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BIRD-LIKE HEAD ON A CHAMELEON BODY: NEW SPECIMENS OF THE ENIGMATIC DIAPSID REPTILE *MEGALANCOSAURUS* FROM THE LATE TRIASSIC OF NORTHERN ITALY

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Riassunto. Vengono descritti due nuovi esemplari appartenenti al genere *Megalancosaurus* (Reptila, Diapsida), uno dei quali raccolto a Zogno (Val Brembana, Bergamo) da un affioramento del Calcare di Zorzino (Norico, Triassico Superiore) e l'altro vicino a Preone (Udine) da un affioramento della Dolomia di Forni, di età coeva. I nuovi esemplari consentono di ampliare notevolmente la conoscenza dell' osteologia del genere *Megalancosaurus*, di precisare i suoi rapporti tassonomici con i generi affini *Dolabrosaurus* e *Drepanosaurus* e di ipotizzare la presenza di due specie distinte nel genere *Megalancosaurus*. Gli elementi scheletrici del cranio e del collo di uno dei nuovi esemplari mostrano una sorprendente somiglianza con gli uccelli, con gli pterosauri e con il possibile proto-uccello Triassico *Protoavis*, tali somiglianze vengono considerate come dovute a convergenza piuttosto che indicatrici di relazioni tassonomiche. Un'analisi dei caratteri scheletrici degli esemplari di *Megalancosaurus* finora conosciuti confermano l'alto grado di adattamento alla vita arboricola di questi rettili e ad un peculiare metodo di caccia. Recenti ipotesi sulla possibilità che *Megalancosaurus* fosse in grado di planare potrebbero anche avere qualche fondamento, ma in tal caso l'eventuale morfologia della superficie alare e la struttura dello scheletro ricorderebbero molto più da vicino i mammiferi planatori e non gli antenati degli uccelli.

Abstract. Two new *Megalancosaurus* specimens collected from the Norian (Late Triassic) Calcare di Zorzino (Zorzino Limestone) Formation (Bergamo, Lombardy, Northern Italy), and from the coeval Dolomia di Forni (Forni Dolostone) Formation (Udine, Friuli, North-eastern Italy) improve our knowledge of skeletal anatomy and mode of life of this genus. Morphology of observable skull elements and cervical vertebrae in one of the new specimens shows some resemblance to the possible Triassic bird *Protoavis*, while the postcranial skeleton of *Megalancosaurus* is completely non-avian. This may suggest that either *Megalancosaurus* and *Protoavis* developed a similar neck structure as a response to the same functional requirement, or that part of the disarticulated material ascribed to *Protoavis* may indeed belong to a *Megalancosaurus*-like reptile.

Megalancosaurus shows a very high adaptation to arboreal life and a peculiar feeding strategy. Recent suggestions that *Megalancosaurus* may have been a glider and a possible model for bird ancestry are discussed. Some skeletal features of *Megalancosaurus* may indeed be interpreted as gliding adaptation, but evidence is weak, and if this reptile was a glider, however, its gliding bauplan should have been completely different from the one usually accepted for bird ancestors, showing instead more morphological similarities with gliding squirrels, phalangeriids and putative ancestors of bats and pterosaurs (according to a non cursorial model for these latter).

Introduction.

Megalancosaurus is a small diapsid reptile from the Late Triassic of Northern Italy (Calzavara, Muscio & Wild, 1980; Renesto 1994a) which is closely related with the enigmatic diapsids *Drepanosaurus* (Pinna, 1980, 1984; Renesto 1994b; Renesto & Paganoni, 1995; Dilkes, 1998) and *Dolabrosaurus* (Berman Reisz 1992, Renesto & Paganoni, 1995; Dilkes, 1998). Until now the only skull preserved was that of the holotype and details of cranial sutures were largely obscured by dolomitization (Calzavara et al. 1980; Renesto, 1994a). In addition, most of the skeleton posterior to the neck was missing. A complete neck was known in one other specimen, (Renesto, 1994a), but it was also poorly preserved.

A new *Megalancosaurus* collected from the Late Triassic (Norian) Calcare di Zorzino (Zorzino Limestone) Formation from Northern Italy, which has already yielded three other *Megalancosaurus* specimens, shows for the first time a partial skull and a well preserved neck articulated with the rest of the skeleton. Analysis of the new specimen reveals that the morphology of the post-orbital portion of the skull of *Megalancosaurus* is very bird-like in appearance, and that the cervical vertebrae are very similar to the anterior cervical ones of the small specimen of *Protoavis*.

An additional *Megalancosaurus* specimen, recently collected from the Dolomia di Forni (Forni Dolostone) Formation, of the same age, reveals that a hooked spine at the end of the tail was present also in this genus, as in *Drepanosaurus* (Pinna, 1984; Renesto, 1994b) *Megalan-*

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cosaurus was recognized as a scansorial reptile with arboreal habits (Calzavara et al., 1980), while for *Drepanosaurus* and *Dolabrosaurus* different and contrasting life habits were suggested; a fossorial, ground inhabitant (Pinna, 1980, 1984) for the former; and an aquatic habit for the latter (Berman & Reisz, 1992). Recently, Ruben (1998) stated that *Megalancosaurus* was not only arboreal, but also a skilled glider and invoked the presence of a prepatagium. Furthermore, similarities to a possible proto-bird morphology have been suggested by the same author. The functional morphology of the skeleton of *Megalancosaurus* is revised here in the light of both the new available material and a re-examination of previously known specimens.

Institutional abbreviations of the cited specimens: MFSN: Museo Friulano di Storia Naturale (Udine, Friuli, Northern Italy); MBSN: Museo Brembano di Scienze Naturali (S. Pellegrino, Bergamo, Lombardy, Northern Italy); MCSNB: Museo Civico Scienze Naturali "Caffi" Bergamo; MPUM: Museo di Paleontologia Università di Milano (Milano, Lombardy, Northern Italy).

Description of the new specimens

The new specimens are described before the section on systematic palaeontology in order to provide the reader with the new informations about the anatomy of *Megalancosaurus* that are included in the revision of the genus.

Specimen CCSR 63115 (Pl. 1; Fig. 5) housed in the 'Collezione del Centro Studi e Ricerche' Villa Anita, Sigillo Umbro (Perugia, Central Italy), collected in the small quarry close to the village of Endenna (Bergamo, Lombardy, Northern Italy), from an outcrop of the topmost section of the Calcare di Zorzino (Zorzino Limestone) Formation, Middle-Late Norian (Late Triassic).

Specimen MFSN 18443a (Fig. 9) housed in the Museo di Scienze Naturali di Udine, collected from an outcrop of the lower member of Dolomia di Forni, Norian (Late Triassic), in the Seazza Creek Valley, near the village of Preone (Udine).

Description of specimen CCSR 63115.

The specimen is articulated and nearly complete, preserved mainly on one slab (Pl. 1A) while some dorsal sacral and caudal vertebrae and ribs lie on the counterslab (Pl. 1B). The snout, the tip of the tail and the right anterior limb are lacking.

Measurements (in mm). Measurements taken on specimen CCSR 63115 are listed here and compared with other known *Megalancosaurus* specimens quoted with their catalogue number. Specimen MPUM 6008 was reported as field number P11 24 in Renesto (1994a).

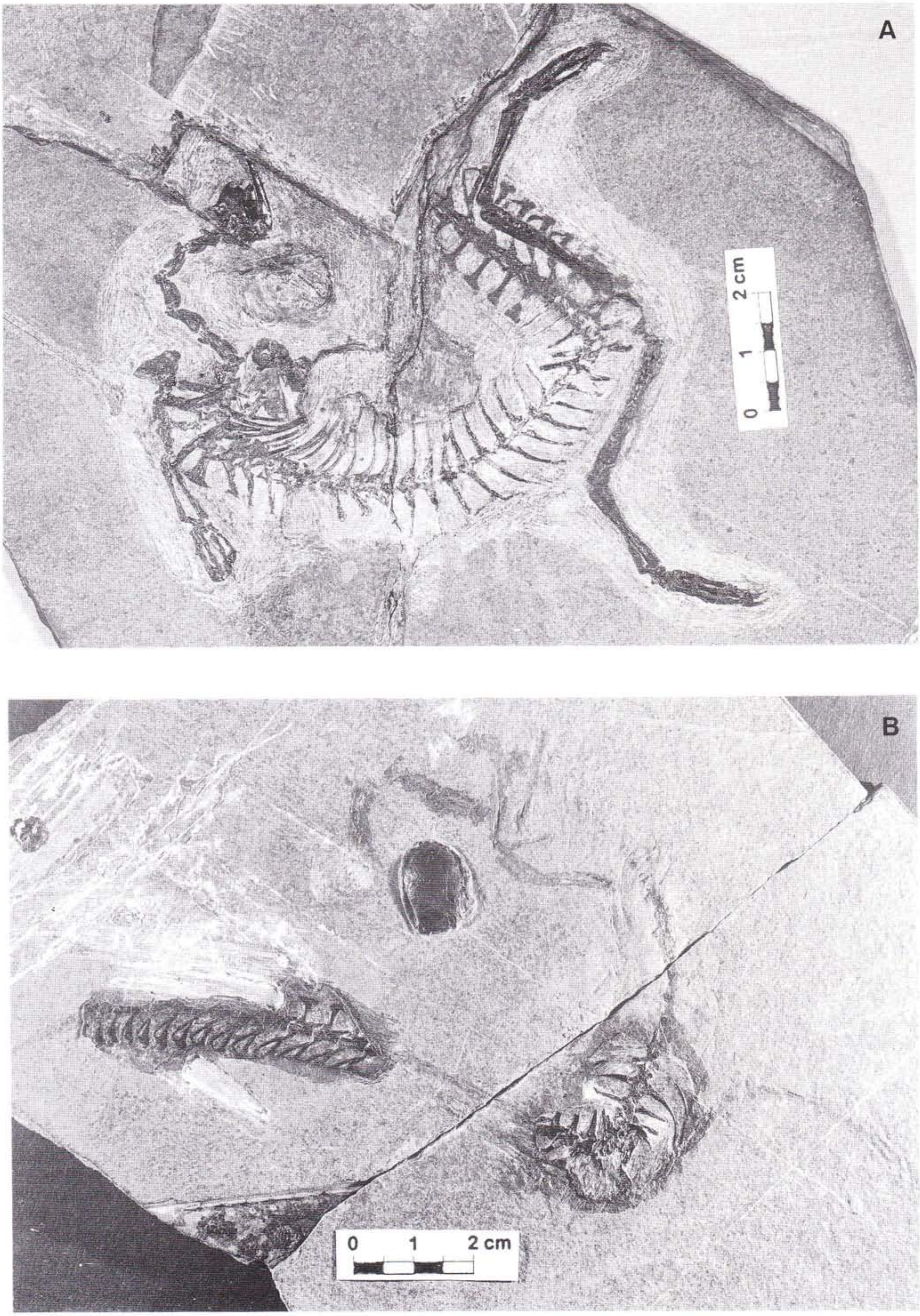
Specimens	CCSR 63115	MFSN 1769	MPUM 6008	MBSN 25	MBSN 26
Lenght of 5th cervical vertebra	7	9	9.5		4.5
Length of 6th cervical vertebra	7.5		10		6
Length of third metacarpal	4	3.5	3		
Length of 1st phalanx of third digit	5	6	6		
Length of the humerus	(21)	22	22.5		18.5
Length of the left radius	11	15	14		
Length of the left ulna	12	15	14		
Length of third metacarpal	4	3.5	3		
Length of the left femur	27			23.5	20
Lenght of the left tibia	17.5			14.5	11.5
Length of the left fibula	16			13	
Length of third metatarsal	4			4	
Length of 1st phalanx of third toe	3			3.5	

The Skull. In specimen CCSR 63115 the right ramus of the lower jaw and some paired elements of the post-orbital region of the skull are preserved as partially articulated elements (Fig. 1).

The frontals are very narrow in their anterior part, forming the dorsal margin of large orbits. These bones become wide at the posterodorsal edge of the orbit, but their most posterior portion cannot be observed, being obscured by the wide parietals, which shifted somewhat anteriorly. The anterior tip of the frontal is obscured by the overlapping lower jaw. Parietals are very large and "bulging", giving an inflated outline to the postorbital region of the skull. The occipital region is well exposed: a small paroccipital process can be observed, similar to

PLATE 1

Megalancosaurus preonensis specimen CCSR 63115. A) the specimen on the main slab; B) the counterslab; the black rounded object is a coprolite.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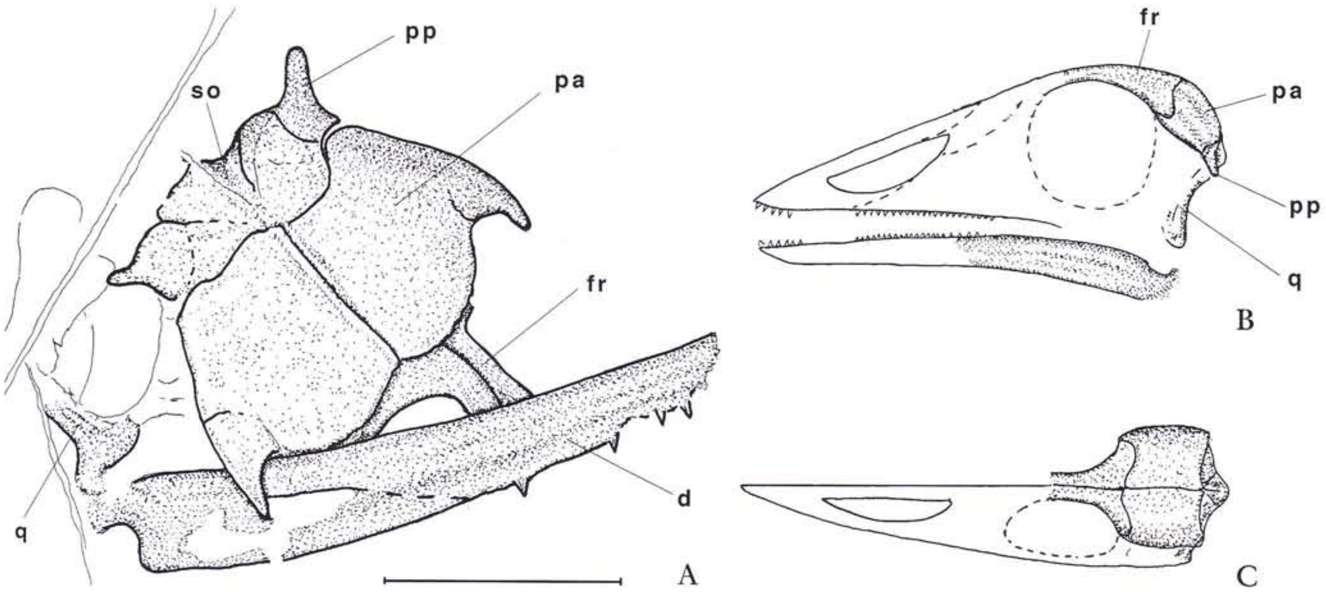


Fig. 1 - *Megalancosaurus preonensis*, specimen CCSR 63115. A) skull remains as preserved; B-C) tentative reconstruction of the skull from lateral and dorsal view, respectively. The bones preserved in speciment CCSR 63115 are drawn stippled, other data are from the holotype. Abbreviations are d) dentary, fr) frontal, pa) parietal, pp) paroccipital, q) quadrate, so) supraoccipital. Scale bar equals 0.5 cm.

that of the Eichstätt specimen of *Archaeopteryx* (Elzanovski & Wellnhofer, 1996). Medial to the posterior portion of the squamosal, a subtriangular (?) epiotic bone is again similar to the that of the Eichstätt specimen of *Archaeopteryx* (Elzanowski & Wellnhofer, 1996); this latter bone medially contacts a stout, triangular supraoccipital. The distal portion of the quadrate is partially visible, and exhibits a rod like structure with an expanded orbital process, although it cannot be reconstructed with confidence. Neither the squamosal nor its articulation with the quadrate are visible.

The preserved portion of the left lower jaw is apparently exposed in lateral view; it is slightly bent ventrally as in the holotype (Calzavara et al., 1980). The mandible lacks teeth posteriorly as it occurs in the holotype, while some very small conical teeth are present in the anterior half. The teeth are set in shallow sockets, and have a subthecodont implantation. The posterior end of the lower jaw, behind the articular area for the quadrate is missing, and only the outline of the articular notch for the quadrate can be observed. A "gap" is detectable at the level of the suture between angular and surangular; it is not considered a mandibular fenestra because the bone margins are broken, and a mandibular fenestra is absent in the *Megalancosaurus* holotype, it is suggested here that it may represent a weak area corresponding to the position of the mandibular fossa.

Vertebral column. The vertebral column of specimen CCSR 63115 consists of eight cervical, 23 dorsal; 3 sacral and up to 39 caudal vertebrae, which is consistent with other *Megalancosaurus* specimens (Renesto, 1994a). The neck (Fig. 2) is exposed on its lateral (right) side, and only the atlas and axis complex is obscured by a crack in the slab and by some overlapping by the third cervical vertebra. The vertebral column is broken between the fifth and sixth cervical vertebrae, but the posterior cervical vertebrae, articulated with the dorsal series, clearly indicates a former dorsally oriented bending of the neck, possibly due to post-mortem contraction of ligaments, as it is frequently found in many reptiles with elongate neck like the prolacertiforms *Tanystropheus* (Wild, 1973) and *Macrocnemus* (Peyer, 1937), and many dinosaurs.

The centra are rather elongate and narrow; their anterior face is concave, while the posterior one is distinctly convex, that is they are procoelous. The prezygapophyses are short and facing forward and upward, forming a convex surface which allowed great vertical mobility to the neck. In ventral view, the protruding zygapophyses show a peculiar buffer-like outline, resembling some primitive pterosaurs in this feature. The neural canal was very large, as indicated by the size of the collapsed walls. The neural spines are low and their axis is inclined anteriorly; the length of the neural spines is about half the length of the centrum. Finally, the ventral margins of the centra are keeled posteriorly, forming a structure nearly identical to the "hypapophyses" quoted by Chatterjee (1991, 1995, 1998) for *Protoavis*.

The anterior dorsal vertebrae (Fig. 3A) show the very characteristic pattern observed in other *Megalancosaurus* specimen (Renesto, 1994a; Fig. 3B). The neural arches are high, and the neural spines of the second, third, fourth and fifth dorsal vertebrae are very high and enlarged anteroposteriorly, while those of the second and third dorsal vertebrae are fused together surround-

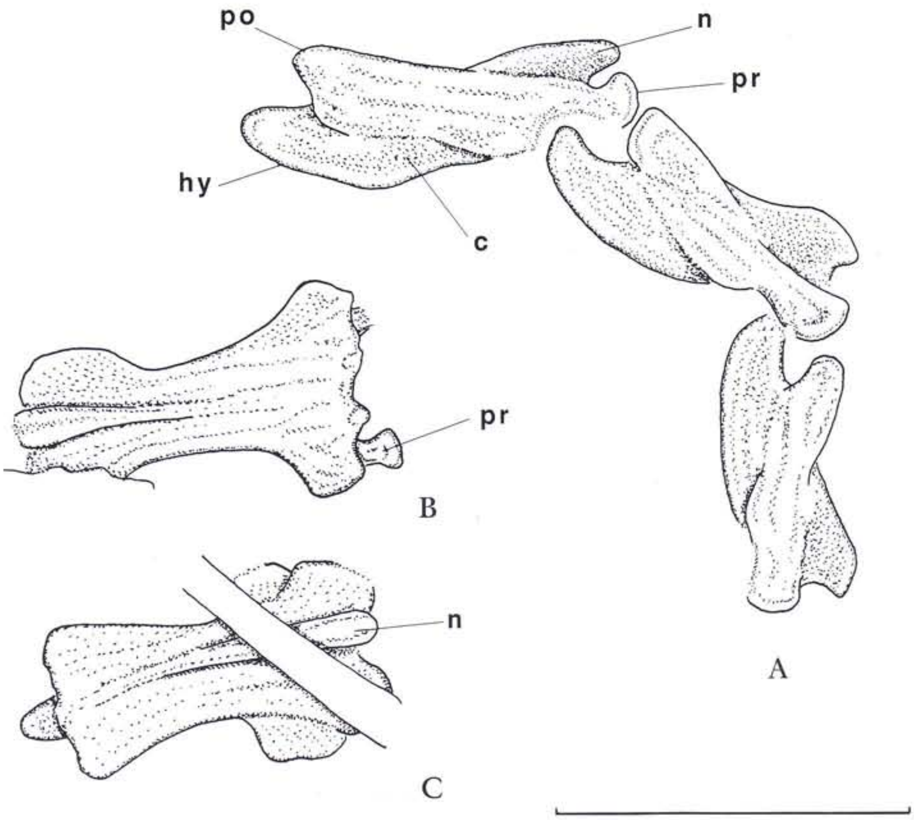


Fig. 2 - *Megalancosaurus preonensis.* A) cervical vertebre 4-6 as preserved in CCSR 63115. B) seventh cervical vertebra of MPUM 6008, ventral view; C) sixth cervical vertebra of MPUM 6008, dorsal view. Abbreviations are: c) centrum, hy) "hypapophysis", n) neural spine, po) postzygapophysis, pr) prezygapophysis. Scale bar equals 1 cm.

ing a wide, oval fenestra. Posterior to the fourth dorsal vertebra, the distal width of the neural spines decreases rapidly, but they remain very high. The prezygapophyses of the anterior dorsal vertebrae are elongate and thin, and they lie very close to the axis of the vertebral column, fitting into hollows on each side of the neural arches of the preceding vertebra. This rendered considerable rigidity to the entire anterior dorsal region. The posterior dorsal vertebrae are exposed from posterior view but they are very poorly preserved (Fig. 4A). The neural canal is still high and the single posteriorly directed process recognized in other *Megalancosaurus* specimens is detectable in the better preserved elements; it lies at the base of the neural spine between the two hollows that house the prezygapophyses of the succeeding vertebra (Fig. 4B). The morphology of the centra progressively change down the length of the dorsal vertebral column. The anterior centra are low and elongate, becoming gradually more and more short posteriorly.

There are at least three sacral vertebrae but they are poorly preserved, their morphology is similar to the one of the posterior dorsal vertebrae, but in the most posterior sacral vertebra a very small, but distinct perforation can be seen the middle of the convex posterior articular surface of the centrum, and it is suggestive of a notochordal condition. This character is not present in the anterior dorsal vertebrae of this nor any other *Megalancosaurus* specimens, and it was not reported for sacral vertebrae of other specimens (Renesto, 1994a). However, the posterior articular surfaces of sacral centra are less accessible to observation in other specimens. The caudal vertebrae can be divided into three categories according to their morphology. The centra of the first 3-4 caudal vertebrae are rather short, approximately of the same size of posterior dorsal and sacral ones. They bear high and narrow neural spines curved caudally in their distal portion and blunt, short and upward directed prezygapophyses with vertically oriented articular facets (Fig. 4A). The haemal spines are fused with the posterior end of the ventral margin of each centrum. The fourth and fifth caudal vertebrae are similar to the preceding ones with haemal spines that are deep and ventrally enlarged, but their structure cannot be reconstructed completely. Posterior to these proximal caudals, the caudal vertebrae assume the form that is peculiar for this genus (Renesto, 1994a; Pl. 1, 3): the centra become elongate, the prezygapophyses are horizontally directed and laterally envelop the preceding vertebra. The neural spines become expanded dorsally assuming a "T" shape; the haemal spines become very deep and longer than the corresponding neural spines. They are also ventrally enlarged with a posteriorly convex and anteriorly concave outline and an oval fenestration can be observed in the haemal spines of the 4th-20th caudal vertebra. Posterior to the 20th caudal vertebra the "stem" of the T-shaped neural spine decreases markedly in height, and the haemal spines lose the fenestration. Starting from the 30th caudal vertebra a slant in the insertion of the haemal spines occur, and they now lie at the anterior end of the ventral margin of each centrum (Fig. 5). Also their cur-

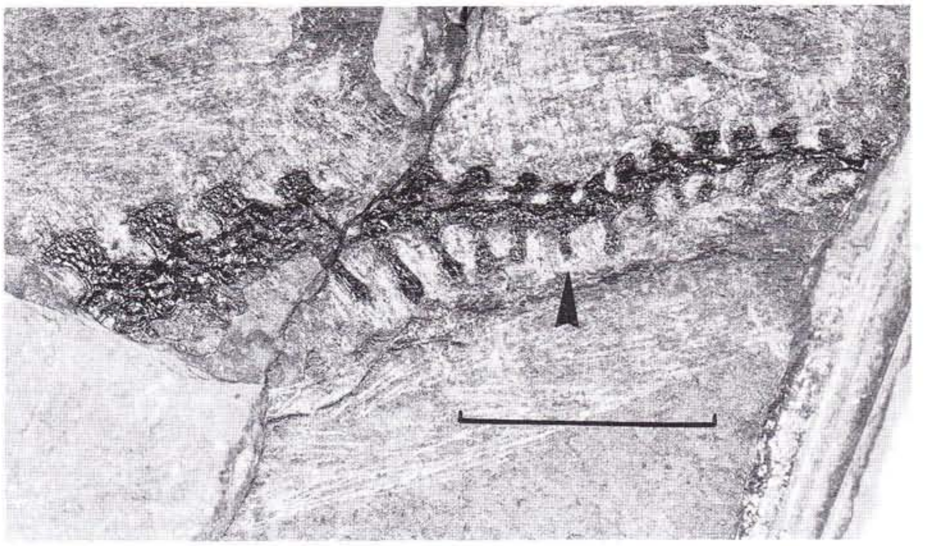


Fig. 5 - *Megalancosaurus preonensis* specimen CCSR 63115. Posterior portion of the tail, lateral (left) view. The black arrow indicates where the inversion of the attachment of haemal spines occurs. Scale bar equals 1 cm.

fused among anterior dorsal ribs. The coracoids are flat and thin, and bear thin irregular grooves on their outer surface; their poor preservation does not permit further discussion. As in MPUM 6008 the ventral portion of the pectoral girdle seems to be extended posteriorly (Renesto, 1994a) and it is possible that the posterior most portion may represent paired sternal plates. The scapula (Fig. 3) lacks some portions of the scapular blade, but the morphology described for other *Megalancosaurus* specimens, however, is clearly detectable: the scapular blade is very high (up to 19 mm) and narrow (1 mm wide), gently curved medially, with a small expanded ventral region. The glenoid seem to be situated almost entirely on the coracoid and it faces outward but also slightly posteriorly.

Pelvic girdle. The ilium (Fig. 4B) shows a very high (8 mm) and narrow (2.5 mm wide) iliac blade, which is

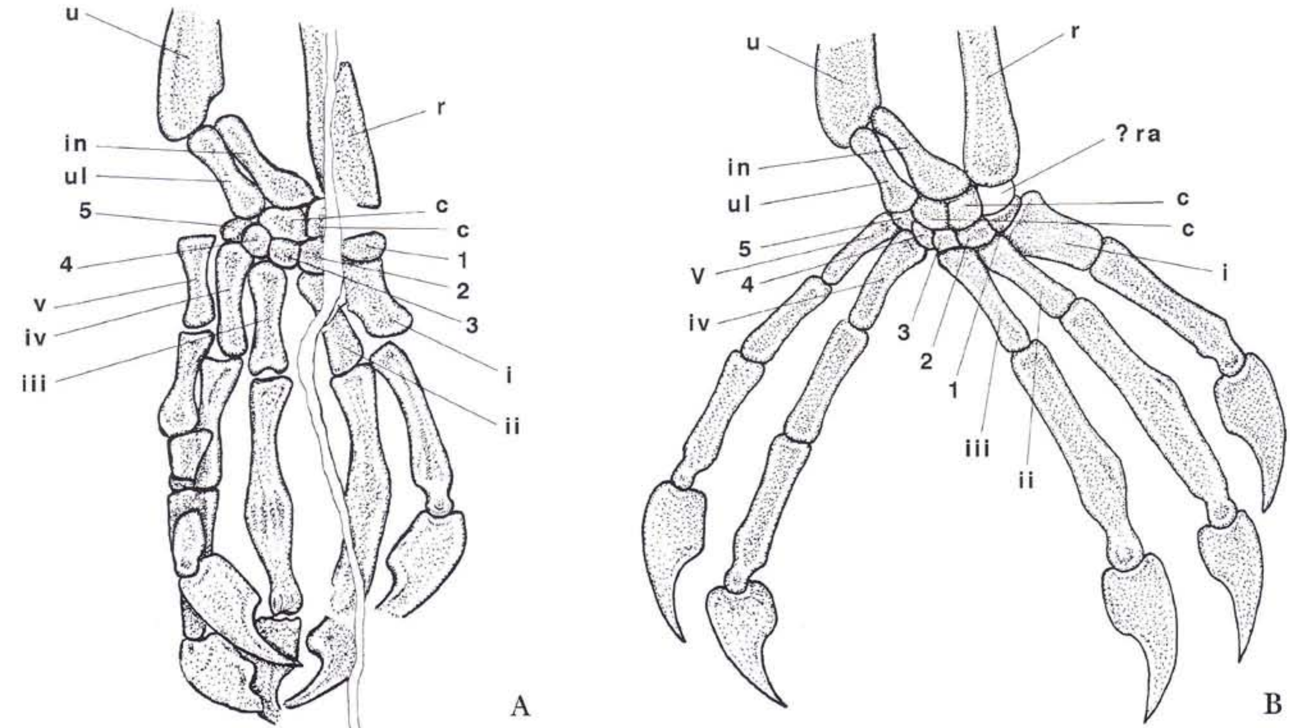
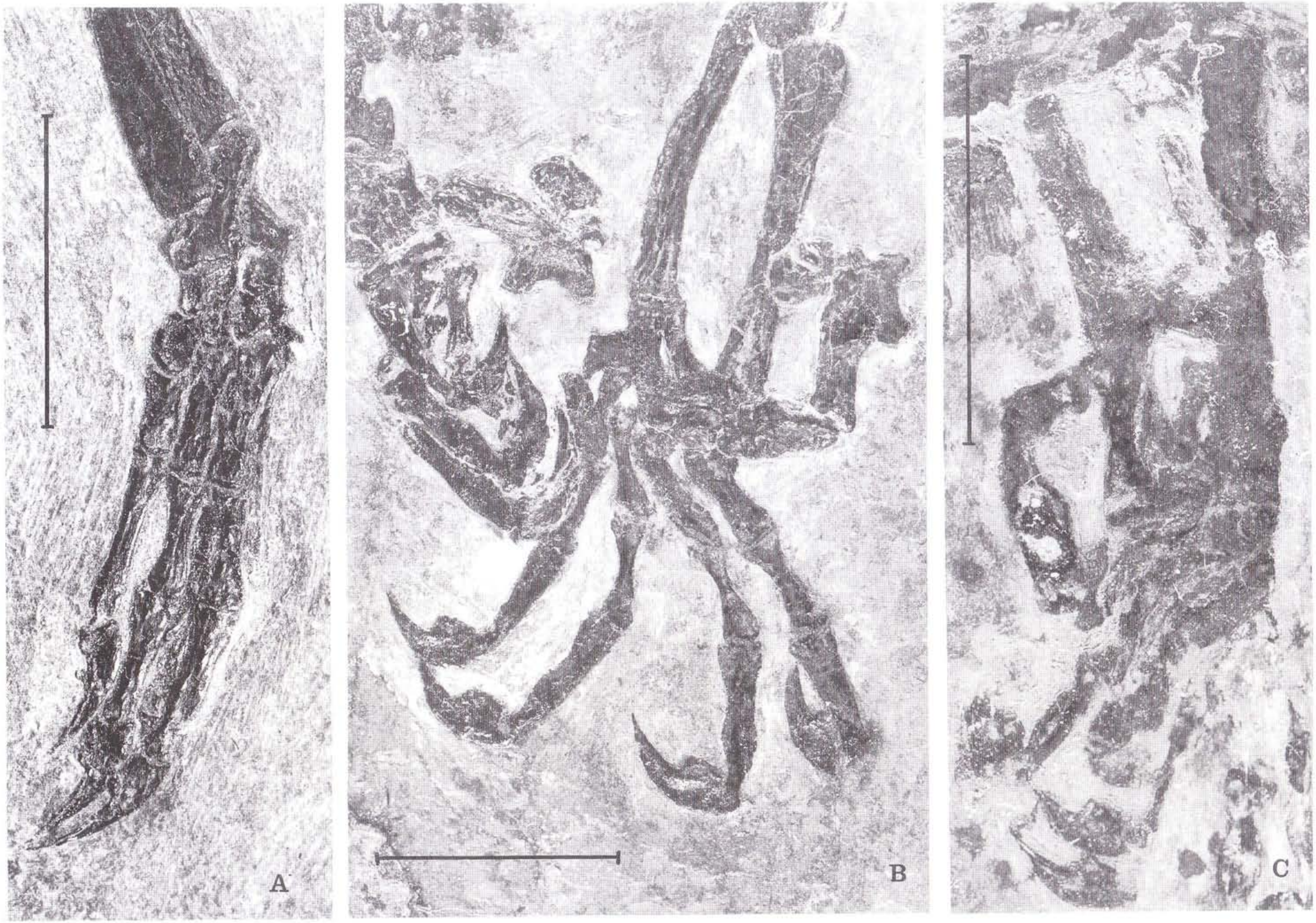


Fig. 6 - *Megalancosaurus preonensis* specimen CCSR 63115. A) left carpus and manus as preserved; B) reconstruction of the pattern of carpus and manus in *Megalancosaurus*. Abbreviations are c) centrale, in) intermedium, ra) radiale, r) radius, u) ulna, ul) ulnalre, 1-5)distal carpals, i-v metacarpals. Scale bar equals 0.5 cm.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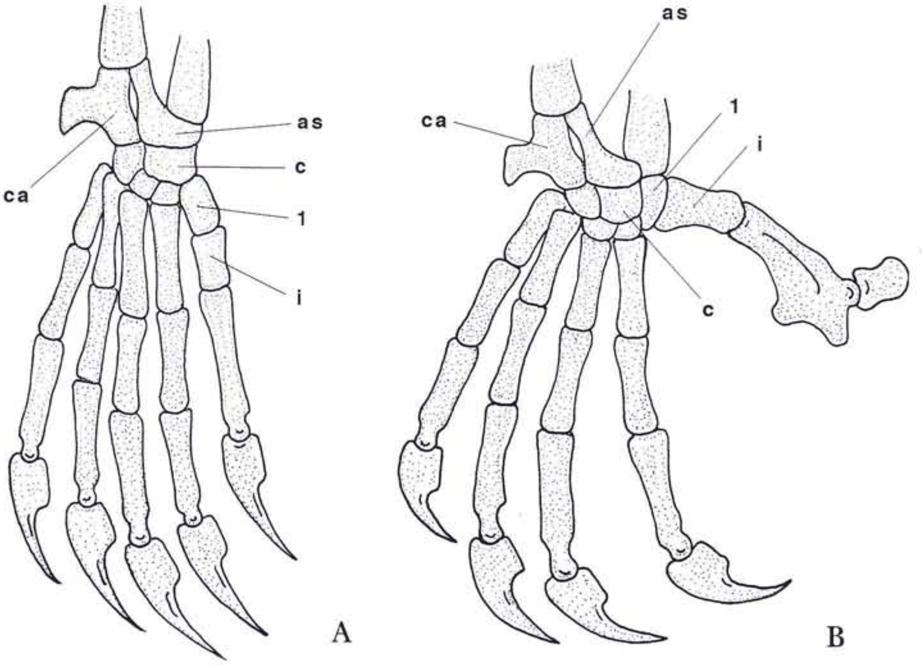

Fig. 8 - Comparison between the patterns of tarsi and feet of specimen CCSR 63115 (A) and MBSN 25 (B). Abbreviations as for Fig. 7. Not to scale.

of the pes. The first phalanx is distally enlarged with a distinct ventral process and the second phalanx is a small rounded bone with blunt distal end, rather than being claw shaped. The implications of the difference in the structure of the pes will be discussed later.

Supraneural bones. In the description of specimen MPUM 6008 of *Megalancosaurus* the presence of a couple of problematic bones were reported (Renesto, 1994a: 42 and fig. 5A). They were considered as scattered bones of uncertain identity. However, similar elements are present also in CCSR 63115 in approximately the same position (Fig. 3A). They are fan-shaped, and with a small ventral process. In specimen CCSR 63115, these bones lie in contact with the anterior end of the expanded portion of the fused neural spines of the third and fourth dorsal vertebra, where apparently a notch is present to house the small process. A reexamination of other *Megalancosaurus* specimens, shows that these bones are indeed present in the same position also in the poorly preserved specimen MBSN 26 (Pl. 3-4). Thus they are present in all specimens in which the anterior dorsal region is preserved. These bones always lie close to, or in contact with, the anterior end of the expanded neural spines (Pl. 3), suggesting that this may be their natural position. These structures might either be neomorph or a dermal ossification, but apparently these bones did not cover the surface of the body. Their presence and functional significance remains problematical.

Description of specimen MFSN 18443a.

This specimen consists of the distal portion of a tail (Fig. 9). As for other specimens collected in the Dolomia di Forni, dolomitization has obscured many of the details, so that, for the most part only the outline of the bone can be observed. The morphology of the most anterior caudal vertebrae show the same pattern as described for other *Megalancosaurus* specimens, showing elongate centra, "T" shaped neural spines and deep, distally wide haemapophyses with oval fenestration.

By comparison with other *Megalancosaurus* specimens the preserved caudal vertebrae can be identified tentatively as 13-38. In addition the terminal vertebra is modified into a hooked and very sharp spine (Fig. 9-10) as in *Drepanosaurus* (Pinna, 1980, 1984; Renesto, 1994b). This character was previously unknown in *Megalancosaurus*, but the morphology of the preceding caudal vertebra is peculiar of that genus, thus seems reasonable to consider MFSN 18443a as belonging to *Megalancosaurus* rather than to an other drepanosaurid genus.

Systematic palaeontology.

The newly discovered specimens add significantly to our knowledge of the genus *Megalancosaurus* but also raise some interesting questions. There are sufficient diagnostic characters present in CCSR 63115 and MFSN 18443 to confidently refer both specimens to the

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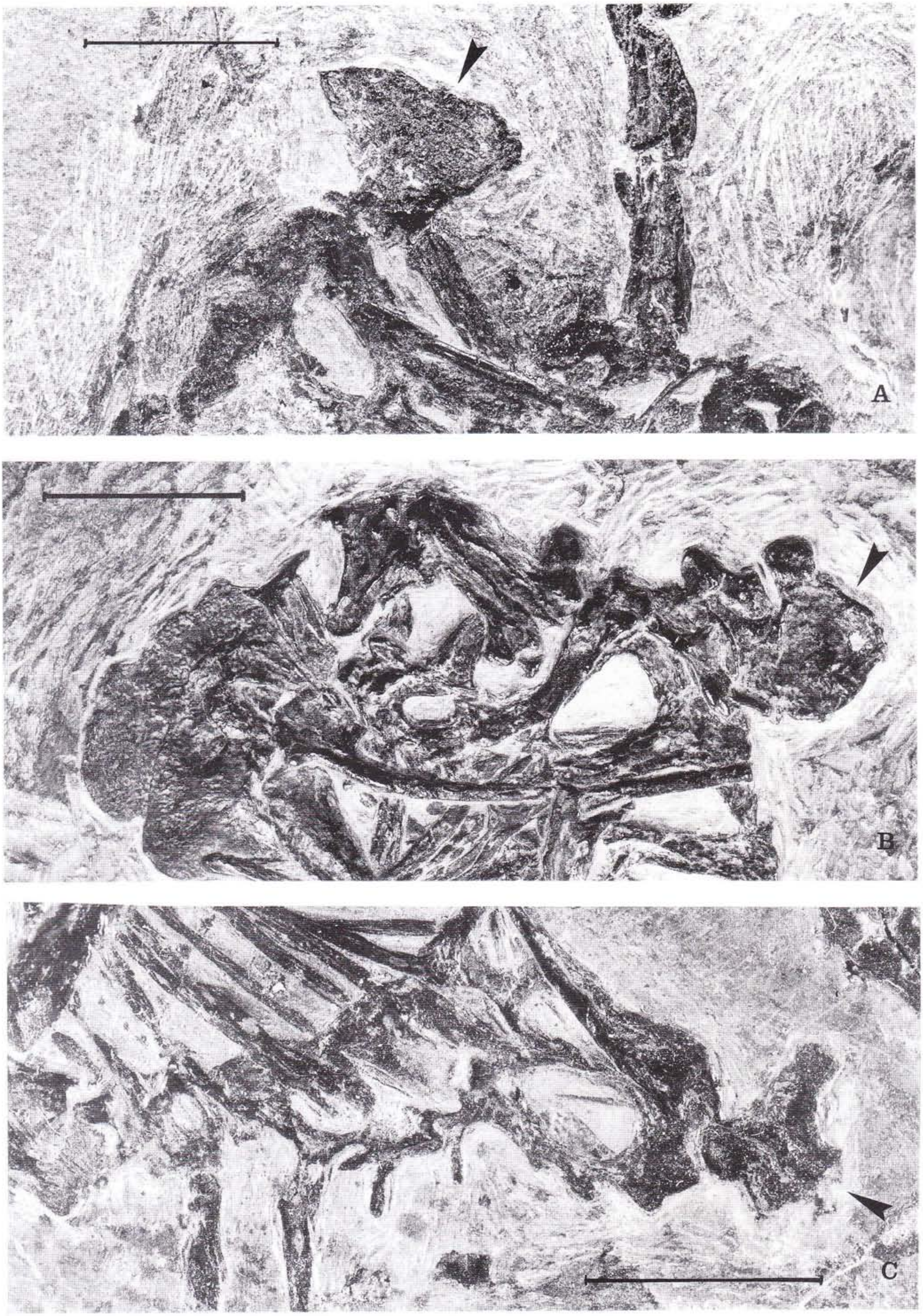
PLATE 3

Supraneural bones (indicated by black arrows) as preserved in different *Megalancosaurus* specimens, A) specimen CCSR3115; B) specimen MPUM 6008; C) specimen MBSN 26. Scale bars equal 1 cm.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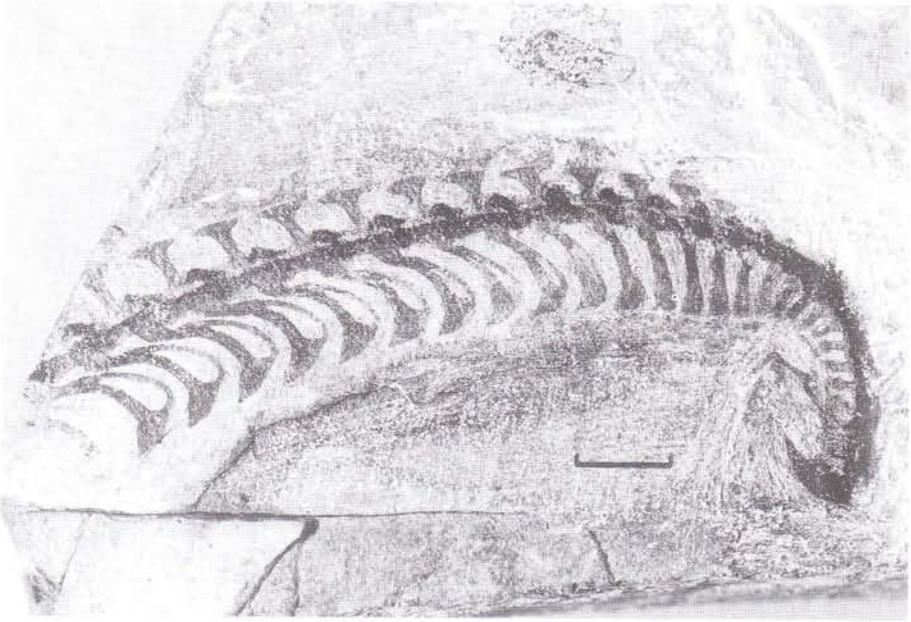

Fig. 9 - *Megalancosaurus preonensis*. Specimen MFSN 18443a: scale bar equals 1 cm.

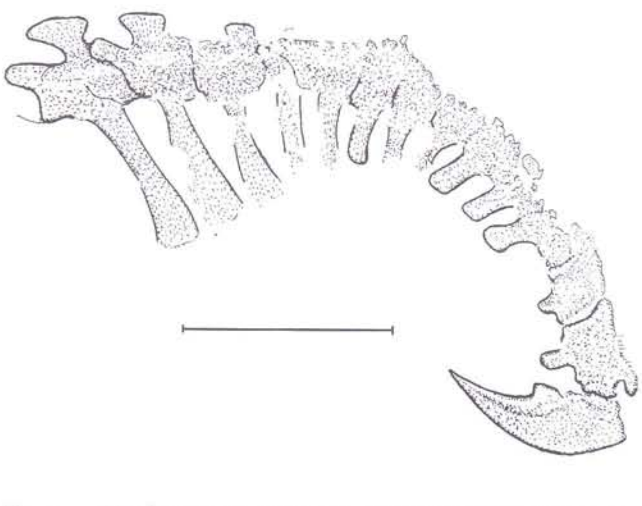

Fig. 10 - *Megalancosaurus preonensis*. specimen MFSN 18443a: the end of the tail. Scale bar equals 1 cm.

genus *Megalancosaurus*. However the presence of an hooked terminal spine on the tail of MFSN 18443a and the pattern of the pes of CCSR 63115 rise some important taxonomic issues. *Megalancosaurus* was placed within a distinct family, the Megalancosauridae (Renesto, 1994a) while *Drepanosaurus* and *Dolabrosaurus* were grouped in the Drepanosauridae (Berman and Reisz, 1992). Further studies on *Drepanosaurus* and a reinterpretation of some features of *Dolabrosaurus* (Renesto 1994b; Renesto & Paganoni, 1995) indicate that *Megalancosaurus* is probably more closely related to the other two genera than was previously thought. The new specimens lend further support to this hypothesis and the distinction between Megalancosauridae and Drepanosauridae is no longer tenable. The family Drepanosauridae was erected by Olsen and Sues in 1986 and diagnosed by Berman & Reisz in 1992, thus it has priority over Megalancosauridae Renesto 1994; as a consequence the latter name must be dropped and the diagnosis for the family Drepanosauridae should be revised. This revision is not undertaken here, however, because a small reptile from the Triassic of the Newark Supergroup (USA) informally known as the "Deep Tailed Swimmer" (Olsen, 1980) has been recognized to be a drepanosaurid (Colbert and Olsen submitted paper) and another undescribed small reptile from the Late Triassic Calcare di Zorzino (Northern Italy), labelled as MCSNB 4751 is undoubtedly a new drepanosaurid (Fig. 11). Even if a detailed study of MCSNB 4751 has not yet carried out, it can be observed that this reptile shows at least characters 1-7, 9-11, 13-14, 16-18 of those listed as possible drepanosaurid synapomorphies in the following section. MCSNB 4751 shares with some *Megalancosaurus* specimens a modified and opposable first toe, but, as it can be pointed out from Tab. 1, it cannot be assigned nor to *Megalancosaurus* neither to any known drepanosaurid genus. The oncoming descriptions of both MCSNB 4751 and of the "Deep Tailed Swimmer" will undoubtedly increase our knowledge of the group in the near future, leading to a more complete and reliable revision. For this reason while the diagnosis for the genus *Megalancosaurus* is emended here, only a list is given for the

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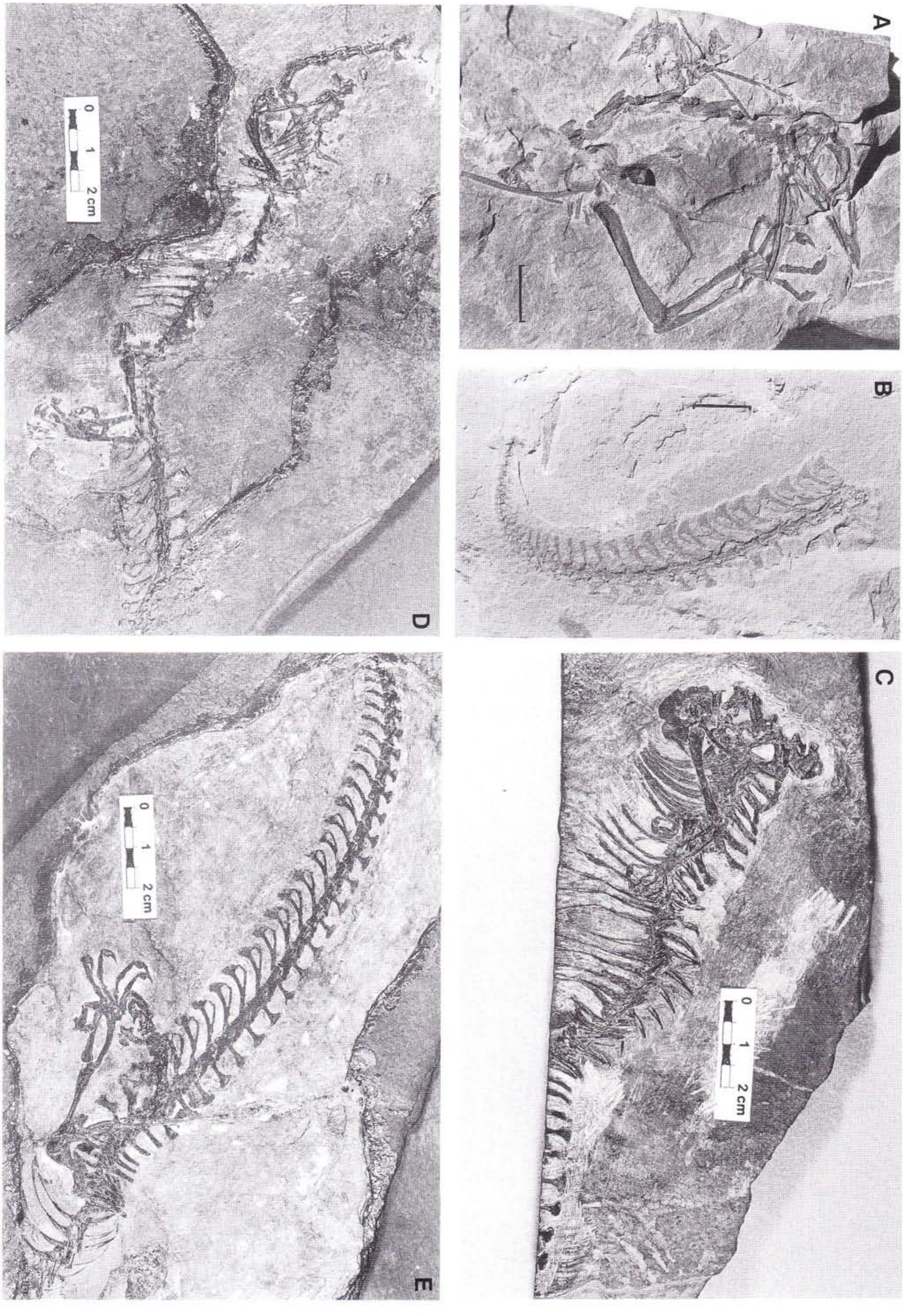
PLATE 4

Megalancosaurus specimens so far described: A) holotype (MFSN 1769); B) MFSN 1801; C) MPUM 6008; D) MBSN 26; E) MBSN 25. Scale bar equals 1 cm where not indicated otherwise.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characters linking *Megalancosaurus* with the Drepanosauridae, and the relationships of this group with other diapsid reptiles will not be discussed here. In this paper the Drepanosauridae are considered as archosauromorph reptiles of uncertain affinity, following Dilkes (1998).

List of characters shared by the Drepanosauridae.

Small to medium sized (10-50 cm) diapsid reptiles with share the following characters:

1) barrel shaped trunk and long, deep, laterally compressed "leaf"-like tail; 2) dorsal vertebrae with high neural spines (height of the neural spines approximately four times that of the centrum); 3) anterior dorsal vertebrae anteroposteriorly expanded at their distal end; 4) zygapophyses lying very close to midline; 5) caudal vertebrae in the middle section of the tail with high neural spines and deep haemal spines, at least 40% longer than the neural spines, 6) caudal vertebrae with prezygapophyses overlapping nearly half of the preceding centra; 7) haemal spines attached at the posterior end of the ventral margin of the first 30 caudal centra, 8) the insertion of the haemal spine in the more posterior caudal vertebrae is placed at the anterior end of the ventral margin of the centra (a feature probably linked with prehension and, at least in some genera, with the presence of a terminal spine); 9) ribs mostly holocephalous, slender and triangular in section; 10) gastralia absent; 11): shoulder girdle with a very high, narrow, rod-like scapula, gently bent anteriorly; 12) coracoid flat, somewhat expanded; 13) pelvic girdle with a high iliac blade, a rather narrow pubis and an ischium that is elongate posteriorly; 14) femur shaft not sygmoidal, 15) tarsus comprising a "L" shaped astragalus and a calcaneum with discrete lateral process (these two bones are fused together in *Drepanosaurus*); 16) fifth metatarsal straight; 17) penultimate phalanges in both manus and pes at least 50% longer than preceding ones; 18) ungual phalanges with the shape of narrow, very long, and sharp claws, provided with a well developed flexor process; 19) presence of rod-like elongate ulnare and intermedium; this character is shared at least by *Megalancosaurus* and *Drepanosaurus* and it is possibly present also in the Deep Tailed Swimmer (Olsen & Colbert subm. paper), thus it seems reasonable to add it to the list.

Class: **Reptilia** Laurenti, 1768

Subclass: **Diapsida**, Osborn 1903

Infraclass: Archosauromorpha, Huene 1946

Family Drepanosauridae Olsen and Sues 1986

Referred genera:
Drepanosaurus Pinna 1980
Megalancosaurus Calzavara, Muscio & Wild 1980
Dolabrosaurus Berman and Reisz 1992

Genus *Megalancosaurus* Calzavara, Muscio & Wild, 1980

Type species: *Megalancosaurus preonensis* Calzavara, Muscio and Wild, 1980

Revised diagnosis. Drepanosaurid with triangular skull, enlarged post-orbital region and long and narrow snout, parietals large, squamosals small with small posterior process. Frontals narrow anteriorly, forming dorsal margins of large orbits; nares anteroposteriorly expanded; lower jaw slightly bent ventrally in its anterior portion, 8 elongate cervical vertebrae with low neural spines, buffer-like prezygapophyses and posterior hypapophyses; presence of supraneural bones contacting the expanded neural spines of the third dorsal vertebra. *Megalancosaurus* is different from *Dolabrosaurus* and *Drepanosaurus* in the presence of ventrally expanded haemal spines bearing an oval fenestration; fusion of the neural spines of dorsal vertebrae 2-3 (not in *Drepanosaurus*); neural spines of the caudal vertebrae distally expanded anteroposteriorly, assuming a distinct "T" shape (not in *Drepanosaurus* and in *Dolabrosaurus*), ulna narrow (flattened and enlarged in *Drepanosaurus*) with well developed olecranon; opposable digits in the anterior limb (not in *Drepanosaurus*), claws on the digits of the manus of similar size (the claw on the second digit is enormous in *Drepanosaurus*); posterior ribs fused with corresponding vertebrae (also in *Dolabrosaurus*, not in *Drepanosaurus*); phalangeal formula for the manus 2, 2, 2, 3, 3, (3, 2, 2, 2, 2 in *Drepanosaurus*, unknown in *Dolabrosaurus*). All these differences are summarized in Tab. 1, and compared also with the possible drepanosaurid MCSNB 4751 (Fig. 11).

Megalancosaurus preonensis Calzavara, Muscio and Wild 1980

Holotype: specimen MFSN 1769, Calzavara Muscio & Wild, 1980, fig. 2-5.

Distribution. Middle - Late Norian (Late Triassic) of Northern Italy.

Below the genus level, the difference between the morphologies of the allux of CCSR 63115 with respect to MBSN 25 and 26 (Renesto, 1994a) rises problems because in the holotype of *M. preonensis* the pes is not preserved and no other significant difference among the holotype and other specimens can be seen. In fact, those specimens with the modified pes (Pl. 2 B- C), either lack the anterior half of the body or it is very poorly preserved (Renesto, 1994a). On the other hand, CCSR 63115 (with a "normal" pes) shares all the features of the holotype, as does MPUM 6008 (Renesto, 1994a; Pl. 3B) and these may be referred to *M. preonensis* with confidence. The two specimens with modified and opposable first toe (Renesto, 1994a) may represent a different

Fig. 11 - Specimen MCSNB 4751. Scale bar equals 1 cm. The drepanosaurid characters are indicated with the numbered black arrows as follows: 1) barrel shaped trunk 2) long, deep, laterally compressed "leaf"-like tail 3) anterior dorsal vertebrae with high neural spines, anteroposteriorly expanded at their distal end; 4) zygapophyses lying very close to midline; 5) caudal vertebrae in the middle section of the tail with high neural spines and deep haemal spines, 6) caudal vertebrae with prezygapophyses overlapping nearly half of the preceding centra; 7) haemal spines attached at the posterior end of the ventral margin of the first 20 caudal centra, 8) ribs mostly holocephalous, slender and triangular in section; 9) gastralia absent; 10) shoulder girdle with a very high, narrow, rod-like scapula, gently bent anteriorly; 11) pelvic girdle with a high iliac blade, a rather narrow pubis and an ischium that is elongate posteriorly; 12) femur shaft not sygmoidal, 13) tarsus comprising a "L" shaped astragalus and a calcaneum with discrete lateral process; 14) fifth metatarsal straight; 15) penultimate phalanges in both manus and pes at least 50% longer than preceding ones; 16) ungual phalanges with the shape of narrow, very long, and sharp claws, provided with a well developed flexor process. The empty triangles without number indicate the modified and opposable first toes.

	Megalancosaurus	*Drepanosaurus*	*Dolabrosaurus*	MCSNB 4751
Neural spines of dorsal vertebrae 2-3	Fused together	Not fused	unknown	Not fused
Neural spines of the sacral vertebrae	Same height as in posterior dorsal vertebrae	Lower than in posterior dorsal vertebrae	Lower than in posterior dorsal vertebrae	Lower than in posterior dorsal vertebrae
Neural spines of the caudal vertebrae	"T" shaped	Only slightly enlarged distally	Only slightly enlarged distally	Only slightly enlarged distally
Haemal spines of the caudal vertebrae	Bearing an oval fenestration	Not fenestrated	Not fenestrated	Not fenestrated
Terminal vertebra of the tail	modified into a spine	modified into a spine	unknown	Not modified
Posterior dorsal ribs	Fused to the neural arches	Not fused	Fused to the neural arches	Not fused
ulna	narrow	very broad	unknown	narrow
ungual of second digit of the manus	similar to other unguals	Enormously enlarged	? similar to other unguals	similar to other unguals
Phalangeal formula for the manus	2, 2, 2, 3, 3	3, 2, 2, 2, 2	unknown	2, 3, 4, 5, 4
Phalangeal formula for the pes	2*, 3, 3, 3, 3 * first toe modified in some specimen	2, 3, 3, 3, 3	unknown	? 2, 3, 4, 5 4 first toe modified

Tab. 1 - List of the character that used to diagnose the genus *Megalancosaurus*, in comparison with *Drepanosaurus*, *Dolabrosaurus* and the possible drepanosaurid MCSNB 4751.

morphotype. The difference between the two morphotypes cannot be due to preservational bias because the pes of MBSN 25 is almost as well preserved as that of CCSR 63115. Malformation seems not plausible because two specimens share this feature and a modified first toe is present also in MCSNB 4751 which do not belong to *Megalancosaurus*. Thus the difference may possibly be considered as due to sexual dimorphism or, less probably, it may indicate the presence of two subspecies.

The presence of a terminal spine in MFSN 18443a raises another issue. Again this character was not reported for previous *Megalancosaurus* specimens. MFSN 1801 consists of the middle and posterior portion of the tail (Pinna, 1987; Renesto, 1994a; Pl. 3E); but it lacks the hooked spine, despite tails are of comparable size to MFSN 18443a. This character, if confirmed, represents an interesting point, because it may indicate that the morphotypes, or the two sexes, could possibly be distinguished by the presence or absence of the spine in addition to the pattern of the tarsus and pes. This assumption, however must be treated with caution, because dolomitization renders it very difficult to be confident that the very end of the tail is indeed preserved in MFSN 1801. The presence of a spine at the end of the tail might be a character of one or both morphotypes (or sexes), thus it is referred to in the diagnoses.

Functional morphology.

Megalancosaurus was first considered to be arboreal (Calzavara et al., 1980), and the detailed description of the postcranial skeleton gave further support to this interpretation (Renesto, 1994a). However *Megalancosaurus* was recently cited as aquatic by Padian & Chiappe (1998: 72) without any explanation, while Ruben (1998), proposed that this reptile was not only a good climber with arboreal habits, but also a skilled glider.

The study of specimen CCSR 63115 confirms that the skeleton of *Megalancosaurus* is even more specialized to life among tree branches than previously suspected, and a re-analysis of other known specimens, allows to conclude that the gliding hypothesis for this reptile may be feasible, but no true evidences can be found.

Any hypothesis on the functional morphology of *Megalancosaurus*, should take into account the huge amount of specialized features present in its skeleton and put them together in a consistent model. According to previous descriptions (Renesto, 1994a) and new available data, in *Megalancosaurus* there are: 1) a triangular skull, posteriorly inflated with a narrow, "beak-like" snout, 2) a long neck with high vertical mobility; 3) a "notarium-like" structure, with this term it is indicated here the presence of a sort of supraneural plate formed by expansion and fusion of the neural spines of anterior dorsal vertebrae, which is superficially similar to the notarium of some pterodactiloyd pterosaurs; 4) a barrel shaped trunk, that is very rigid owing to the position of the zygapophyses (close to the midline) and to the fusion of the ribs with the walls of the neural arches, 5) a high pectoral girdle with clavicles, possibly also with sternal plates, along with a very high and extremely narrow scapula which is vertically oriented, and a glenoid facing laterally and posteriorly; 6) a pelvic girdle with a very high anteriorly inclined iliac blade; 7) slender and rather long limbs; 8) carpus and tarsus allowing a high degree of rotation of both the manus and pes 9) manus with opposable digits and stout, long claws, 10) pes with long toes ending in very long, narrow and sharp claws and at least in one morph with an opposable clawless first toe. 11) tail long, stiff in the middle portion (due to the long prezigapophyses, lying close to the midline and laterally enveloping the preceding vertebra), but with good possibilities of flexion in the vertical plane at its base and forming a robust "hook" at the end; in addition this latter bears, at least in one morph, a pointed, claw-like terminal spine. 12) tail laterally compressed and leaf- like in appearance.

The long narrow snout and the small conical teeth are useful for grasping and keeping insects. The very large eyes and inflated parietal region may be indicative of good vision, useful for locomotion and precise prey location among tree twigs and possibly good limb coordination.

The morphology of the cervical vertebrae is similar to that of some pterosaurs (e. g. the buffer-like zygapophyses are present also in some rhamphorhyncoid pterosaur) and it may be suggested that the neck of *Megalancosaurus* was very flexible only on the vertical plane, but torsion was eliminated by the "hypapophyses" and lateral mobility was limited by the buffer-like zygapophyses. The presence of very high neural spines in the anterior dorsal vertebrae suggest that robust muscles or tendons may have been originated from these structure permitting the neck to be held upright. The hypapophyses, in addition, allowed the insertion of a well developed longus colli, for the extension of the neck. All these features permitted the neck of *Megalancosaurus* to be both retracted and suddenly projected forward, as in some projectile feeders.

The height of the neural spines all along the dorsal region and the rigidity of the rib cage are consistent with the ability to raise the neck and the trunk off the substrate by development of a robust transversospinalis system (Hildebrand, 1974; Rieppel, 1989; Tschanz, 1986). Further support to this hypothesis comes from the shape of the ilium (Renesto, 1994a).

The supraneural plate formed by the anterior dorsal vertebrae, together with the problematic supraneural bones is the most difficult feature to be explained. In pterodactyloid pterosaurs the supraneural plate served to articulate the free end of the scapula and is also the area for the insertion of a very powerful latissimus dorsi, a retractor and elevator of the humerus (Brinkman, 1981; Jenkins & Goslow, 1983; Peterson, 1971, 1984; Wellnhofer, 1991) this muscle plays an important role in raising the humerus backwards above the glenoid level.

The morphology of the scapula and coracoid has been already described and a functional similarity with chameleons has been proposed (Renesto, 1994a). However, the discovery of clavicles, and possibly of sternal plates, complicates this interpretation. Clavicles would render the pectoral girdle more solid, and prevent to some extent a lateral swing during walking, a feature that allows greater reach to the forelimb of chameleons. Thus the clavicles of *Megalancosaurus* may have limited the anterior extension of the fore limb, and at the same time provided more rigidity to the girdle. If the scapula was connected to the supraneural plate as in pterosaurs, the shoulder girdle was indeed rigid. The pattern of the carpus and of the tarsus in *Megalancosaurus* are functionally very similar to each other: there are two elongate and inclined proximal elements (ulnare-intermedium/astragalus-calcaneum), followed by a row of robust, square ones. The elongate elements may have improved mobility, enhancing flexion and rotation at the wrist and ankle level for better grasping abilities(Jenkins & Mc Clearn, 1984). It may be hypothesized that the stout structure of the shoulder region may have allowed good brachiation and quick movements of the fore limbs. Thus, without excluding their use for locomotion on narrow branches, the anterior limbs may have been also useful for seizing or holding firmly the prey. The hands of *Megalancosaurus* with opposable digits may have been capable of catching and holding preys like insects, grasping to the cuticle with the very stout and sharp claws.

The lateral expansion on the sides of the ungual phalanges of the pes indicate that very long cheratinous sheaths were present in life. This occurs frequently in climbing vertebrates (Hildebrand, 1974; Cartmill, 1985; Bennett, 1997). The modified first toe in *Megalancosaurus* specimens MBSN 25 and 26, and in *Dolabrosaurus* (according to the reinterpretation by Renesto & Paganoni, 1995), as well as in specimen MCSN 4571, is preserved as it suffered strong hyperextension, suggesting the presence of a robust ligament in life for the abduction of the toe. This character is present in some climbers, and may represent an useful device for single extremity grasping on slender supports (Cartmill, 1985), but, however, if the modified first toe was sex related feature, it may have served perhaps to hold the partner during mating on unstable supports like narrow twigs.

The shift of the insertion of the haemal spines in the posterior portion of the tail is probably related to a prehensile tail and to the presence of the terminal spine. It is worth noting that the same feature also occurs in *Dolabrosaurus* (Berman & Reisz, 1992), which suggests that *Dolabrosaurus* may also have been arboreal in habit.

The terminal hooked spine, is rather an odd structure that can be explained as a device for a particular kind of prehension. Chameleons grasp twigs and branches by curling the narrow tail which is circular in section. The deep, leaf-shaped tail of *Megalancosaurus* was less suited for this task, but the terminal hook may have been a functional substitute. The tight articulation of the spine with the preceding vertebra would have kept the spine in a nearly fixed position: it pointed anteriorly and lay almost parallel to the axis of the tail both in *Drepanosaurus* and in *Megalancosaurus* forming a stiff hook. In such a position it may have been useful not only to grasp on twigs, but also to "lock" the animal by clinging in crevices or in cracks of the substrate, counteracting gravity. The same device may have also been useful when *Megalancosaurus* was hanging in an head down position.

In summary, the morphology of the end of the tail and posterior limbs of all known drepanosaurids follows the pattern of climbing vertebrates with prehensile tails and grasping hind feet that may be used together forming a stable three point support base for stance or feeding, also hanging head down (Cartmill, 1985). It has to be noted that the first caudal vertebrae bear narrow neural spines that are inclined posteriorly, allowing to rise the tail at its base to some extent. In *Drepanosaurus* the neural spines of the posterior sacral and proximal caudal vertebrae were low, perhaps for the same reason (Pinna, 1984).

It is suggested here that *Megalancosaurus* may have hunted by ambush among foliage, moving slowly or perhaps, remaining still in a tripod stance, with the neck and anterior limbs in a retracted position. When the prey was at a suitable distance, it was seized with a sudden extension of the limbs and of the long neck. The victim was then held firmly with the grasping hands (Fig. 12). This would have rendered *Megalancosaurus* hunting mode more similar to that of a praying mantis rather than to that of a chameleon.

Gliding adaptations?

Similarities between *Megalancosaurus* and phalangeriids (a group of small scansorial mammals which comprises adept gliders along with other non-gliding genera) have already been noted (Renesto, 1994a).

Gliding is advantageous under many aspects for small arboreal animals (Hildebrand, 1974; Scholey, 1986; Norberg, 1985; Feduccia, 1996) and it developed independently in several taxa of reptiles and mammals (and also in amphibians).

Recently Ruben (1998) proposed a gliding bauplan for *Megalancosaurus* and considered it as a plausible model for the morphology of a putative ancestor of birds. According to this author the characters supporting gliding abilities in *Megalancosaurus* should be the presence of a bird-like scapula; long, only partially extendable forelimbs (due to the structure of the olecranon) possibly supporting propatagial membranes; of a notarium-like structure, and of a rudder-like tail (Ruben, 1998). The author suggested that "*Megalancosaurus* may well provide valuable insights into intermediate stages leading to the origin of the Aves" (Ruben 1998: 73A).

Climbing abilities are often a prerequisite for gliding and the energy required to maintain the limbs in a spread position and thereby stretch the gliding membrane is lower than that needed for climbing (Rayner, 1988). As a result, any climber might be a potential glider, if has a possibility to develop a flight surface. It should be stated however, that no evidence for a patagium was found in *Megalancosaurus*; this might be due to preservational bias but it has also to be taken into account that all the characters of the anterior limb and shoulder girdle quoted by Ruben (1998) as supporting gliding abilities in *Megalancosaurus*, can also be explained otherwise, as detailed in the previous section.

The stiff, deep, leaf-like proximal and middle portion of the tail may seem an efficient rudder in a gliding *Megalancosaurus* as suggested by Ruben (1998), but, on the other hand, it is very long with respect to the span of the putative membrane, consequently the animal may have had problems of balance during gliding. In gliding phalangeriids the tail is long indeed and it acts as a rudder, but it is flattened *dorsoventrally*, providing further lift during gliding. In the drepanosaurid the *laterally* flattened tail could not provide any lift. It is probable that the expanded proximal and middle portion of the tail played some other role, like display, or even heat absorption and dissipation if appropriately oriented. In any case the deep tail of the drepanosaurids seems improbable as a sculling organ for swimming as suggested by Berman and Reisz (1992) for the related genus *Dolabrosaurus*, since lateral undulation was restricted or even impossible (Renesto, 1994a, b). Furthermore it is not easy to explain the function of a curled end (sometimes with an terminal spine at its tip) for swimming.

Even if it cannot be excluded that *Megalancosaurus* may have been adapted for gliding, there is no clear evidence supporting this hypothesis. If it was a glider, however, its bauplan should have been different from the one currently accepted for bird ancestors (Fig. 13). In fact an hypothetical gliding *Megalancosaurus* should have had a patagium extending between anterior and posterior limbs. Consequently the presence a patagium that reached the posterior limb, excluded the possibility of a bipedal gait, and bipedality is considered to have developed prior to the attainment of gliding/flying abilities in pre-birds, both by supporters of the cursorial and of the arboreal theory for the origin of bird flight (Padian, 1985; Peters, 1985; Peters & Gutmann, 1985; Rayner, 1985a, b, 1988; Schaller, 1985). According to all these authors the upright position of the hind-limbs in pre-birds precluded their integration in a gliding membrane and flying apparatus (Fig. 13A), thus only the fore limbs

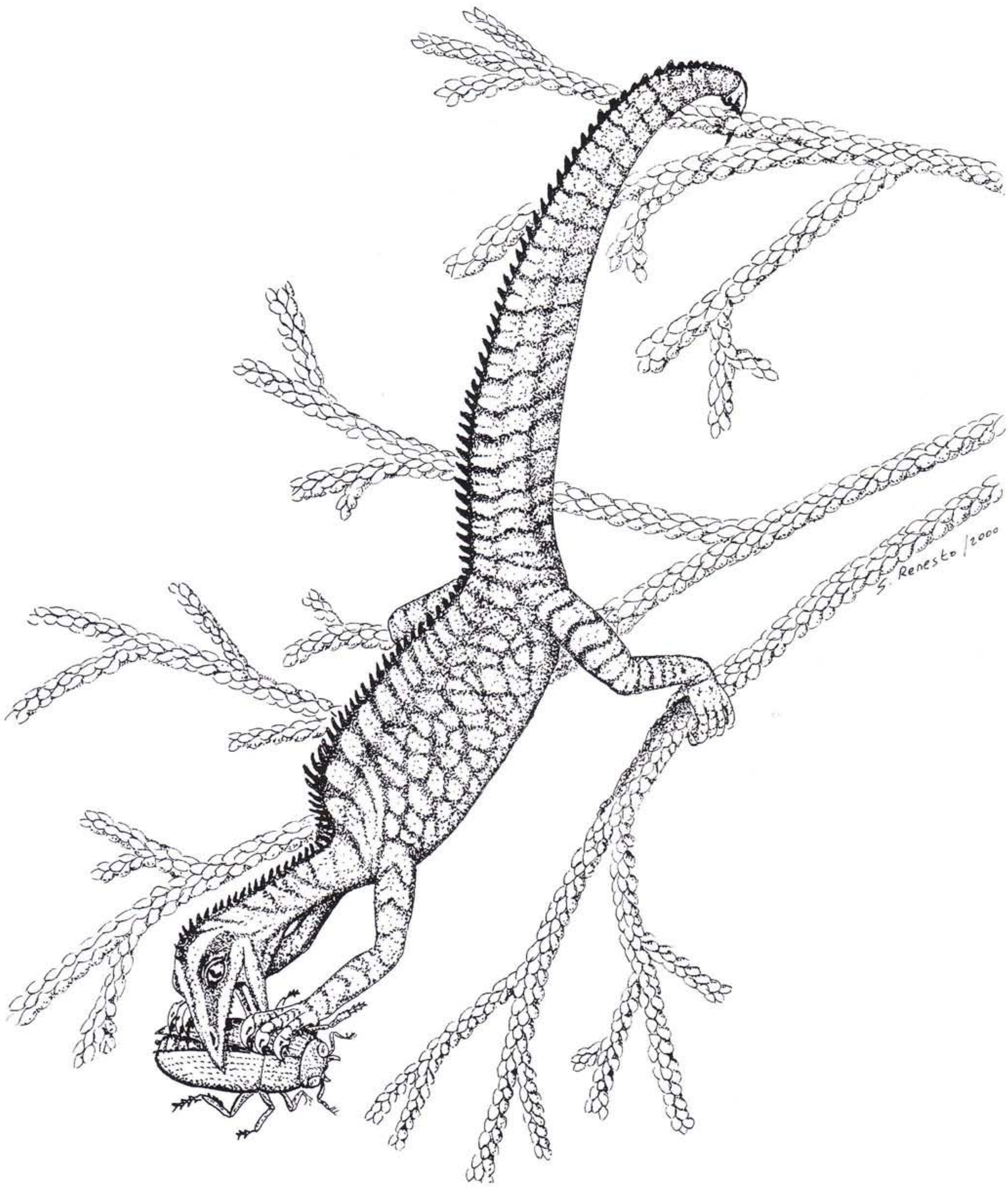

Fig. 12 - Restoration of *Megalancosaurus*, feeding on a coleopteran, while clinging into the scale-like leaves of *Brachyphyllum* twigs with the claws of the posterior limbs and with the terminal spine of the tail.

could have offered support to a lateral extension of the membrane. In pre-birds, the gliding surface was interrupted by the posterior limbs, and further lift posterior to the hind limbs were required to avoid pitch caused by the presence of a still elongate reptile-like tail (Peters & Gutmann, 1995; Schaller, 1985). For this reason the presence of a further posterior horizontally flattened surface necessary for a stable gliding apparatus (i. e. the feathered tail) was of fundamental importance in these animals (Peters & Gutmann, 1985). This view is accepted here and it is stressed that *Megalancosaurus* with its sprawling gait along with a laterally (not dorsoventrally)

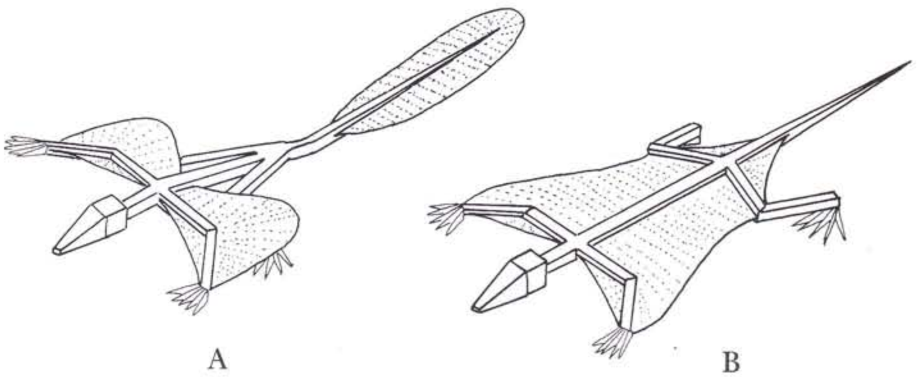

Fig. 13 - Comparison between different gliding patterns: A) prebirds; B) generalized glider, bat and pterosaur ancestors; if *Megalancosaurus* was a glider, its pattern should fall within B. Redrawn from Peters & Gutmann (1985).

compressed tail, that could *not* provide any kind of lift, cannot represent a functional model for bird ancestors, notwithstanding any possible gliding adaptation.

Morphological similarities between *Megalancosaurus*, and *Protoavis*.

Specimen CCSR 63115 permits a reconsideration of the structure of the three disarticulated cervical vertebrae that can be observed in specimen MPUM 6008 and they are now identified as the fifth, sixth and seventh one. These vertebrae are preserved, in dorsal, lateral and ventral view respectively (Fig. 2 B-C, Fig. 14E).

The analysis of the preserved elements of the skull of specimen CCSR 63115 and of the neck both in specimen CCSR 63115 and in specimen MPUM 6008, reveals the existence of a high morphological similarity with the same structures in the possible Triassic bird *Protoavis*, according to the description and reconstruction by Chatterjee (1991, 1999). This resemblance is particularly evident in the cervical vertebrae.

Megalancosaurus and *Protoavis* skull are superficially very similar, being narrow and pointed anteriorly with an inflated the postorbital region; the lower jaw is also similar in shape, with a ventrally bent anterior portion.

An even deeper similarity between *Protoavis* and *Megalancosaurus* could be found however in the cervical vertebrae (Fig. 14). By comparison with Chatterjee's reconstructions (1991, 1995, 1998, 1999) the anterior cervical vertebrae of *Protoavis* (based on specimen 9201) share with *Megalancosaurus* the same general outline of the cervical vertebrae, as well as other features. In both taxa the prezygapophyses have a convex surface and are vertically oriented with. The presence of "hypapophyses" and of elongate, narrow centra that are concave anteriorly and convex posteriorly, together with low neural spines are common in both forms. Interestingly, the cervical vertebrae are also approximately of equal size (their length being 10-11 mm in MPUM 6008, and 10-12 mm in the small specimen of *Protoavis*).

Having not examined directly the *Protoavis* material first hand I cannot give a detailed comparison between the two taxa, neither comment further the similarities. However, since the bones ascribed to *Protoavis* specimens were found disarticulated and the doubts cast on their association into specimens or even into a single taxon (Ostrom, 1991, 1996; Chiappe, 1995) may be founded, then the possibility that at least the anterior cervical vertebrae of the small specimen of *Protoavis* might instead represent scattered elements belonging to the skeleton of a *Megalancosaurus*-like drepanosaurid reptile should be seriously considered. *Dolabrosaurus* remains have been collected from the Chinle Formation (Berman & Reisz, 1992), a *Drepanosaurus*-like shoulder girdle from the same formation is currently under study (J. D. Harris, pers. comm.), and their occurrence, along with the Deep tailed Swimmer in the Triassic of the Newark Supergroup (Colbert & Olsen subm.), is consistent with the possibility of a drepanosaurid reptile in the Dockum Group.

Conclusions.

New available data on *Megalancosaurus* confirm the high degree of adaptation toward arboreal life for *Megalancosaurus* and possibly for other drepanosaurids.

At present there is little evidence supporting gliding abilities and evidence is insufficient to support the hypothesis of relationships with powered flyers.

However, if small drepanosaurids like *Megalancosaurus* may perhaps have been gliders, their overall structure was similar to that one of gliding squirrels, of bats (Rayner, 1988) and pterosaurs ancestors, that is consistent with a "from trees down" model as hypothesised by Peters & Gutmann (1985); Schaller (1985); Wild (1984) and Bennet (1997).

In should be taken into consideration that if these reptiles were gliders, they may simply represent a further attempt to exploit the aerial environment, as often occurred during the Middle - Late Triassic in many unrelated groups. These include the kueheneosaurids (Robinson, 1962; Colbert, 1970), *Longisquama* (Sharov, 1971a; Haubold & Buffetaut, 1987), *Sharovipteryx* (Sharov, 1971b; Gans et al., 1987). All these reptiles were

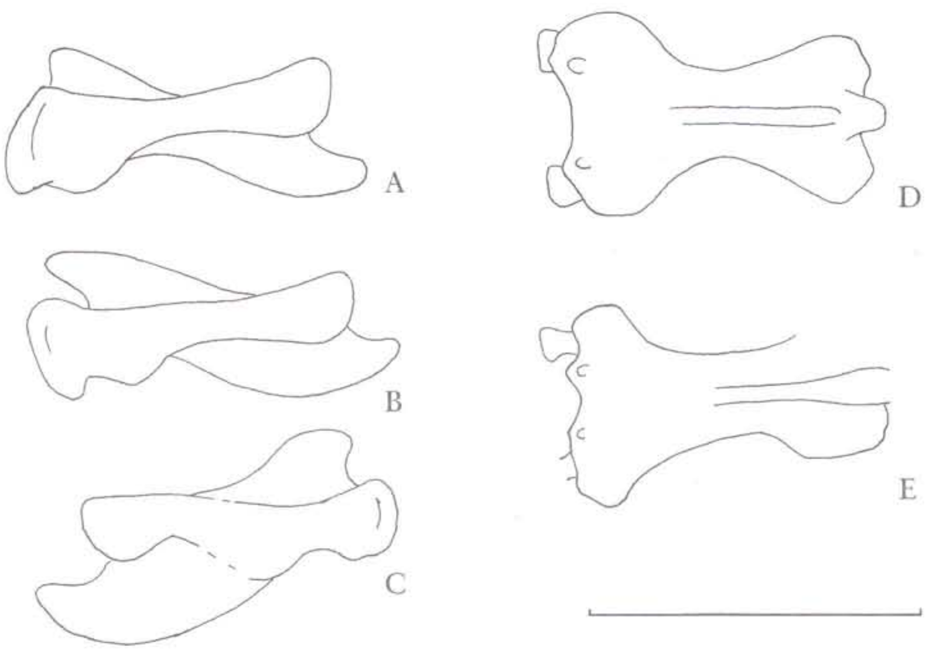

Fig. 14 - Comparison among the cervical vertebrae of *Protoavis* and of *Megalancosaurus*. A) fourth cervical vertebra of *Protoavis*, lateral (left) view; B) fifth cervical vertebra of *Megalancosaurus preonensis* specimen MFSN 1769 (the holotype) in lateral (left) view; C) fifth cervical vertebra of *Megalancosaurus preonensis* specimen CCSR 63115 in lateral (right) view; D) fifth cervical vertebra of *Protoavis* in ventral view; E) seventh cervical vertebra of *Megalancosaurus preonensis* specimen MPUM 6008 in ventral view. Scale bar equals 1 cm. A) and D) redrawn from Chatterjee 1991, 1999.

small and many were probably arboreal. Apart for the drepanosaurids from the Italian localities, these reptiles were collected in continental deposits, thus they may have lived on the tree canopy. The Italian drepanosaurids lived on isles surrounding the intraplatform marine anoxic basins in which these animals fossilized. These basin were connected to the open sea only by narrow and long tidal channels (Renesto & Tintori, 1995), and it represented probably an obstacle for many aquatic reptiles. This may in part explain why terrestrial reptiles are more frequently found than aquatic ones in the lithostratigraphic units in which Italian drepanosaurids have been found (Dalla Vecchia, 1995; Renesto, 1994 a, b, c; 1995a b; Renesto & Tintori, 1995; Renesto & Dalla Vecchia, in press; Wild, 1978, 1984, 1991, 1994). Insects and plants remains were also found in Lombardy units and in the Dolomia di Forni (Whalley, 1986; Dalla Vecchia, 1991; Jadoul et al., 1992).

Finally, the morphological similarity between the necks and (to a lesser extent) the skulls of *Megalancosaurus* and *Protoavis* is intriguing; in fact the peculiar morphology of the anterior cervical vertebrae has considered as one of the synapomorphies linking *Protoavis* to true birds by Chatterjee (1999), especially for the presence of hypapophyses. However, hypapophyses has been reported for varanoid lizards (Romer, 1956) and for crocodilians (E. Frey, pers. comm.) and the possibility that the cervical vertebrae of *Protoavis* might belong to a *Megalancosaurus*-like reptile should be considered.

Taking into account that all *Megalancosaurus* specimens are perfectly articulated, and no doubts on the association of skeletal elements can be casted, it is concluded here that the bird like features of the skull and of the neck, along with the postcranial structures like the rod like scapula, the orientation of the glenoid, the hollow limb bones and the shape of the claws cannot be considered characters linking *Megalancosaurus* with birds, because they may merely represent functional adaptations and some are widespread among different diapsids. In addition, if *Megalancosaurus* is considered to be related to birds, it will imply that the Drepanosauridae as a whole should be related to birds, or conversely that the huge amount of drepanosaurid characters in the skeleton of *Megalancosaurus* developed as convergences, and this latter hypothesis seems less plausible.

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