral view and slight degree of flexure is consistent with this interpretation. All three elements bear a shallow ridge running longitudinally down each side (Fig. 4). The remarkable similarity of the proximal end of UMZC 2004.8 (Fig. 4B) to that of the amphicoelous caudal centra also supports this referral, but because the Italian fossils are compressed, it is not possible to make a direct comparison.

Given the rather unique structure of certain other drepanosaur elements – such as the scapulocoracoid, the curious first pedal digit in some *Megalancosaurus* individuals, or the extraordinary large claws on the *Drepanosaurus* manus – it is not unreasonable to expect to find additional very diagnostic elements in the Cromhall sediments. In this respect, a fragmentary bone with a glenoid (Fig. 7) is potentially part of a drepanosaur scapulocoracoid. Below the glenoid is a small perforating foramen that would be situated within the coracoid. However, the remainder of the bone is missing, and it is impossible to determine whether or not it originally had the approximately oval, flat form displayed by *Drepanosaurus* and *Hypuronector*. Above the glenoid, the bone continues as a strap-like process, but it too is very incomplete. Given its incompleteness, the possibility that it represents part of a drepanosaur ilium cannot be excluded. In fact, it shows some resemblance to the iliac blade and acetabulum of the most recently discovered *Megalancosaurus* specimen, CCSR 63115 (Renesto, 2000). Indeed, the blade of UMZC 2004.9 is somewhat compressed rather than thick and sub-circular in cross section. This would be more consistent with interpretation as an iliac blade rather than a scapula.

Some interesting, small and rather delicate marginal jaw elements were described by Fraser (1988) from Cromhall Quarry. They included two types of premaxilla and two types of maxilla. Recognizing that such elements rarely permit specific diagnoses, Fraser (1988) only provided very broad



Figure 5. *Megalancosaurus* caudal series, MFSN 18443a. Scale bar represents 10.0 mm.

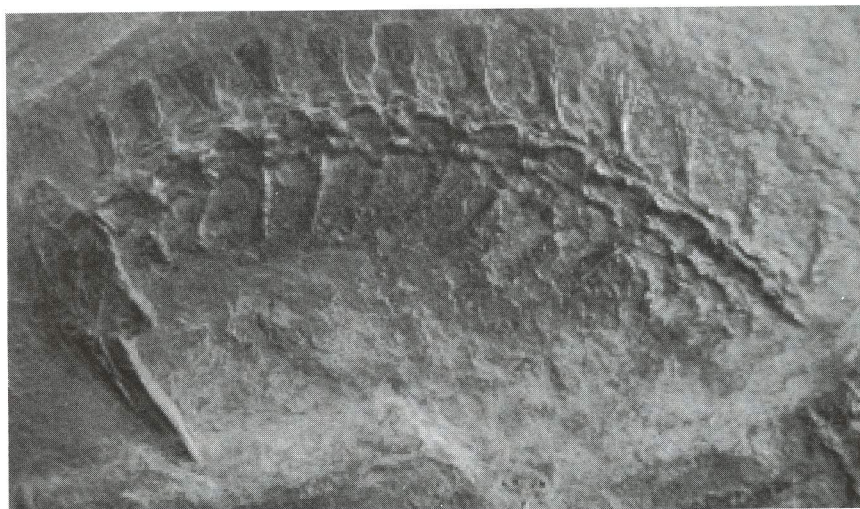


Figure 6. *Drepanosaurus* caudal series, MCSNB 5728. Scale bar represents 10.0 mm.

taxonomic commentary, but suggested the possibility of prolacertiform, thalattosaurian, or pterosaurian affinities. It is worth pointing out here that these elements are also consistent with some of the known cranial material of drepanosaurs, and that their structure is very similar to jaw bones in the holotype of *Megalancosaurus* as well as the small undescribed drepanosaur MCSNB 4751. On the other hand, *Hypuronector* apparently was quite distinct in having a dentary with an edentulous anterior region (Colbert & Olsen, 2001).

DISCUSSION

The new material confirms the presence of at least one drepanosaur in the fissure fills of Cromhall quarry. However, the relationship to drepanosaurs from elsewhere is more difficult to determine.

Renesto (2000) divides the caudal series of *Megalancosaurus* into three regions: the first 3-4 vertebrae are rather short, and bear high and narrow neural spines that are curved caudally in the distal portion. The chevron is fused to the posterior end of the centrum. In the mid section of the tail, the caudals take on a different form. The centra become more elongate and the neural spines are expanded distally to form a "T"-shape in lateral view. The haemal spines are also expanded and bear a fossa (Fig. 5). Finally, in the most distal region, the haemal spines lose the fenestration and the T-shaped spines decrease in height. Furthermore, the haemal spines migrate onto the anterior margin of the centrum and are angled forwards. None of the Cromhall caudals exhibit the morphology displayed in the mid or distal regions of the *Megalancosaurus* tail, and while they are closer to those from the anterior region, the Cromhall caudals are noticeably longer than the distinctly short *Megalancosaurus* anterior caudals.

Drepanosaurus lacks the complexity of the *Megalancosaurus* caudal series and consequently, in some respects, *Drepanosaurus* caudals (Fig. 9) appear closer to the Cromhall forms. Likewise the caudals of *Dolabrosaurus* (Berman & Reisz, 1992: figs. 3, 4), but in terms of size and

overall shape, the unnamed taxon MCSNB 4751 and *Hypuronector* are the closest matches to the new Cromhall caudals.

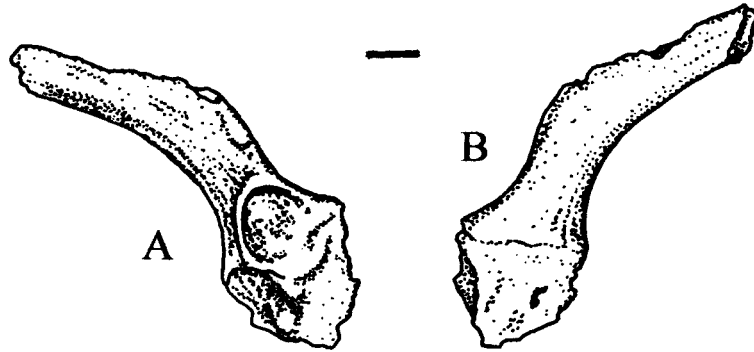
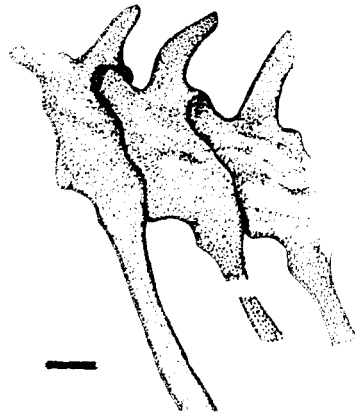


Figure 7. UMZC 2004.9, tentatively referred to as a partial drepanosaur scapula, in A) lateral, and B) medial views. Scale bar represents 1.0 mm.

UMZC 2004.4 bears a striking resemblance to the caudals of *Hypuronector* (Colbert & Olsen, 2001: fig. 9), even having a notochordal amphicoelous centrum. Colbert & Olsen (2001) state that the caudal vertebrae of *Megalanocosaurus* are procoelous, and not amphicoelous. However, we contend that because of the closely articulated nature of the tail in all known *Megalanocosaurus* specimens, it is not possible to directly observe the articular surfaces of the centra to determine whether they are amphicoelous or not. Nevertheless, an examination of CCSR 63115 shows that the sacral vertebrae were notochordally amphicoelous (Renesto, 2000; fig. 4), and we suggest that there is no evidence to indicate that this condition did not continue into the caudal series. In this context, it is worth pointing out that while the Cromhall cervical vertebrae referred to drepanosaurs are procoelous, the described dorsal vertebra and all the characteristic caudals are notochordal amphicoelous. This raises the possibility that, in at least some drepanosaurs, there is a change along the

length of the vertebral column from procoely in the cervical series to notochordal amphicoely in the dorsal and caudal series. It appears that the nature of the articulation surface in the cervicals of *Hypuronector* cannot be readily determined on the basis of the described specimens. Thus, it is conceivable that they are procoelous, even in *Hypuronector*. Certainly, changes in the nature of the centra articulations are known in other tetrapods, including certain chelonians, where the same cervical series can exhibit procoelous, opisthocoelous and amphicoelous vertebrae together (Romer, 1956: 243).

Figure 8. Anterior caudal vertebrae in the small undescribed drepanosaur, MCSNB 4751. Scale bar represents 1.0 mm.



The new caudals are also particularly close to those of the very small drepanosaur MCSNB 4751, figured by Renesto (2000: fig. 11). This specimen is currently being described by Rupert Wild (pers. comm.). Both appear to have equally slender neural and haemal spines (Fig. 8).

Colbert & Olsen (2001) argued that *Hypuronector* used its “deep tail” to propel itself, or scull, through the water. However, Renesto (2000) argued that the tail was incapable of lateral undulation, and therefore could not have generated any significant propulsive force. Indeed, Renesto (2000) considered drepanosaurs to be exclusively arboreal. The new material tends to reinforce Renesto’s arguments. It provides for the first time good, three-dimensional preservation of drepanosaur vertebrae, and it is difficult to

envision any significant lateral movement between successive caudal vertebrae. The closely positioned, almost vertically oriented, zygapophyses, coupled with the anterior “inclination” of the vertebrae, would have severely restricted side-to-side movement. At the same time, dorso-ventral flexure of the caudal axial column would have been facilitated. Since the new caudal vertebrae closely resemble those of *Hypuronector*, this speaks against an aquatic habit for *Hypuronector*, or at least against the use of the tail to scull through the water.

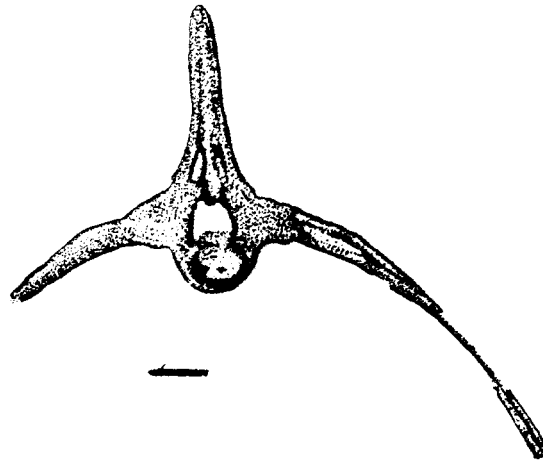


Figure 9. Anterior caudal of *Drepanosaurus*, MCSNB 5728. Scale bar represents 1.0 mm.

As first suggested by one of us (Renesto, 2000), the claw-like spike at the end of the tail is most probably an adaptation to an arboreal lifestyle. Renesto noted the similarity of the tail to that of a chameleon and suggested that, in *Megalancosaurus*, it served as a prehensile device for wrapping around shoots and branches. In such an environment the spike might provide more stability, perhaps even permitting a kind of tripod stance, thereby freeing the front legs for locomotion (gap bridging) or prey capture.

The taxonomic position of the Drepanosauridae is still uncertain, and awaits a detailed phylogenetic analysis of basal archosauromorphs and lepidosauromorphs.

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