THE SKULL AND LOWER JAW OF THE HOLOTYPE
OF *MEGALANCOSAURUS PREONENSIS* (DIAPSIDA, DREPANOSAURIDAE) FROM THE UPPER TRIASSIC OF NORTHERN ITALY

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Abstract. The skull of the holotype of the Late Triassic diapsid reptile *Megalancosaurus preonensis* is described for the first time. Its study revealed affinities with archosauromorph reptiles along with striking similarities with basal pterosaurs, apart for the absence of an antorbital fenestra.

Riassunto. Viene descritto per la prima volta in dettaglio il cranio dell'olotipo del Diapside *Megalancosaurus preonensis* del Triassico Superiore. Lo studio morfologico del cranio di *Megalancosaurus* rivela affinità con i rettili arcosauromorfi e, nonostante l'assenza della finestra antorbitale, sorprendenti somiglianze con gli pterosauri primitivi.

Introduction

Megalancosaurus Calzavara, Muscio & Wild, 1980 is a small drepanosaurid reptile from the Norian (Late Triassic) of the Friuli Venezia Giulia and Lombardy regions of Northern Italy. The skull of the incompletely preserved holotype has a bird-like appearance owing to the sharply pointed snout and the inflated parietal region. For this reason Feduccia & Wild (1993), Feduccia (1996), and Ruben (1998) considered it as an avian ancestor. However, detailed studies of further specimens (Renesto 1994a, 2000) revealed that the postcranial skeleton was highly specialized and completely non- avian. Padian & Chiappe (1998) suggested it was an aquatic prolacertiform, while Renesto (1994a, 2000), Renesto & Paganoni (1995) and Renesto & Fraser (2003) repeatedly pointed out the obvious adaptations to arboreal life. Despite the fact that at least six specimens are presently ascribed to this genus, the skull and lower jaw are still poorly known, because they are preserved only in the holotype (specimen MFSN 1769, Figs. 1-2 and 4). The parietal region and part of the lower jaw are also preserved in a second specimen (MPUM 8437, Renesto 2000, p.160, fig.1, and Fig. 4 in this paper).

The holotype of *Megalancosaurus* was briefly described by Calzavara et al. (1980) but they did not produce any reconstruction or interpretative drawing of the skull. Padian & Chiappe (1998) published two drawings of the cranial region obtained from photographs, which are simple sketches of the skull pattern that do not reflect the true cranial osteology of the specimen.

The main problem with the holotype of *Megalancosaurus* is that the block has splitted directly through the specimen leaving the skull broken sagittally, with two mirror halves on each slab. In addition the grain of the recrystalized dolostone does not allow a good definition of the bone contour. Furthermore, cracks in the rock run across the skull, damaging or obscuring some key regions.

Here we describe the skull of *Megalancosaurus* in detail, on the basis of the holotype and of the partial skull preserved in MPUM 8437, in order to clarify as much as possible the anatomy of the skull of *Megalancosaurus*. These details have great significance for further studies on the phylogenetic position of the drepanosaurid clade.

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Systematic palaeontology

Diapsida

Drepanosauridae Olsen and Sues, 1986

Megalancosaurus Calzavara, Muscio and Wild, 1980

Megalancosaurus preonensis Calzavara, Muscio and Wild, 1980
Figs. 1-2, 4

1980 *Megalancosaurus preonensis* Calzavara, Muscio & Wild, p. 59, figs. 2-5.

1994a *Megalancosaurus preonensis* Renesto, p. 39.

1993 *Megalancosaurus preonensis* Feduccia & Wild, p. 654.

1996 *Megalancosaurus preonensis* Feduccia, p. 7.

1998 *Megalancosaurus preonensis* Ruben, p. 73.

1998 *Megalancosaurus preonensis* Padian & Chiappe, p. 71.

2000 *Megalancosaurus preonensis* Renesto, p. 170.

Holotype: specimen MFSN 1769 Calzavara, Muscio and Wild 1980, figs. 2-5.

Examined material: the holotype, MFSN 1769, housed in the Museo Friulano di Storia Naturale (Udine), and specimen MPUM 8437 of the collection of the Dipartimento di Scienze della Terra dell'Università degli Studi di Milano.

Distribution: Dolomia di Forni, Middle Norian (Late Triassic), Friuli (Northern Italy) and Calcare di Zorzino, Middle Norian, Lombardy (Northern Italy).

Methods. The holotype was observed using a Leitz binocular microscope, both dry and wet under alcohol; preliminary drawings of skull sections were made looking at both halves of the specimen under the microscope and using a camera lucida, then re-drawn and combined.

Measurements. The following measurements were taken on the skull of the holotype of *Megalancosaurus preonensis* (MFSN 1769): maximum length of the skull 30 mm; length of the skull from the snout to the occipital condyle: 25 mm; height of the skull at orbit level: 12 mm; maximum (anteroposterior) length of the narial opening: 10 mm; maximum length of the lower jaw: 18 mm.

Description

The skull and lower jaw of MFSN 1769 are preserved on two slabs of gray dolostone (Fig. 1). In slab A (Fig. 1A, 2A, and 4A), a fracture crosses the skull in the posterior part of the narial opening and the middle of the lower jaw. The damage caused by this fracture is responsible for the doubts about the presence of an antorbital fenestra.

In slab B, the snout region is better preserved, but the parietal region is entirely missing.

The skull is exposed mostly in lateral view (but with the surface of the bone stripped away and preserved on the opposing slab), with little distortion apart flattening and reciprocal shifting of the left and right halves of the skull. The lower jaw sits at an angle of approximately 50° and it is still in partial articulation with the skull.

Skull. *Megalancosaurus* has a triangular skull with a tapering and pointed snout that superficially resem-
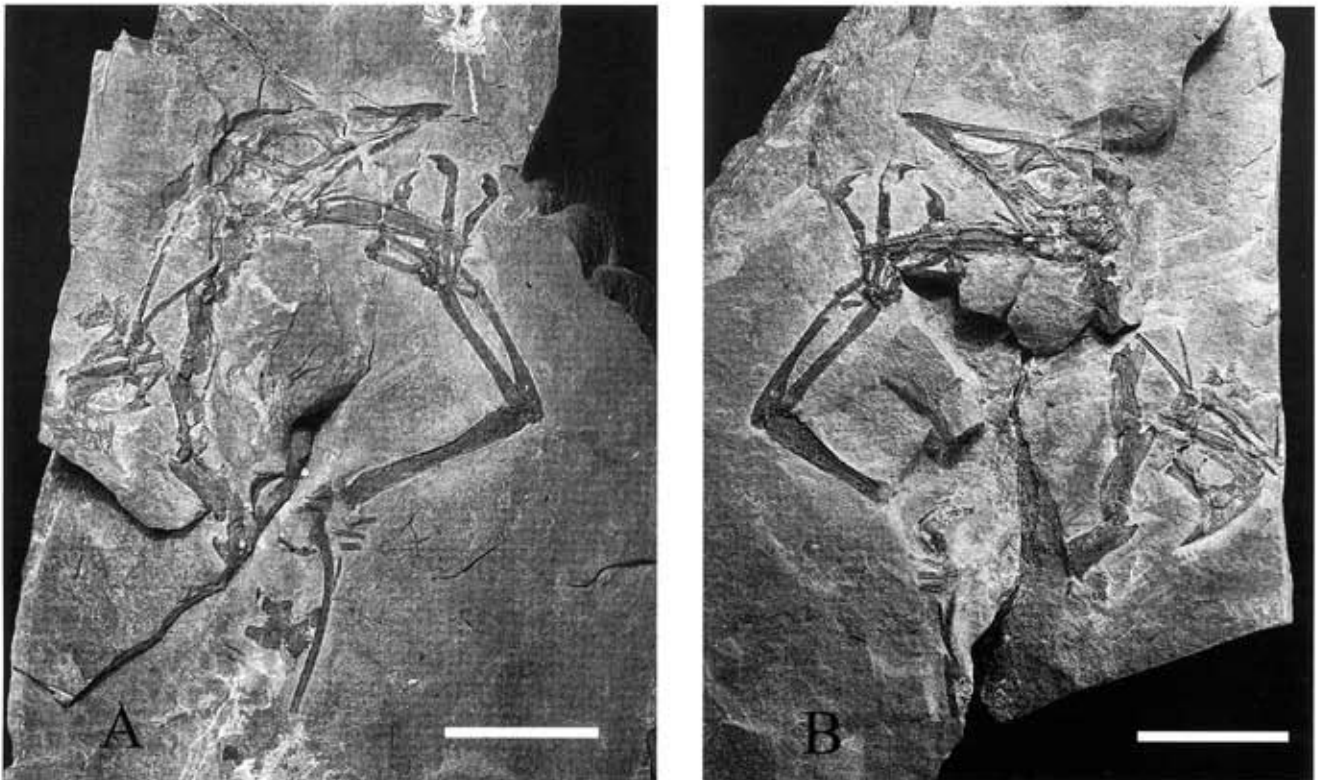

Fig. 1 - *Megalancosaurus preonensis* Calzavara, Muscio & Wild 1980, specimen MFSN 1769 (holotype), preserved in two slabs, A and B. Scale bar equals 2 cm.
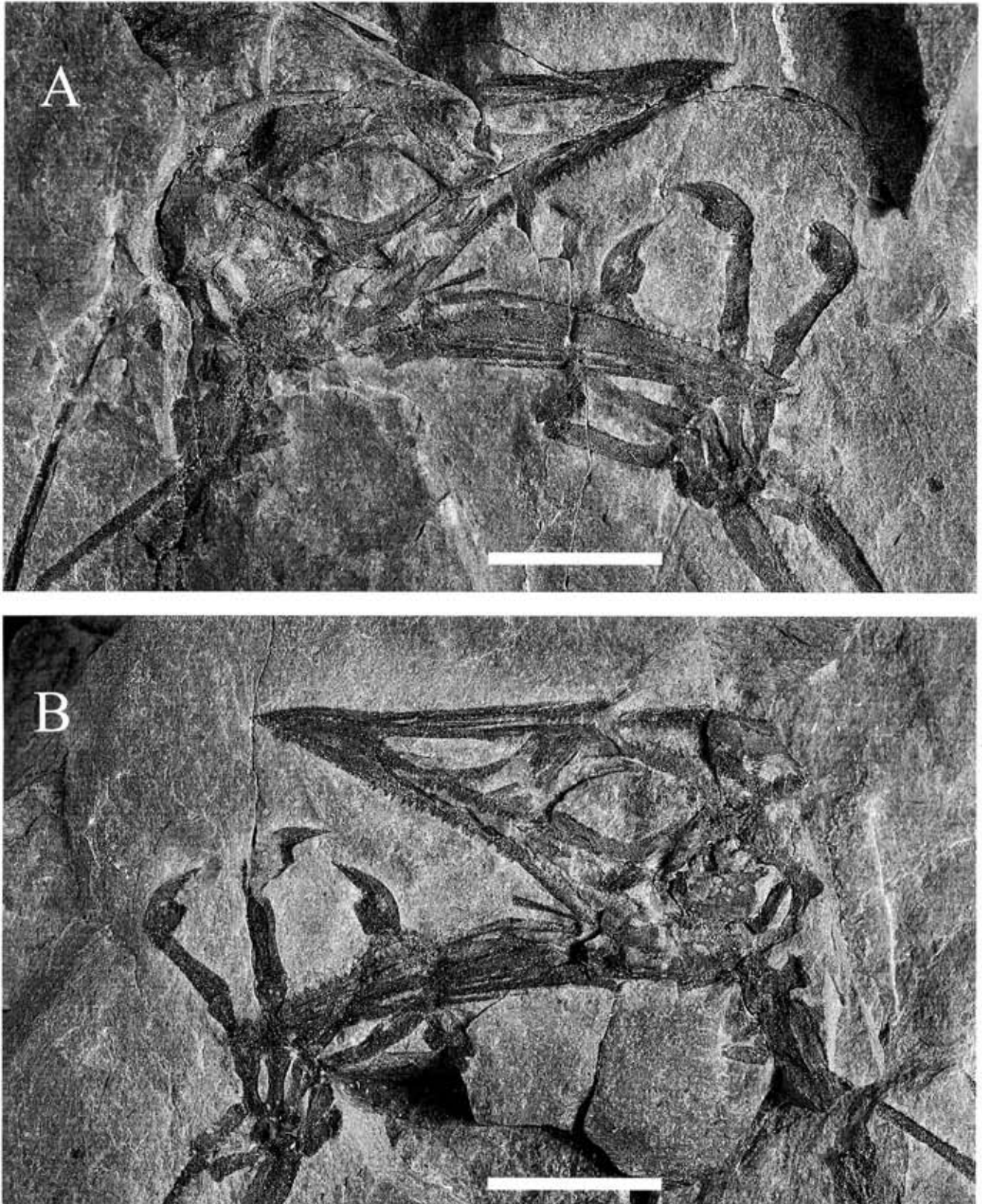
Fig. 2   - *Megalancosaurus preonensis* Calzavara, Muscio & Wild, 1980, specimen MFSN 1769 (holotype), close up of the skull as preserved in slabs A and B. Scale bar equals 1 cm.

bles those of living avian archosaurs (Figs. 1-3). The skull of MFSN 1769 is nearly completely compressed laterally; most bones are crushed, and some are slightly disarticulated and displaced. Cranial elements such as the frontals, jugals, maxillae, nasals and premaxillae have shifted slightly from their original position. Extreme compression of the skull probably caused the partial exposure of the palatal region. As stated above,
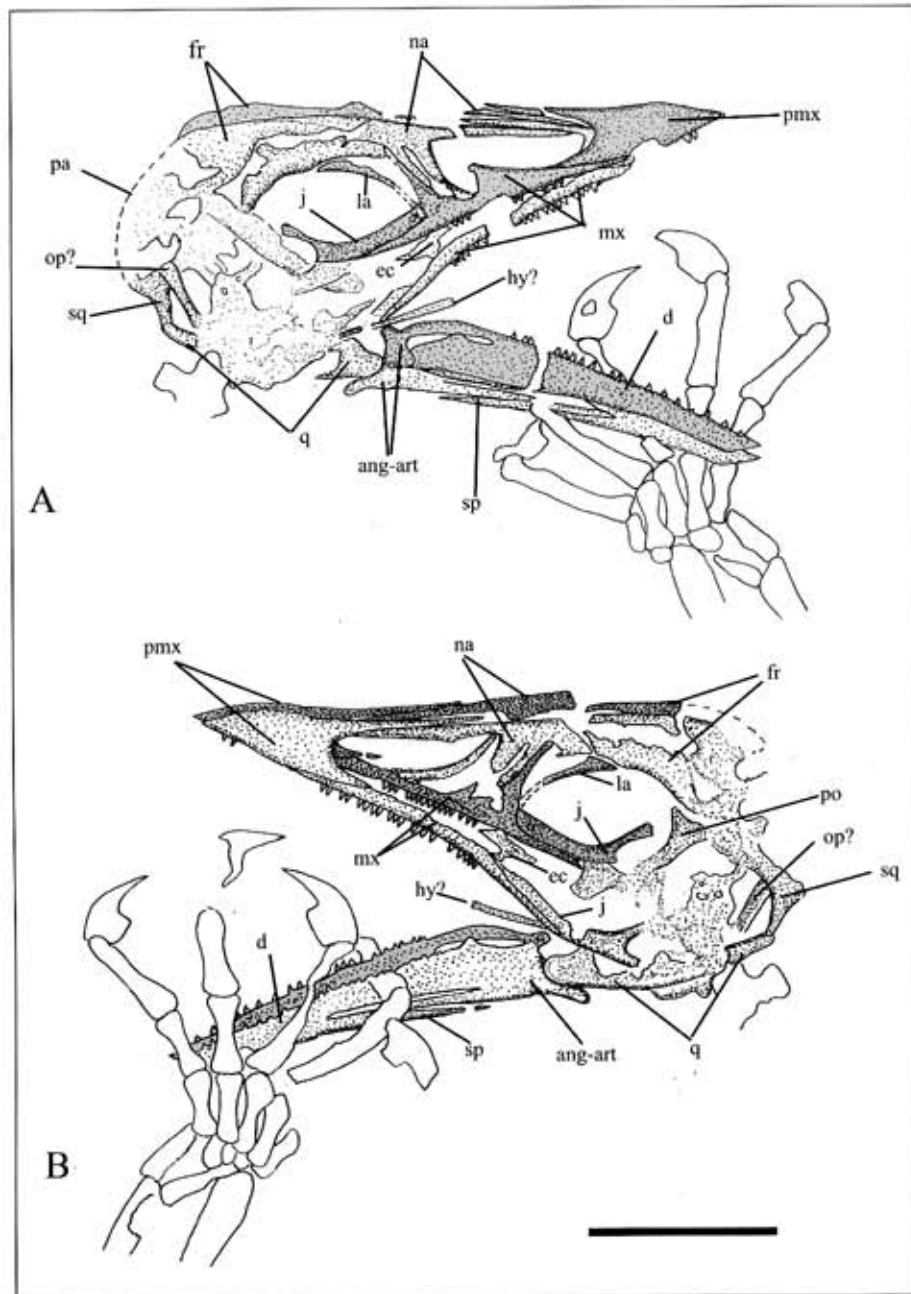
Fig. 3 - *Megalancosaurus preonensis* Calzavara, Muscio & Wild, 1980, drawings of the skull bones of the the holotype as preserved on slabs A and B. Scale bar equals 1 cm. Abbreviations are: ang-art) angular and articular; d) dentary; ec) ectopterygoid; fr) frontal; hy?) hyoid element; j) jugal; la) lacrimal; mx) maxilla; na) nasal; op?) opisthotic; pa) parietal; po) postorbital; pmx) premaxilla; q) quadrate; sp) splenial; sq) squamosal. The bones belonging to the left half of the skull, where recognized, have been coloured in light grey.

the skull is split into two parts roughly along its sagittal plane. In addition, elements of the left half of the skull lie partially on the right slab and vice-versa, this is specially true in the snout region. As a consequence, many bones have their medial surfaces exposed, are seen from the inside and many elements of the palate and braincase are mingled with dermal skull bones. This kind of preservation inevitably leads to a certain degree of subjective interpretation in the identification of some cranial elements. It was nevertheless still possible to reconstruct the overall pattern of the skull.

The left and right premaxillae are slightly separated from each other. They are long tapering bones, sharply pointed at their anterior tips. The inclination of the dorsal margin of the rostral portion of each premaxilla changes its inclination in the middle, so that the anterior tip of the rostrum has a more pronounced slope, that forms a beak-like process. The anterior part of each premaxilla bears two triangular, subthecodont teeth slightly larger and with a broader base than those borne by the maxillae. A posteroventral process of the premaxilla dorsally overlaps the anterodorsal edge of the maxilla; together the two bones form part of the anteroventral margin of the nasal opening. Dorsally, the premaxillae form very long and posteriorly tapering processes that greatly extend between the nasals, but they do not reach the frontals.

The maxillae are relatively large elements, subtriangular in lateral view, with very high but narrow dorsal processes and slender anterior (premaxillary) and posterior (jugal) processes. The ventral margin of each maxilla bears at least 22 small, subthecodont teeth.

They are at least twice as high as they are wide, sharply pointed and slightly compressed laterally, somewhat less robust than those borne by the premaxillae. The anteriormost part of the maxillary margin and the posterior part of the premaxilla are toothless, with apparently no alveoli, indicating that there was a wide diastema between the preserved premaxillary and maxillary teeth. Both the anterior and posterior dorsal margins of the maxilla are concave; the anterior margin is largely, but not completely, excluded from the posteroventral margin of the nasal opening by the nasals. A long and thin process of the maxilla extends posteriorly from the maxilla and contacts the ventral margin of the jugal. The anterior margin of the dorsal process of the maxilla contacts the long ventral portion of the nasal while the posterior margin may have been in contact with an elongate narrow, crescent-shaped lacrimal. The latter expands dorsally, somewhat reminiscent of the element present in the pterosaurs *Eudimorphodon* and *Anurognathus* (Wellnhofer 1978). However it should be noted that Wild (1978) intepreted the same bone in *Eudimorphodon* to be the prefrontal. In *Megalancosaurus* it does not appear to be a separate bone, and we therefore consider it to be the expanded dorsal end of the lacrimal. Anteriorly, the lacrimal has detached from the maxilla and the nasal, as a result of the ventral shift of the frontal. If this position represents the original articulated condition, a small antorbital fenestra is individuated, shaped like a narrow inverted (base up) triangle. However, the overall pattern of skull deformation strongly suggest that the separation of the lacrimal from the maxilla and the nasals is entirely due to disarticulation. Thus an antorbital fenestra is almost certainly absent.

The jugal is strap-like, with a gently curved ventral ramus that forms the ventral margin of the orbit, and a narrow upright dorsal (postorbital) process that forms part of the posterior margin of the orbit and should have contacted the postorbital. The posterior margin of the jugal is gently embayed and a small posterior process is present. It is impossible to ascertain, however, whether or not a quadratojugal was present.

The nasal is wide and bears a very long and narrow anterior process that forms nearly the entire dorsal margin of the nasal opening. This process, along with the concave maxillae, continue almost straight to give the nasal opening a semi-elliptical morphology. The anterior processes of each nasal are separated by the narrow posterior processes of the premaxillae. A wider, but shorter, portion of the nasal extends ventrally, forming the posterior, and a little bit of the posteroventral, margin of the narial openings. The nasals meet together posteriorly, thus excluding the premaxillae from an articulation with the frontals. These latter bones are heavily fractured in the holotype and they have shifted down into the orbits so that their dorsal surfaces are exposed. However, their outline can be observed. The frontals are narrow anteriorly, but widen posteriorly. Their ventral margin is concave and they form most of the dorsal margins of the large orbits. Posterior to the frontals the skull is even more poorly preserved, thus few details of the parietals and squamosals can be discerned. Indeed, the parietals seems to have left only a faint trace in the rock, but a partial three dimensional cast of the inside of the cranial cavity remains with the outline of the skull margin. This cast does not show much detail, but testifies that the parietal region was inflated and large relative to the overall size of the skull, at least by "reptilian" standards. Moreover, its shape matches that of the parietals preserved in MPUM 8437 (Fig. 4; and fig. 1, p. 160 in Renesto 2000). In the latter the parietals are wide and "bulging". Again, the parietals of specimen MPUM 8437 show an "S"- shaped suture with the frontals. The same outline is also visible in the holotype. In this latter specimen, a subtriangular fragment of bone is situated posteroventral to the parietal area and contacts the dorsal end of the quadrate. This position is highly suggestive of the quadrate process of the squamosal. The postorbital region is badly preserved and nothing can be said about it. The quadrate appears to be very long and rod-like, with a small flange anteriorly directed, and no posterior embayment for housing the tympanum. The articular condyle for the lower jaw is small and quite rounded in shape. The long axis of the quadrate is steeply inclined anteriorly, so that the mandibular articulation lies quite anterior to the level of the occiput. This latter region is poorly preserved and obscured by the superimposed atlas/axis complex.

Lower jaw. The lower jaw is long and narrow, deflected slightly ventrally. The two mandibular rami are shifted dorsoventrally with respect to each other, giving an unnaturally deep appearance to the lower jaw, while simultaneously suggesting that the two rami were not or were only weakly fused at their symphysis. It is difficult to detect the suture between the bones of the lower jaw apart from those zones in which they have been partially disarticulated. The dentary spans a little more than two-thirds of the whole length of the lower jaw and bears at least 22 triangular, sharply pointed teeth. However, there are few empty alveoli in the posterior portion of the jaw quadrant, so that teeth number was possibly higher. The first five to six teeth are stouter and more widely spaced than the subsequent teeth, and are distally recurved. The more posterior teeth are straight and closely spaced. All teeth are taller than their mesiodistal length. The posterior mandibular teeth are approximately equal in size to the maxillary teeth. Teeth of different sizes are irregularly distributed along the tooth row.
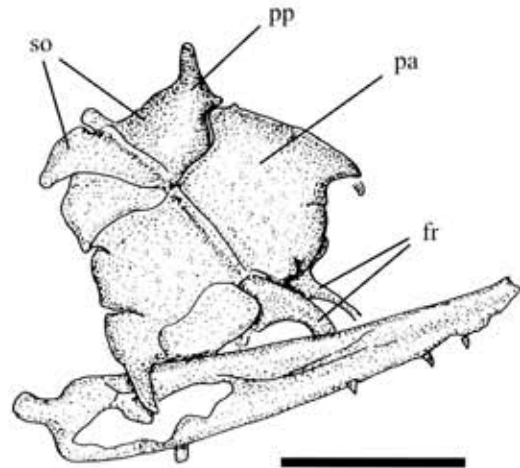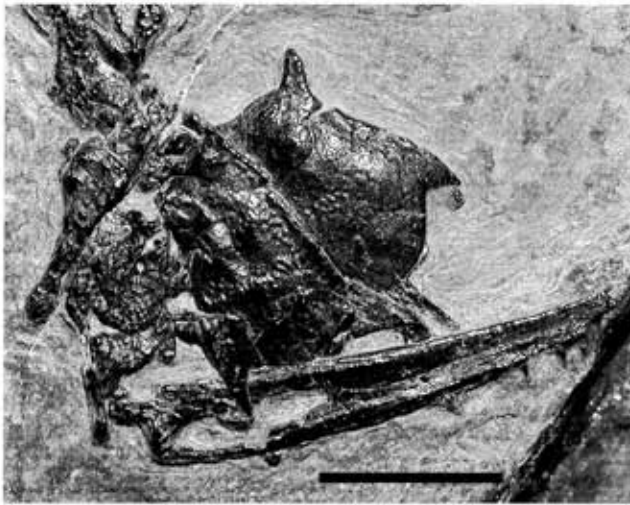
Fig. 4 - *Megalancosaurus preonensis* Calzavara, Muscio & Wild, 1980, photo of the skull region of specimen MPUM 8437 (left) and sketch of the parietal region (right, modified from Renesto 2000). The enlarged posterior portion of the frontal bones is nearly completely shifted below the parietals. Scale bars equal 0.5 cm. Abbreviations are: fr) frontal; pa) parietal; pp) paroccipital; so) supraoccipital.
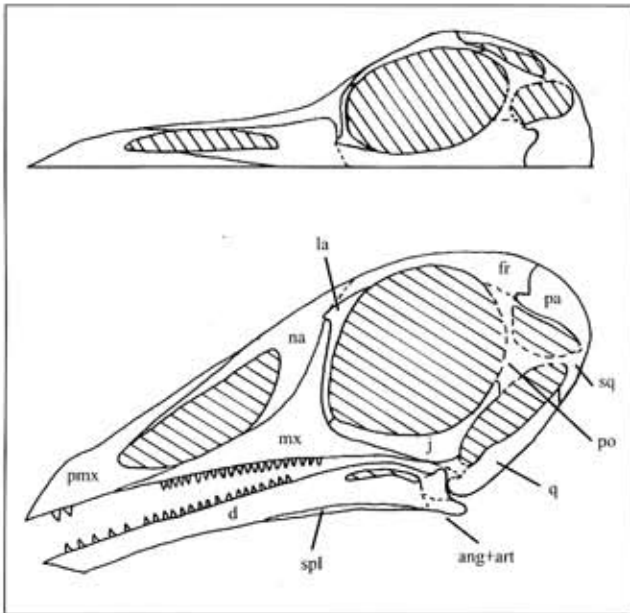

Fig. 5 - Reconstruction of the skull of *Megalancosaurus* in lateral dorsal (above) and lateral (below) views. Abbreviations are the same as in Figure 3.

At its posterior end, the dentary divides into two branches and forms the anterior margin of a slit-like mandibular fenestra that is bounded also by the angular and surangular. The angular and surangular bones cannot be described in detail because it is impossible to detect their sutural margins. A very long and narrow splenial is present ventral to the dentary. It shows a long and tapering posterior process. The articular is short, with a deeply concave articular area for the quadrate and a small retroarticular process that points slightly downwards. Posteriorly, the lower jaw exhibits a characteristic "square" shape similat to that of pterosaurs.

No distinct coronoid process is present, however, the dorsal margin of the lower jaw does show a distinct convexity with the apex in a position where there could have been a coronoid, this is similar to the condition in *Preondactylus* (Dalla Vecchia 1998).

Systematic discussion

Calzavara et al. (1980) considered *Megalancosaurus* to be an archosaur, they believed that an antorbital fenestra was present and they also misinterpreted some elements of the postcranial skeleton. Renesto (1994a) showed that some specimens previously considered as juveniles of *Drepanosaurus* (Pinna, 1980) belonged to *Megalancosaurus*, and that the two genera were closely related and both comprised in the family Drepanosauridae Olsen & Sues, 1986. The systematic position of the Drepanosauridae within diapsids remained uncertain due to the highly derived condition of the postcranial skeleton and also because of insufficient cranial material (completely missing in *Drepanosaurus*).

The family Drepanosauridae was erected by Olsen & Sues (1986) and first diagnosed by Berman & Reisz (1992). *Drepanosaurus* (Pinna, 1980) from the Calcare di Zorzino (Zorzino Limestone, Norian) of Lombardy and *Megalancosaurus* from the Calcare di Zorzino (Lombardy) and Dolomia di Forni (Friuli Venezia Giulia) were the first drepanosaurids to be described. Later *Dolabrosaurus* from the Petrified Forest Formation, Chinle Group, New Mexico (Berman & Reisz 1992), and, most recently, *Hypuronector* (informally known for many years as the "deep-tailed swimmer", Olsen 1980), from the Newark Supergroup (Colbert & Olsen 2001), were added to the family. While these taxa exhibit different sizes and moderately di-

verse body forms, all share some derived features that unequivocally demonstrate their close relationships (Renesto 1994a, b, 2000; Renesto & Fraser 2003); in particular, very slender rod-like, vertically oriented scapula, dorsal vertebrae with high neural spines (sometimes expanded craniocaudally at their distal ends), exceptionally tall neural and haemal spines on the caudal vertebrae, caudal prezygopophyses considerably overlapping the centrum of the previous vertebra, and zygapophyses lying very close to the midline on the caudal vertebrae are diagnostic. 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, 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).

Berman and Reisz (1992) considered drepanosaurids as lepidosauromorphs, while Renesto (1994a, b; 2000) suggested archosauromorph affinities. Analyses by Benton & Allen (1997) and Dilkes (1998) lent further support to the hypothesis that drepanosaurids were archosauromorphs, specifically closely related to Prolacertiformes, an hypothesis also proposed in the recent revision of Prolacertiformes (Protorosauria) by Rieppel et al. (2003). On the other hand, more recently Senter (2004) suggested a completely different view, considering drepanosaurids and the enigmatic diapsid *Longisquama* as closely related to each others and with Coelurosauravids, thus nested outside the archosauromorph-lepidosauromorph dichotomy.

While a more detailed discussion of Senter (2004) drepanosaurid phylogeny will be carried out in the forthcoming description of a new drepanosaurid genus (Renesto & Binelli in progress), the skull of *Megalancosaurus* as reconstructed here (Fig. 5) supports the attribution of the Drepanosauridae to the Archosauromorpha and definitely rules out the hypothesis about the presence of an antorbital fenestra. The skull of *Megalancosaurus* shows many characters considered by most authors (e. g. Benton 1985; Dilkes 1988; Evans 1988; Gauthier et al. 1988; Laurin 1991; De Braga & Rieppel 1997) as indicative of archosauromorph affinities, namely: 1) a premaxilla with a posterodorsal process which runs dorsally between the anterior portion of the nasals, and with a subnarial process forming most of the ventral margin of the anterior portion of the nasal openings; 2) external nares elongate and close to mid-

line; 3) quadrate which extends well below the braincase; 4) an ascending ramus of the maxilla; 5) a mid length constriction of the frontals; 6) a preorbital region longer than the postorbital region; 7) a squamosal reduced to less than one half the height of the lower temporal fenestra.

Of special interest are some features of the skull of *Megalancosaurus* which can also be observed in the skulls of certain basal pterosaurs (Fig. 6). These concern the general shape of the premaxillae and their overlap with the maxilla along the anteroventral margin of the nasal opening (e. g. *Eudimorphodon* and *Dimorphodon* in Wellnhofer 1978; *Austriadactylus* in Dalla Vecchia et al. 2002; also listed as a character of basal pterosaurs by Bennett 1996). The shape of the nasal (cf. *Eudimorphodon*, Wellnhofer 1978; *Austriadactylus*, Dalla Vecchia et al. 2002), the triradiate maxilla with slender processes (Wellnhofer 1978; Dalla Vecchia 1998), the anteroposteriorly elongated and broad narial opening (Wellnhofer 1978; Dalla Vecchia 1998), the strap-like jugal with posterodorsal and posterior processes (cf. *Campylognathoides*; Wellnhofer 1978), the slender "lacrimal" with an expanded dorsal termination, the long, rod-like and anteriorly inclined quadrate (Wellnhofer 1978), squamosal with a small process that hooks down behind the quadrate (Bennett 1996; Welllnhofer 1978) are other features shared by *Megalancosaurus* and pterosaurus. In addition, the parietal region of pterosaurs is rounded (Wellnhofer 1978), although only moderately expanded, as in *Megalancosaurus*.

Despite this large array of similarities with basal pterosaur skulls, *Megalancosaurus* lacks the antorbital fenestra, a character that is always present in basal pterosaurs (Wellnhofer 1978; Dalla Vecchia et al. 2002). Furthermore, the postcranial skeleton of *Megalancosaurus* possesses no shared derived characters with pterosaurs, but both groups clearly represent highly specialized forms very modified from the skeletal plan of their unspecialized ancestors.

Due to the high degree of specialization of the postcranial skeleton, it is impossible to know whether *Megalancosaurus* and its allies represent a group of odd, basal archosauromorphs, possibly related to prolacertiforms (Benton & Allen 1997; Dilkes 1998; Rieppel et al. 2003), rendering the pterosaurian features of the skull convergent due to adaptation to a similar complex environment, or whether the lack of an antorbital fenestra represents a secondary loss and the Drepanosauridae are phylogenetically closer to pterosaurs than previously thought.

The evolutionary implication of the habitat of the small reptiles found in the Norian marine intraplatform basins (the drepanosaurids *Megalancosaurus*, *Drepanosaurus*, "MCSN 4751" Renesto 2000, the prolacertiform *Langobardisaurus* and the pterosaurs *Eudimorphodon*,

Peteinosaurus, *Preondactylus*, and *Austriadactylus*), on islands representing emergent parts of a wide carbonate platform bordering the margins of the huge Triassic supercontinent Pangaea at the western end of Tethys (Marcoux et al. 1993), has not previously been considered. The existence and extension of these flat islands were controlled by sea level fluctuations, sediment deposition cycles, and local tectonics, that operated on a time scale of 1000 to 100,000 years (Bosellini 1967; Bosellini & Hardie 1988). It is plausible that these rapidly changing environmental conditions applied evolutionary pressures much stronger than in the more stable cratonic areas or continental settings in general. In fact, evolutionary change is most likely to occur through rapid variations within small, geographically isolated populations (e.g. Mayr 1982). Colonization by few individuals and the consequent "founder effect" was probably the rule. This also means that we should expect an array of "aberrant" insular reptiles from these carbonate platform islands, with the development of unusual structures and the repeated, homoplastic appearance of others. Recent studies on the cichlid fishes of African lakes (ecologic islands) (Stiassny & Meyer 1999) as well as numerous case histories (e.g. Galapagos finches), demonstrate how dramatically rapid and wide-

spread is the appearance of unusual, specialized structures and of convergent morphologies in insular settings. Probably *Megalancosaurus*, *Drepanosaurus* and "MCSN 4751" (Renesto 2000; Renesto & Binelli in progress), represented insular dwellers that originated from a rapid diversification from the basal drepanosaurid stock. This latter could have been represented by continental forms like *Hypuronector*. This assumption however would not necessarily imply that, in order to reach the islands, *Hypuronector* was aquatic. Most small reptiles can cling easily to floating vegetation and are also considered to be good rafters and consequently can spread from mainlands to islands. An example is represented by the arboreal gecko of the genus *Phelsuma* that colonized the Mascarene islands (Austin, Arnold & Jones 2004; Bauer 1990) where it gave origin to different species in a relatively short time span.

Mode of life

Interpretations of the mode of life of *Megalancosaurus* have been conflicting. Calzavara et al. (1980) considered it an arboreal climber because of the opposable digits in the hand. On the other hand, Padian
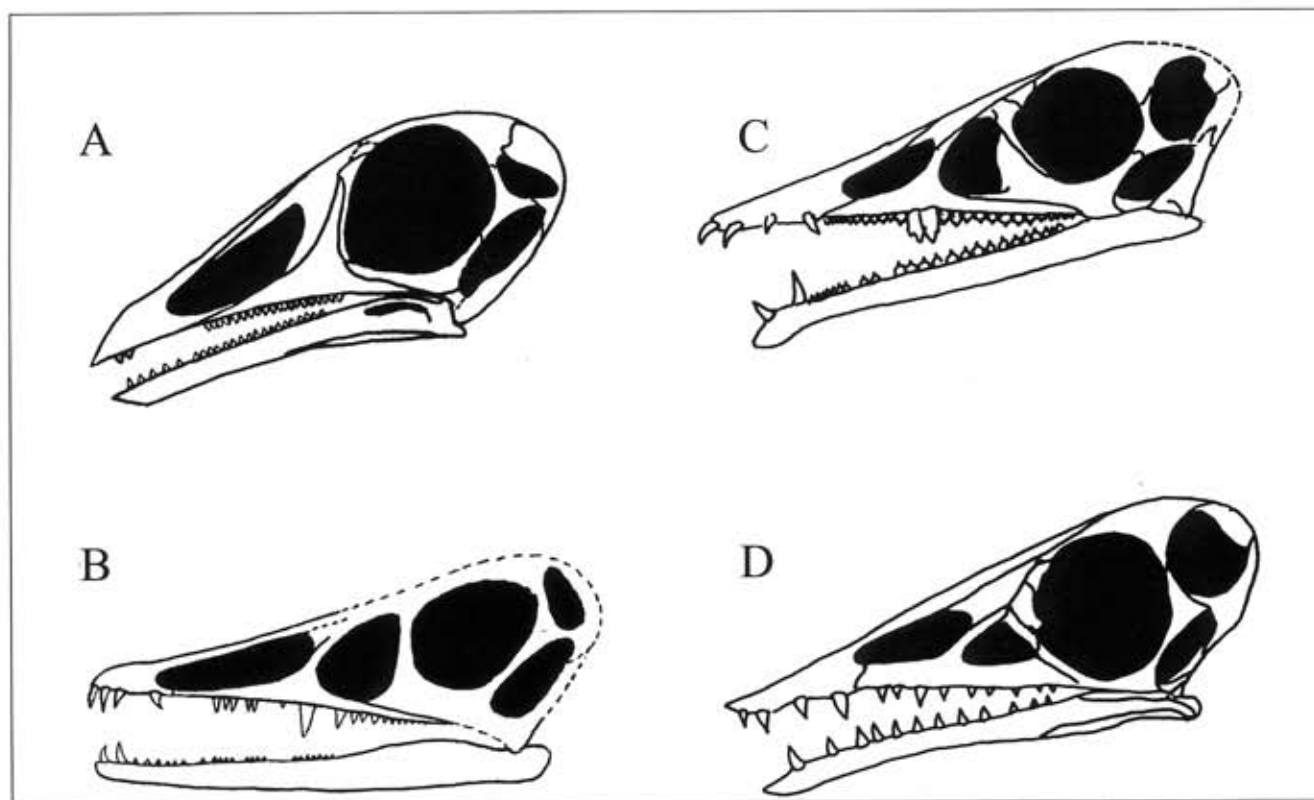

Fig. 6   - Comparison between the skull of *Megalancosaurus* (A) and those of the pterosaurs *Preondactylus* (B), *Eudimorphodon* (C) and *Campylognatoides* (D); (C) and (D) redrawn from Wellnhofer (1978). Drawings not to scale.

& Chiappe (1998) considered it to have been aquatic because they were found in marine sediments. However, most of the reptiles collected in the Norian deposits of Lombardy are non marine (Renesto 1995), and a third of the fossils found in the formation which yielded the holotype of *Megalancosaurus* are terrestrial plants (Dalla Vecchia 1991; 1994).

Ruben (1998) regarded *Megalancosaurus* as an arboreal glider on the basis of the elongate forelimb. Renesto (1994a, 2000), Renesto & Paganoni (1995), Renesto & Fraser (2003) and Fraser & Renesto (2005) discussed in detail the morphological features showing that no adaptations for swimming are present in *Megalancosaurus*, while the postcranial skeleton is highly specialized for a scansorial life, strongly suggesting arboreality. The present analysis of the skull gives further support to this interpretation: the expansion of the parietal region of *Megalancosaurus* gives an inflated appearance to the skull similar to that of birds and pterosaur. In birds the entire volume of the parietal region is occupied by a large brain, while in pterodactyloid pterosaurs the space was occupied also by trabecular bone which partially reduced the area for the brain (Kellner 1996). However, in pterosaurs, the brain was proportionally larger than in non avian archosaurs and other reptiles (Witmer et al. 2003). Endocasts of pterosaur skulls allow us to understand the structure of their brain and inner ear in some detail (Newton 1888; Edinger 1941; Kellner 1996; Witmer et al. 2003). They indicate high development of the optic lobes, flocculi and semicircular canals, features all related to vision, eye-muscle coordination, head rotation and stabilization, as in birds. Unfortunately, the endocast of *Megalancosaurus* does not provide comparable information. The extreme compression and the splitting of the skull of the holotype does not permit any definitive conclusion about the orientation of the orbits, but the three dimensionally preserved skull roof of MPUM 8437 shows that the frontals were very narrow in their anterior portion (Renesto 2000, fig 1 p. 160; Fig. 4 in the present paper) and widen significantly in the posterior part, suggesting that the skull was triangular with a pointed tip and quite narrow anterior to the orbit. Such orientation would permit a great overlap of visual fields perhaps resulting in a good binocular (three dimensional) vision. The lack of any skeletal correlate indicative of a flying or gliding adaptation (Renesto 2000; *contra* Ruben 1998) casts doubts about the hypothesis that the enlarged brain of *Megalancosaurus* served for aerial locomotion, but it pertained to an arboreal way of life. It is reasonable to suppose that the presence of large eyes, and an enlarged brain are indicative of precise eye to limb neuromuscular coordination. This would be particularly useful to

Megalancosaurus, if it moved quickly rather than in a slow chameleon-like fashion. Binocular vision and good eye-limb coordination would also be useful for hunting insects if *Megalancosaurus* may have caught its prey by darting the bird-like head with a sudden extension of the long neck, or, alternatively it could also have grasped them with the prehensile anterior limbs, in a praying mantis style (Renesto 2000).

Life environment

Geological data indicate that the oxygen depleted basins in which the remains of *Megalancosaurus* were deposited were surrounded by carbonate platforms dominated by wide tidal flats and devoid of any volcanic reliefs. Therefore the landscape was flat, with no cliffs or similar geomorphologic highs (see Dalla Vecchia 1991, 1994; and literature herein). Also, the abundant plant remains preserved in the same formation pertain only to bush-like, and possibly succulent (see Viohl 1985) conifers (*Brachyphyllum*, *Pagiophyllum*, etc), possibly cycadeoids, and a long-leafed, probably low and yucca-like plant. Evidence of tall trees (trunks, roots, branches, etc) are absent and the floristic assemblage is thus similar to that found in the Late Jurassic Solnhofen Limestone (cf. Viohl 1985). Nevertheless this kind of environment is not incompatible with the hypothesis of an arboreal life for *Megalancosaurus* since the gliding insectivorous diapsid *Weigeltisaurus* lived in a similar environment (Evans 1982). *Weigeltisaurus* specimens were collected in the Permian Marl Slate and Kupferschiefer Formations of Great Britain and Germany, where the plant record reflects the presence of a rich and diverse, but topographically low, coastal vegetation indicative of arid conditions (Bell et al. 1979; Schweitzer 1968). Nevertheless, *Weigeltisaurus* shows adaptations functionally very similar to those of the extant gliding agamid lizard *Draco* which is also a skilled climber, and its mode of life was almost certainly similar. In conclusion *Megalancosaurus* and other drepanosaurids may well have thrived among the intricate network of narrow twigs of low bushes, feeding upon insects.

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