

DIFFERENCES IN THE HINDLIMB ANATOMY IN THE TWO SPECIES OF THE LATE TRIASSIC DREPANOSAUFOMORPH DIAPSID *MEGALANCOSAUFURUS* INDICATE HABITAT PARTITIONING WITHIN THE ARBOREAL ENVIRONMENT

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Abstract. Discovery of two different morphologies of the hindlimb in specimens ascribed to the Triassic drepanosauromorph diapsid *Megalancosaurus* led to the erection of two distinct species within this genus: *M. preonensis* and *M. endennae*. In the present study a re-examination of the hindlimb architecture of both *Megalancosaurus* species indicates that *M. preonensis* and *M. endennae* exploited different microhabitats within the arboreal environment as for many extant species belonging to the same genus, like caribbean Anoles. *M. endennae*, with a stronger lower leg, a larger grasping foot, an opposable clawless hallux, and deeper and more recurved claws on pedal digits 2-5 was better adapted for locomotion on narrow and intricate supports like narrow twigs on terminal branches. *M. preonensis* with more slender hindlimbs, absence of an opposable hallux and longer, but thinner and less recurved claws on all pedal digits may have been better adapted to live on larger supports and could also have used the long pedal claws as hooks in a sloth-like fashion. In both *Megalancosaurus* species the tail acted both as a prop to assume a stable tripod gait and as a clinging device that ensured grip during bridging as in other arboreal drepanosauromorphs which skeleton is adequately known. The overall hindlimb adaptation of *Megalancosaurus* species are more similar to that of some small arboreal mammals rather than that of chameleons.

INTRODUCTION

The Drepanosauromorpha Renesto, Spielmann, Lucas & Tarditi Spagnoli, 2010, are one of the most peculiar clades of diapsid reptiles among the terrestrial faunas of the Late Triassic. Some authors place the Drepanosauromorpha outside the crown group diapsids (Muller 2004; Senter 2004,

Pritchard et al 2017); however, other authors (Dilkes 1998; Renesto & Binelli 2006, Renesto et al. 2010) nested the Drepanosauromorpha within archosauromorphs. The Drepanosauromorpha comprises several genera: *Hypuronector* Colbert & Olsen, 2001, *Dolabrosaurus* Berman & Reisz, 1992, *Drepanosaurus* Pinna, 1980, *Megalancosaurus* Calzavara Muscio & Wild, 1980, *Vallesaurus* Renesto & Binelli, 2006. More recently other drepanosauromorph genera have been erected on the basis of fragmentary material: *Avicranium* Pritchard & Nesbitt, 2017, repre-

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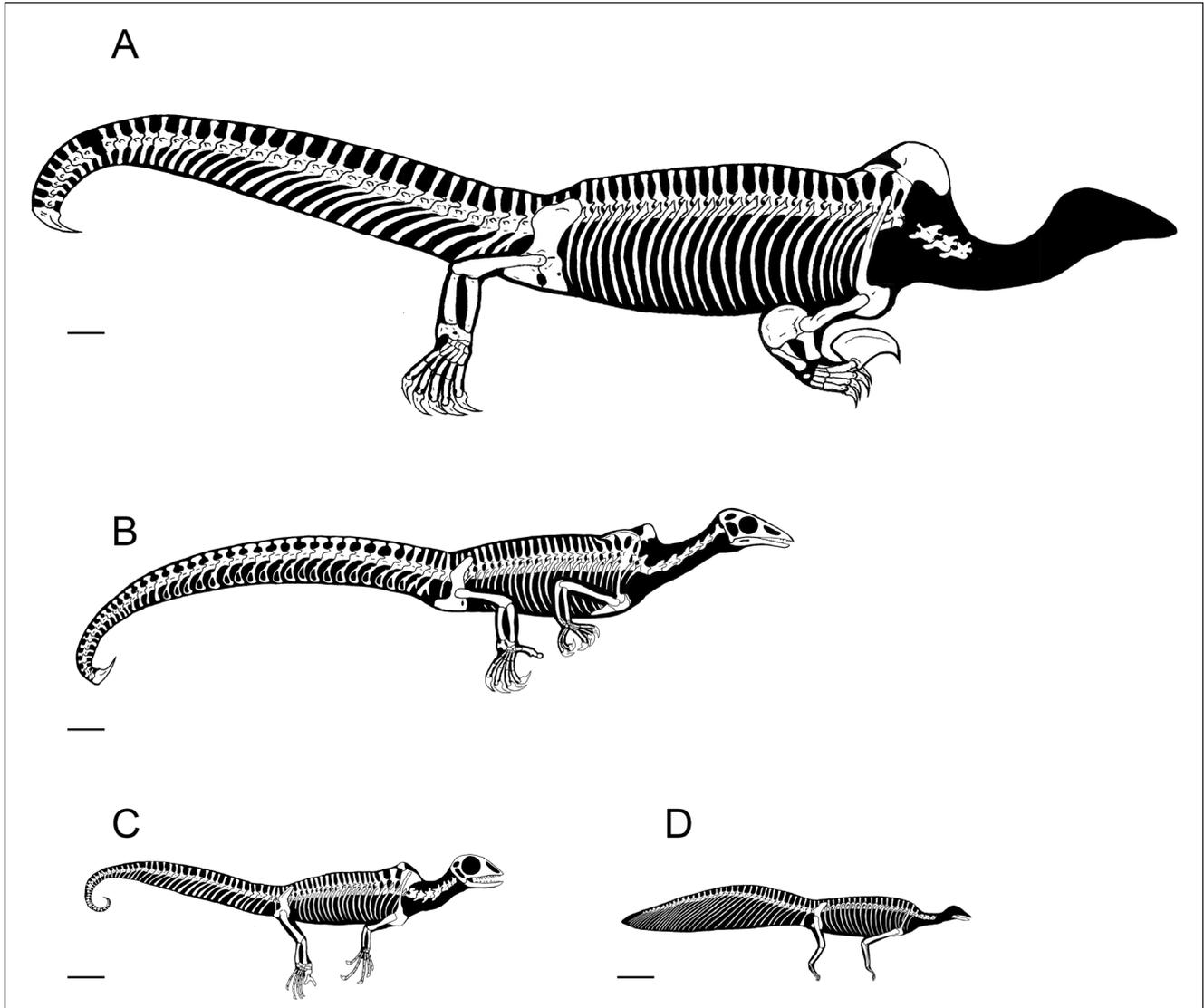


Fig. 1 - Skeletal reconstruction and body outline of the drepanosauromorph genera which skeleton is adequately known. A) *Drepanosaurus*; B) *Megalancosaurus*; C) *Vallesaurus*; D) *Hypuronector*. Scale bars equal 1 cm.

sented by an isolated skull, *Ancistronychus* Gonçalves & Sidor, 2019, and *Skybalonyx* Jenkins, Pritchard, Marsh, Kligman, Sidor & Reed, 2020, both known only by isolated manual claws. Further isolated drepanosauromorph elements probably belonging to different drepanosauromorph taxa are known, but not named (Harris & Downs 2002; Renesto & Fraser 2003; Fraser & Renesto 2005; Renesto et al. 2009). The geographical distribution of drepanosauromorphs was very wide, ranging from USA to United Kingdom and Italy (Berman & Reisz 1992; Colbert & Olsen 2001; Harris & Down 2002; Renesto et al. 2009, 2010). The genus *Kyrgyzsaurus* (Alifanov & Kurochin, 2011) from Kirgizistan is also considered close to Drepanosauromorpha. The

stratigraphical record of known drepanosaur taxa ranges from the Late Carnian to the Norian-Rhaetian (Late Triassic).

The overall body architecture of the Drepanosauromorpha (Fig. 1) is rather constant in the genera which skeleton is adequately known and has been thoroughly described in several articles (see Renesto et al. 2010 and references therein, and also Pritchard & Nesbitt 2016) and there is general consensus that the drepanosauromorph skeletal bauplan in these genera reflects adaptation to arboreal life.

On the other hand, the massive unguals of *Ancistronychus* Gonçalves & Sidor, 2019, and of *Skybalonyx* Jenkins et al., 2020, indicate that these two genera may have been terrestrial diggers.



Fig. 2- *Megalancosaurus preonensis*, A-B) the holotype MFSN 1769, part and counterpart preserved on two slabs; C) MPUM 6008. Specimens not examined for this study. Scale bars equal 1 cm.

The genus *Megalancosaurus* was firstly described by Calzavara et al. (1980) on the basis of one incomplete specimen (Fig. 2A, B) from an outcrop of the Norian (Upper Triassic) Dolomia di Forni Formation in Friuli (northern Italy). Subsequent findings of more complete specimens (Fig. 2C, Fig. 3-5) from outcrops of the coeval Calcare di Zorzino Formation in Lombardy (northern Ita-

ly), allowed a nearly complete reconstruction of the osteology of *Megalancosaurus* (Renesto 1994, 2000; Renesto & Dalla Vecchia 2005). Further studies (Renesto 2000; Renesto et al. 2010) revealed the presence of substantial differences in the morphology of the hindlimb in different specimen of *Megalancosaurus* which were otherwise identical even in size (Tab. 1). Renesto (2000, p. 172) suggested that

	<i>M. preonensis</i> MFSN 1769	<i>M. preonensis</i> MPUM 6008	<i>M. preonensis</i> MPUM 8437	<i>M. endennae</i> MBSN 25	<i>M. endennae</i> MBSN 26
Skull	27	-	-	-	-
5th cervical	9	10	7.5	-	6
1 st phalanx of digit 3	6	6	5	-	-
Humerus	22	22,5	21	-	18.5
Radius (left)	15	14	11	-	-
Ulna (left)	15	14	12	-	-
3 rd metacarpal	3.5	3	4	-	-
1 st phalanx digit 3	6	6	5	-	-
Femur (left)	-	-	27	23.5	20
Tibia (left)	-	-	17.5	14.5	11.5
3 rd metatarsal left			4	4	
First phalanx third pedal digit			3	3.5	
Length of mt plus phalanges of 3 rd pedal digit			17.5	19	
Tibia/femur			64%	60%	
3 rd pedal digit/tibia			90%	130%	

Tab. 1 - Measurements (length) in mm for different specimens of *Megalancosaurus*. Studied specimens are in bold.

the differences in the tarsus and pes between the two *Megalancosaurus* morphotypes could either have been related to sexual dimorphism or may have been indicative of the presence of two subspecies. The hypothesis of sexual dimorphism was subsequently dismissed and the differences were considered as indicative of two distinct species (Renesto et al. 2010): the type species *Megalancosaurus preonensis* Calzavara Muscio & Wild, 1980, and a new species, *Megalancosaurus endennae* Renesto, Spielmann, Lucas & Tarditi Spagnoli, 2010. The erection of two distinct species was based on the assumption that in reptiles sexual dimorphism may be strong in display structures or in overall size, while in functionally related structures sexual dimorphism is expressed mostly by differences in their sizes and relative proportions among body and limb sections (Pietruszka 1988; Perez-Mellado & De La Riva 1996; Fitch 1981; Borczyk et al. 2014; Motani et al. 2015), rather than by a strongly different morphology as is the case of *Megalancosaurus*, even when differences in microhabitat are present (Kuo et al. 2009). Sexual dimorphism is present instead in the limbs of some mammals. For instance, the carpus of certain small arboreal didelphid marsupials is sexually dimorphic (Lunde & Schutt 1999; Voss & Jansha 2009): the wrist of males bears prominent tubercles which are supported by carpal ossifications and were interpreted as clasping devices for copulation (Lunde & Schutt 1999). However, even if sexual dimorphism, albeit less probable, cannot be ruled out completely as alternative explanation of the presence of two morphotypes in *Megalancosaurus*, an evaluation of the validity of the two separate *Megalancosaurus* species is out of the scope of the study, which aim is to

propose a functional interpretation of the different hindlimb morphology shown by the two *Megalancosaurus* morphotypes, which was not investigated in previous studies. For this reason the two *Megalancosaurus* species names are maintained here as a reference to the different morphotypes.

In the present paper the morphology of the hindlimbs of *Megalancosaurus* is revised in detail and the functional and ecological significance of the differences between the two species are considered as suggestive of adaptations to different microhabitats within the arboreal environment.

Institutional acronyms

The specimens are indicated with the following institutional acronyms preceding the catalogue numbers: MPUM (Museo di Paleontologia dell' Università di Milano, Milano Italy); MBSN (Museo Brebano di Scienze Naturali, San Pellegrino, Italy) MFSN (Museo Friulano di Scienze Naturali, Udine Italy) MCSNB (Museo Caffi di Scienze Naturali, Bergamo, Italy). NMMNHS (New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA), CM (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania USA), MSNM (Museo di Storia Naturale di Milano, Milano Italy).

LIST OF SPECIMENS ASSIGNED TO *M. PREONENSIS* AND TO *M. ENDENNAE*

Direct comparison between *Megalancosaurus* specimens is difficult due to the lack of elements shared by all specimens, along with poor preservation or incompleteness of some, holotype included.

MPUM 8437 which has a straight, clawed hallux is nearly complete and identical in all shared characters with the holotype of *M. preonensis* (MFSN 1769), thus Renesto et al. (2010) assumed that *M. preonensis* was the species lacking of the opposable

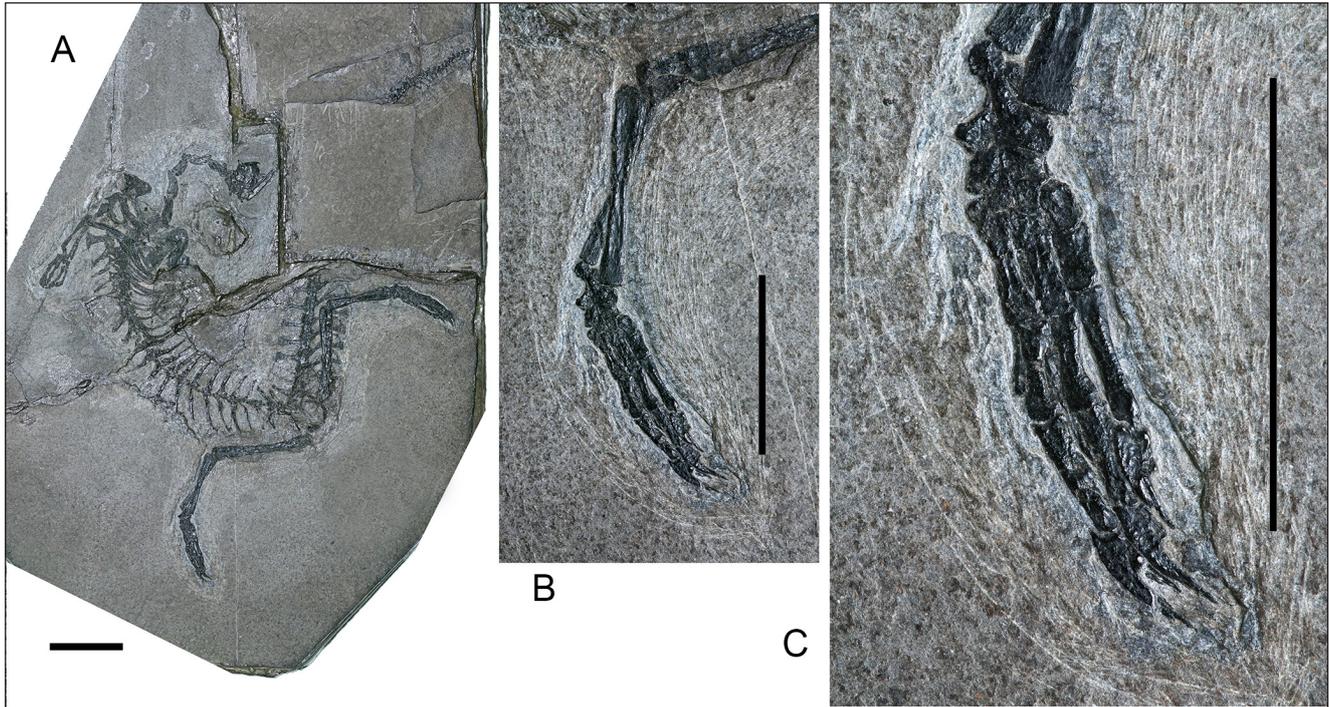


Fig. 3 - *Megalancosaurus preonensis*, specimen MPUM 8437: A) the entire specimen; B) detail of the hindlimb; C) detail of the tarsus and pes. Scale bars equal 1 cm.

clawless hallux, while specimen MBSN 25 and 26 that have an opposable hallux were assigned to *M. endennae*. Specimen MPUM 6008 was also assigned to *M. preonensis* by Renesto et al. (2010) on the basis of identical shape of the forelimb and pectoral girdle. However, this assignment remains dubious due to the absence of the hindlimb in MPUM 6008 and the absence or poor preservation of the anterior limb and pectoral girdle in specimen MBSN 25 and 26, ascribed to *M. endennae*. In the present paper the specimen assignment of Renesto et al. (2010) is maintained however, since the status of MPUM 6008 is irrelevant for the study.

Megalancosaurus preonensis

MFSN 1769 (Fig. 2A, B), *Megalancosaurus preonensis* holotype (Calzavara et al. 1980), consisting of the skull, incomplete cervical series, the first three-four dorsal vertebrae fused in the notarium-like structure, few disarticulated ribs, the complete right forelimb and scapula. Collected from the Dolomia di Forni.

MPUM 8437 (Fig. 3), *Megalancosaurus preonensis*; the specimen is articulated and almost complete, the skull lacks of most of the preorbital portion, and the right forelimb is missing along with the tip of the tail. Collected from the Calcare di Zorzino.

Specimen MPUM 6008 (Fig. 2C), *Megalancosaurus "preonensis"*. It consists of an incomplete specimen consisting of the last three cervical vertebrae, the entire dorsal series of the vertebral column with associated ribs, two sacral vertebrae and the dorsal tip of the neural spines of the first twelve caudal vertebrae; the pectoral girdle and forelimbs are complete while the dorsal tip of the ilium is the only preserved portion of the pelvic girdle and the hindlimb is entirely missing. Collected from the Calcare di Zorzino.

Megalancosaurus endennae

MBSN 25, (Fig. 4) *Megalancosaurus endennae* holotype, a partial skeleton consisting of the last four dorsal vertebrae, the sacral vertebrae and most of the tail, along with the pelvic girdle and the posterior limbs. Collected from the Calcare di Zorzino.

MBSN 26 (Fig. 5A), *Megalancosaurus endennae*; incomplete specimen consisting of fragment of the skull, a complete cervical series, portions of the dorsal and sacral vertebral series with associated ribs along with the first 10-11 caudal vertebrae, pectoral and pelvic girdles. Fore- and hindlimbs are present, the opposable clawless hallux is preserved in hyperextended position as in MBSN 25, albeit poor preservation does not allow a detailed analysis. Collected in the Calcare di Zorzino.

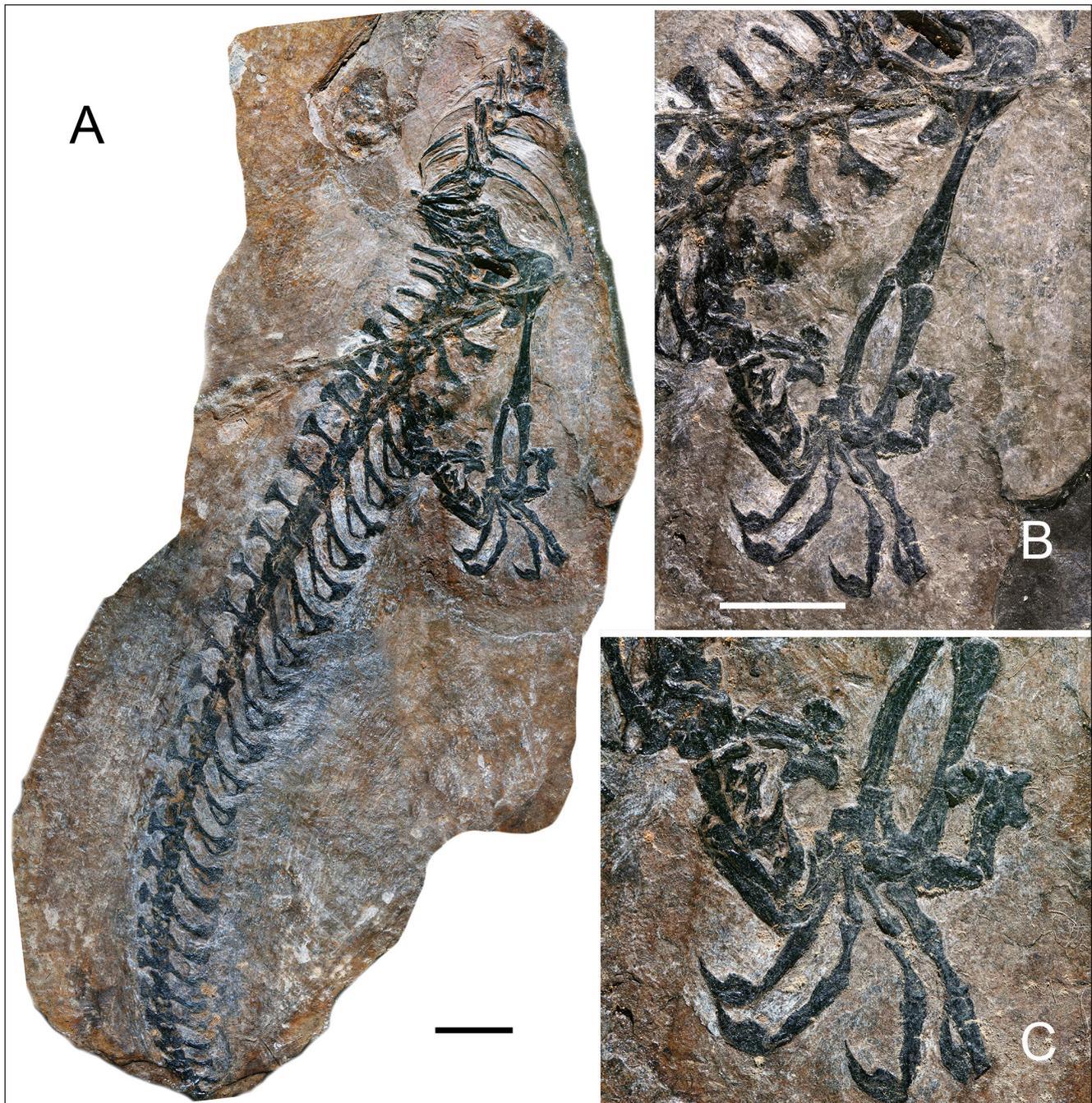


Fig. 4 - *Megalancosaurus endennae* holotype, specimen MBSN 25; A) the entire specimen; B) detail the whole hindlimb; C) detail of the crus and the pes. Scale bars equal 1 cm.

Specimen ascribed to *Megalancosaurus* sp.

Two further specimens have been collected in the Dolomia di Forni, both consist only of the posterior portion of the tail, and thus cannot be assigned to either *Megalancosaurus* species: MFSN 18443, (Fig. 5B) consisting of the last 26 caudal vertebrae, with associated terminal hook, and MFSN 1801 (Fig. 5C) consisting of the last 32 caudal vertebrae, but lacking of the terminal hook.

OSTEOLOGY OF *MEGALANCOSAURUS*

Several descriptions of *Megalancosaurus* have been published (Renesto et al. 2010 and references therein), thus its skeletal architecture (Fig. 6) is only briefly summarized here, apart for the hindlimb anatomy that is described in detail in the further section.



Fig. 5 - A) *Megalancosaurus endennae* MBSN 26; dorsally hyperextended halluces are visible; B) *Megalancosaurus* sp. MFSN 18443; C) *Megalancosaurus* sp. MFSN 1801. Specimens not examined for this study. Scale bars equal 1 cm.

The skull of *Megalancosaurus* is known in detail only for *M. preonensis*, while only part of the occipital region is preserved in specimen MBSN 26 of *M. endennae*. The skull (Fig. 6A) is triangular in shape, with long narrow and pointed jaws, large orbits and a reduced postorbital portion like in other drepanosauromorphs in which the skull is known, like *Vallesaurus cenensis* (Renesto & Binelli 2006), and *Avicranium renestoi* (Pritchard et al. 2017), thus superficially resembling that of birds or of pterosaurs. The vertebral column consists of 8 cervical, 23 dorsal, 3 sacral and at least 39 caudal vertebrae; the cervical vertebrae (Fig. 6B) are elongate, with procoelous centra, low neural spines, distinct hypapophyses and buffer-like zygapophyses like those of some primitive pterosaurs (Renesto 2000). The dorsal vertebrae (Fig. 6D) show very high neural spines at least three times higher than long, with the first three vertebrae fused together and bearing anter-

oposteriorly expanded dorsal portions of the neural spines thus forming a notarium-like structure (Fig. 6C) which is surmounted by two flat, fan-shaped bones; sacral vertebrae resemble the posteriormost dorsal ones in shape and possess short transverse processes; caudal vertebrae (Fig. 6E) show well developed praezygapophyses and those of the mid and posterior portion of the tail bear vertical facets that extend until the middle of the preceding vertebra, rendering the tail very stiff and restricting motion to a vertical plane. Haemapophyses are more than two times deeper than anteroposteriorly wide, distally expanded and forked until the fourth-fifth caudal vertebra, then become closed and encircle a drop-like fenestration until the 20th caudal vertebra, while the associated neural spines become T-shaped starting from the fifth caudal vertebra. The last caudal vertebra forms a sharp pointed spine anteroventrally directed (Fig. 6F). Cervical ribs are absent while

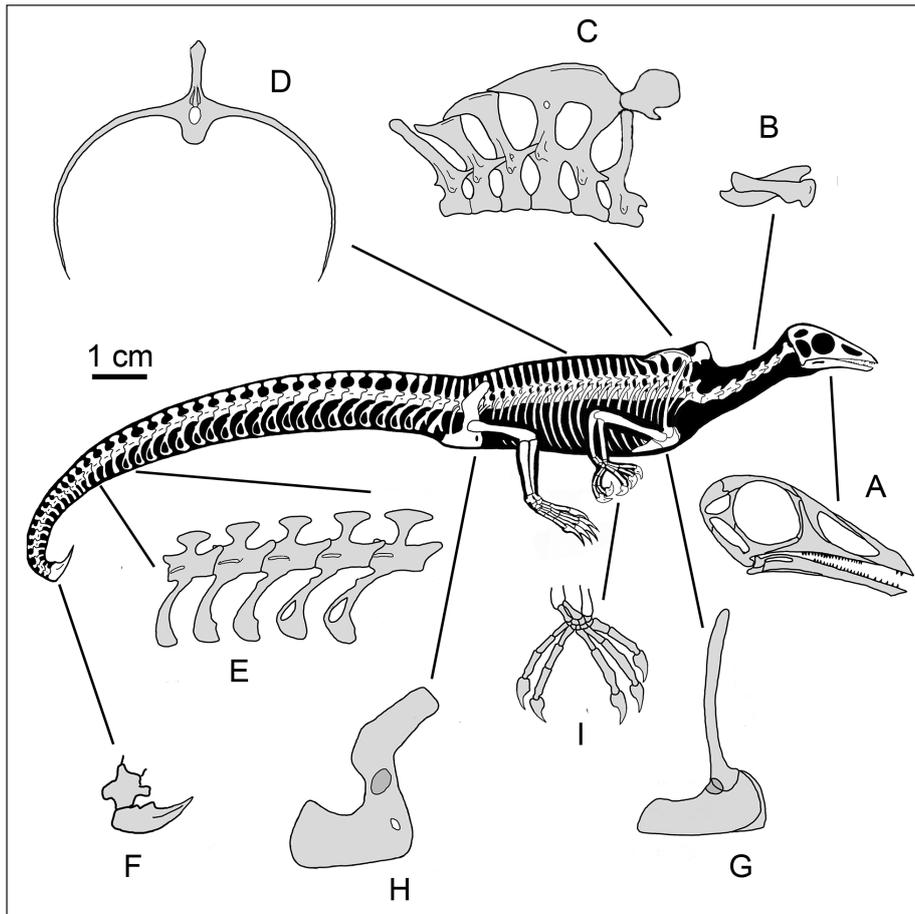


Fig. 6 - Details of *Megalancosaurus* skeletal architecture which are shared by both *M. preonensis* (figured in the reconstruction) and *M. endennae*: A) skull; B) cervical vertebra in lateral view; C) notarium-like structure of the anterior dorsal vertebrae with extra bone in lateral view; D) mid-dorsal vertebra with fused ribs in anterior view; E) mid caudal vertebrae in lateral view; F) hook (modified vertebra) at the end of the tail; G) pectoral girdle in lateral view; H) pelvic girdle in lateral view; I) hand in dorsal view. Scale bar equals 1 cm ad is referred to the skeletal reconstruction of the entire specimen.

dorsal ribs (Fig. 6D) are narrow and deeply curved, giving a barrel-like shape to the trunk. Posterior to the first five-six ones, the dorsal ribs are fused to the walls of the neural arches. No caudal ribs or distinct pleurapophyses are present, but small lateral ridges are visible in those specimens in which bone details are not obscured by dolomitization (MPUM 8437, MBSN 25, 26 and MFSN 1801).

The pectoral girdle (Fig. 6G) consists of high and narrow, strap-like scapulae, small clavicles fused in a furcula-like structure (Castiello et al. 2015), flat subrectangular coracoids, and short paired sternal plates.

The pelvic girdle (Fig. 6H) consists of an anteroposteriorly narrow, but very tall ilium, an anteroposteriorly narrow pubis and an anteroposteriorly broad ischium. The iliac blade is three times taller than long, and it is inclined cranially, forming an angle of about 40° with the body axis in MBSN 25. The anterior limb is slender with a straight humerus bearing a distinct deltopectoral crest, a narrow radius and ulna, the latter bearing a well developed olecranon. In the carpus (Fig. 6I) the ulnare and intermedium are elongate and allowed pronation and

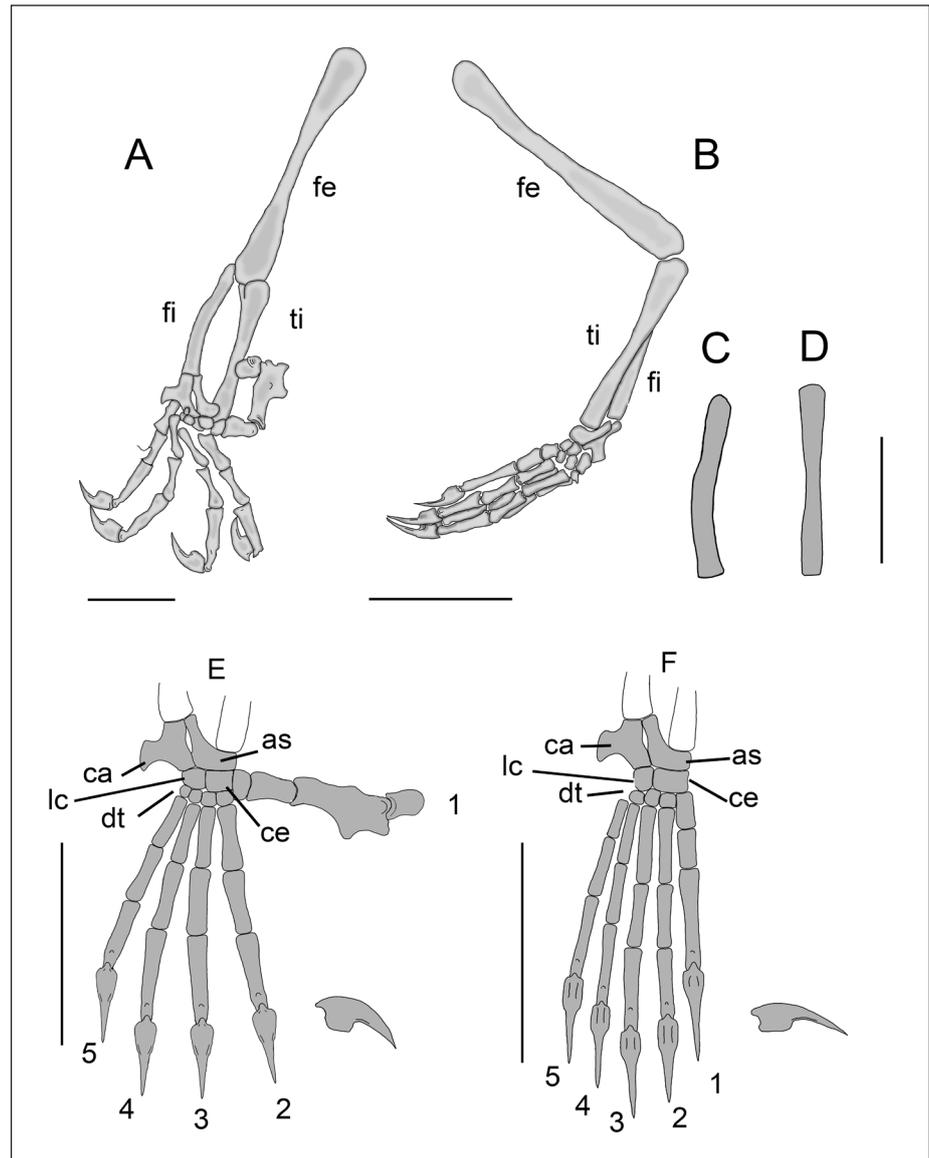
supination of the manus, which first three digits are opposable to the other two.

Hindlimb anatomy of *M. preonensis* and *M. endennae*.

Material examined. Two specimens of *Megalancosaurus* were examined in detail for this study: MPUM 8437 (Fig. 3) assigned to *Megalancosaurus preonensis* and MBSN 25 (Fig. 4) the holotype of *Megalancosaurus endennae*, both collected in the Bergamo Prealps at the Zogno locality (Lombardy, Northern Italy) in the upper levels of the Calcare di Zorzino (Zorzino Limestone), Late Norian.

Hindlimb architecture. In both species the femur (Fig. 7A, B) has a straight and narrow shaft without sigmoidal curvature. The proximal and distal portions are expanded, being more than two times larger than the midshaft. The proximal head has an oval outline that articulates with the acetabulum suggesting that there was a high degree of mobility at the coxofemoral level. In both MPUM 8473 and MBSN 25 it can be observed that the articular area for the tibia and the fibula lie at the same level. In

Fig. 7 - Comparison between hindlimb structure of *Megalancosaurus endennae* and *M. preonensis*: A) hindlimb of *M. endennae* and B) of *M. preonensis*; C) fibula of *M. endennae* and D) of *M. preonensis*; E) tarsus and pes of *M. endennae* and F) of *M. preonensis*. Abbreviations are: as, astragalus; ca, calcaneum; ce, centrale; dt, distal tarsals; fe, femur; fi, fibula; lc, lateral centrale; ti, tibia; 1-5 pedal digits. Scale bars equal 1 cm.



the two species the tibia is 64–60% the length of the femur (Tab. 1) and the fibula is slightly shorter than the tibia. The calcaneum is a proximodistally elongated bone with a narrow dorsal process similar to that of the astragalus, on its lateral side a large hatchet-shaped calcaneal tuber is present. The astragalus has an L shape, it contacts the tibia and the medial border of the proximal end of the calcaneum. The two bones can rotate to some extent with respect to the crus allowing a high degree of pronation and supination of the foot, possibly allowing to assume a reversed hind foot posture, as occurs in many arboreal mammals (Cartmill 1985). Distal to the calcaneum a large subrectangular medial centrale and a smaller lateral centrale are present. Four suboval distal tarsals are present.

Metatarsal 2–5 show a straight shaft with slightly expanded distal heads in both morphotypes. The first metatarsal is short and stout, with no distinct shaft. The phalangeal formula is 2,3,3,3,3. Preungual phalanges are much longer than the preceding ones, with a well developed rounded trochlea for the articulation of the unguis phalanx which forms an elongate and very sharp claw, the latter provided with a well-developed ventral process for the insertion of tendons of powerful flexors muscles.

The differences in hindlimb anatomy between the two species concern the limb proportions, the shape of the fibulae, of the tarsus and of the pes. In *M. endennae* the fibula has a curved shaft thus forming a distinct medial concavity that creates a wide spatium interosseum (Fig. 7C, 11B). In *M. preonen-*

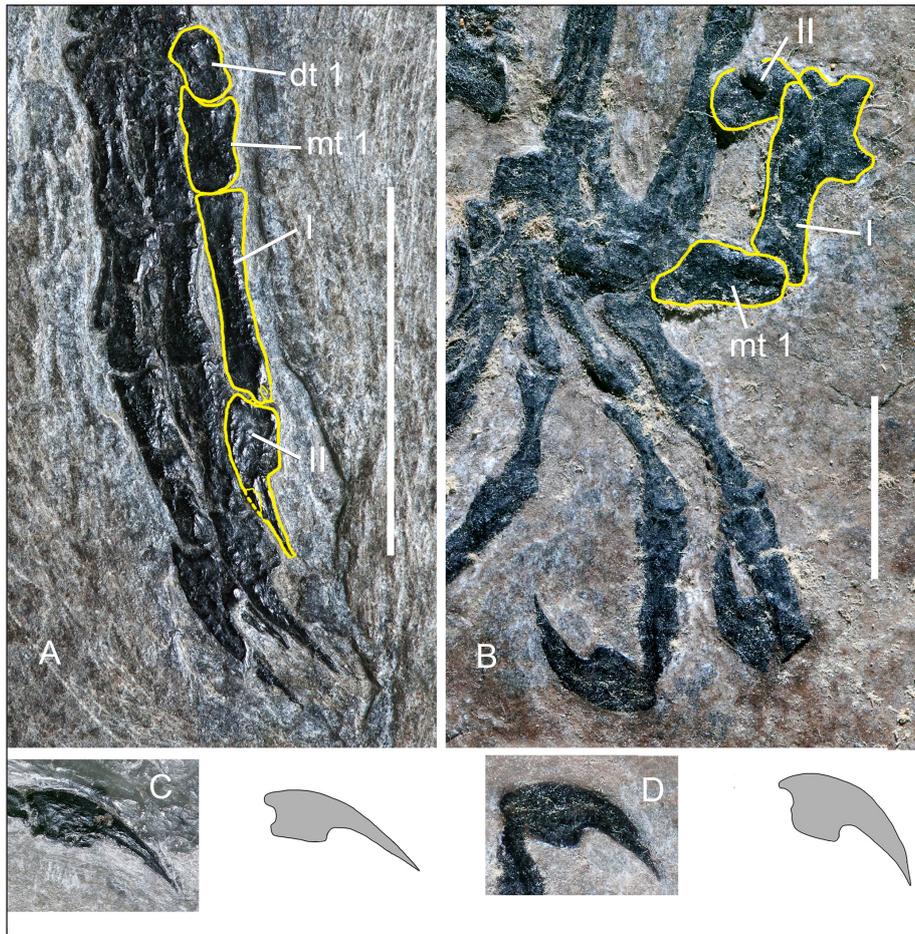


Fig 8 - A-B) Drawing of the shape of the hallux of *M. preonensis* (A) and *M. endennae* (B) outlined on a photo of the specimen. C-D) photo and drawings of the ungual phalanges of the right third pedal digit of *M. preonensis* MPUM 8437 (C) *M. endennae* MBSN 25 (D). Abbreviations: dt1, first distal tarsal; mt1, first metatarsal; I first phalanx; II second phalanx. Scale bars equal 5 mm (A-B)

sis, (MPUM 8473) the fibula is partially overlapped by the tibia in both hind limbs, however the visible portions (the distal head the distal half of the shaft and the proximal head) indicate that the main axis of the fibula shaft is straight like that of the tibia (Fig. 7D, 11A), thus the two bones surround a very narrow spatium interosseum. In specimen MBSN 26 (Fig. 5A) only scraps of the fibula are preserved and its shape cannot be reconstructed.

The most striking difference between the two species, however lies in the hallux. In *M. endennae* (Fig. 7E, 8B) the first metatarsal is much stouter than metatarsals 2-5, subtriangular in shape (much wider at its proximal end than at its distal one), and it is oriented at a right angle to the other metatarsals, so that the hallux is opposed to the other four digits. The proximal phalanx of the hallux is stout, curved ventrally, on its dorsal surface a robust area for the insertion of the tendon of extensor muscles forms a distinct “hump”. Also, a prominent tubercle is present on the ventral margin of the bone, close to distal end, which likely housed the insertion of a very strong tendon of flexor muscles. At the

distal end of the first phalanx a small trochlea is visible, on which is articulated a small second and last phalanx that does not form a claw, being instead suboval in outline. In both specimens ascribed to *M. endennae*, the hallux is distinctly bent dorsally, with the second and last phalanx touching the shaft of the tibia. This may be interpreted as due to a strong dorsal hyperextension due to contraction of powerful extensor muscles. The latter phalanx is preserved in a hyperextended position in both limbs and given the rounded shape of the trochlea, it is feasible that it was highly mobile. In *M. preonensis* (Fig. 7F, 8A) the first metatarsal and the hallux show the same morphology of the other four pedal digits and ends with a sharp claw.

In *M. endennae* the ungual phalanges (Fig. 8B, D) are dorsoventrally deeper than in *M. preonensis*, with a shorter anterior portion and a more pronounced curvature. In *M. preonensis* (Fig. 8A, C) the ungual phalanges are less curved, slightly longer and dorsoventrally narrower than in *M. endennae*, ending in an extremely sharp tip. In both *M. preonensis* and *M. endennae* a distinct lateral shelf for the insertion

of a well-developed keratinous sheath was present on the ungual phalanges, suggesting that in life the claw was distinctly longer. This shelf, however, is more developed in *M. preonensis*, thus it is feasible that the keratinous sheath in this species was proportionally longer, even if less curved.

FUNCTIONAL INTERPRETATION

Differences in claw morphology and curvature between *M. endennae* and *M. preonensis*

The shape and curvature of the claws has been considered useful clues to establish adaptation to different environments. Zani (2000) reported that, in lizards, increases in claw curvature, toe width and adhesive lamella number are correlated with increases in clinging performance on smooth substrates, while increases in claw height and decreases in toe length are correlated with increases in clinging performance on rough substrates. Usually, slightly curved claws are typical of terrestrial taxa especially in mammals and birds but also in some reptiles, while long, stout and strongly recurved claws are typical of perching birds and climbing lizards (Zani 2000). Most climbers among birds and mammals (e. g. woodpeckers, bats and squirrels, Cartmill 1985), and reptiles (Zani 2000), possess recurved sharp-pointed claws that are laterally compressed to fit better into crevices of the substrate (Cartmill 1985; Tulli et al. 2009; Cobb & Sellers 2020), while predators among birds and mammals also have distinctly recurved and sharply pointed claws, but they are more robust and conical in section, less compressed laterally than the claws of climbers (Cartmill 1985).

No data are available about toe skin or other soft parts of drepanosaurs feet, while claw shape and curvature can be compared with extant taxa. The claws of both *Megalancosaurus* species (Fig. 8C, D) are long, very sharp and strongly compressed laterally but their curvature is somewhat lower than that of many adept climbers. Spielmann et al. (2006), calculated the claw curvature index of several drepanosauromorph genera (*Drepanosaurus*, *Megalancosaurus* and *Vallesaurus*). For *Megalancosaurus* were examined both specimens still ascribed to *M. preonensis* and MBSN 25, which was subsequently designed as the holotype of *M. endennae*. The range of values for the claw curvature index of all *Megalancosaurus* specimen resulted to be lower than expected for adept climbers. In par-

ticular *M. preonensis* resulted to have a distinctly low curvature index (62°) while the index for *M. endennae* (86°) was closer to the limit for adept climbers (100° or more). Spielmann et al. (2006) however, concluded that the significance of the claw curvature index may vary depending to the postcranial skeletal architecture: if there are several unequivocal adaptations for arboreal life, as in *Megalancosaurus*, the presence of highly recurved claws is less significant or may represent a further adaptation for a particular niche within the arboreal environment, thus the low curvature indexes of the pedal claw in *Megalancosaurus* do not speak against the adaptation toward arboreal life. The different curvature indexes between *M. preonensis* and *M. endennae* most probably reflect adaptation to different microhabitats within the arboreal environment. It could be hypothesized that the lesser degree of curvature might have been compensated by strong capacity of flexing the other phalanges, however in *M. preonensis* there are no evidences of more developed areas for the insertion of stronger flexor muscles than in *M. endennae*. In addition, the architecture of the pes with reduced phalangeal formula (2,3,3,3,3) along with the presence of a stiff, elongate penultimate phalanx, may have hindered the possibility to perform an effective grip without using the claws to cling in some way to the substrate. The higher and more recurved claws of *M. endennae* may have allowed locomotion on a wider variety of substrates of different thickness and inclination, in an intricate framework of small twigs. The shape of the claw of *M. preonensis* is strikingly similar to that of sloths (Fig. 10) and, as suggested above, the presence of lateral shelves may be indicative of the presence of a long and keratinous sheath as in sloths; this may suggest that the claws may have enabled *M. preonensis* to cling on larger substrates or eventually, albeit speculative, it can be proposed that *M. preonensis* could hang itself below narrow supports, in a sloth-like fashion (Mendel 1985), exploiting the prehensile tail as a further support.

Pedal phalangeal proportions as a clue to arboreal life habits. The pedal phalangeal index (*sensu* Meng et al. 2017) has been defined as the ratio between the length of the proximal + intermediate (preungual included) phalanges and the length of the metatarsal. In mammals and reptiles, the PPI value increases from terrestrial to arboreal to gliding (Meng et al. 2017).

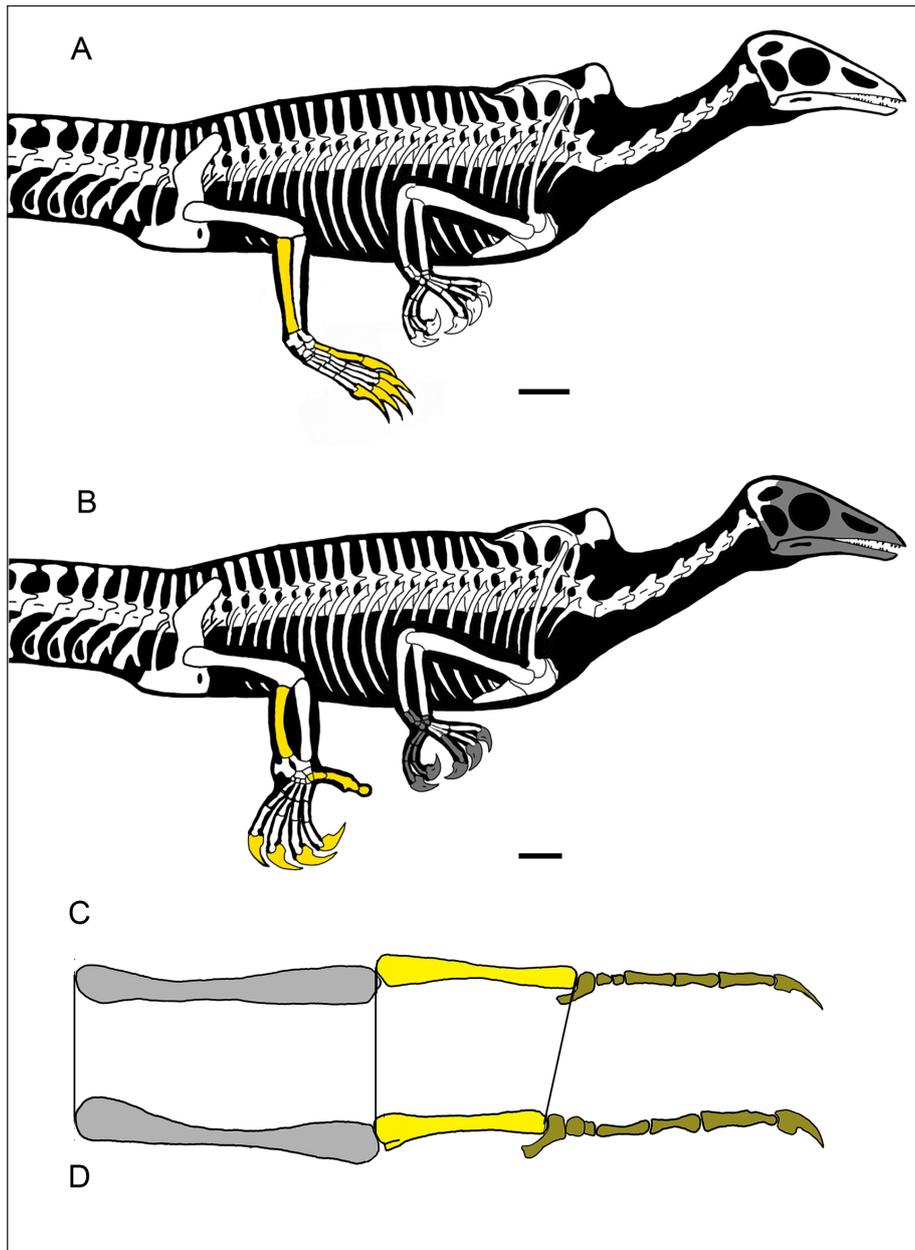


Fig. 9 - A-B) reconstruction of *M. preonensis* (A) and of *M. endennae* (B) with the differences in the hindlimb architecture highlighted in yellow. C-D) different proportions between limb sections of *M. preonensis* (C), and *M. endennae* (D). Grey areas in the reconstruction of *M. endennae* represent elements not preserved in any specimen. Scale bars in A-B equal 10 mm; C-D drawn not to scale.

In all drepanosauromorph taxa in which the hands and feet are adequately known, the pedal proximal and intermediate phalanges are exceedingly elongate relatively to the metatarsals and to the limb bones. We calculated the pedal phalangeal index of *Megalancosaurus* specimen, and it resulted to be extremely high (200% for *M. preonensis*, and 182% for *M. endennae*), comparable to that of bats, or of dermopterans, both of which use pedal, or four limb upside-down, suspension in roosting (Byrnes & Spence 2011). The pedal phalangeal index of *Megalancosaurus* is also comparable to that of some Jurassic gliding mammaliaforms (Meng et al 2017) and of Permian weigeltisaurids (Pritchard et al. 2021). This character may give further support

to the interpretation that despite the low curvature of the claw, *Megalancosaurus preonensis* was arboreal.

M. preonensis (Fig. 2A, B; 9A) had pincer-like, prehensile hands with opposable fingers like all *Megalancosaurus* specimen in which the hand is preserved, but non-prehensile feet. This pattern is rather unusual, since in most small climbing vertebrates which have only one pair of limbs with opposable digits, these are the hindlimbs as in tarsiers and marmosets among primates and *Petaurus*, *Acrobates* and other sugar gliders among marsupials (Shapiro et al 2014). In Anoles (Foster & Higham 2012), in the arboreal environment the forelimbs may play a more propulsive role than on the ground, however the hindlimbs (along with a prehensile tail,

if present) are the only way to ensure firm stability when moving from one support to another. When bridging the gap between two branches, the risk of falling is strongly reduced if the stability of a stiff trunk is provided by a firm grip on the original substrate with the feet. For this reason, the presence of prehensile feet ensuring a firm grasp is more important than the ability to grasp with the hands. Unless some kind of fleshy pad was present in life, as in the pigmy anteater, it is feasible that the lack of an opposable hallux in *M. preonensis* may have limited its mobility on narrow substrates, while on larger surfaces like tree trunks and large branches, it could have climbed up and down with ease given the high mobility of the coxofemoral joint, as testified by the shallow acetabulum and the subspherical proximal head of the femur, along with the possibility of hind foot reversal (Cartmill 1985).

Megalancosaurus endennae (Fig. 5A, 8B, 9B) had an opposable, clawless hallux as it occurs in many small arboreal mammals like basal primates, plesiadapiforms and marsupials (Bloch & Boyer 2002; Lemelin 1999; Szalay 1988).

In Anoles, the species that live on narrow perches have shorter limbs to lower the center of mass and avoid the risk of tumbling from the support (Losos 1990, 2009; Losos et al. 1997). The length of the metatarsal plus the phalanges of the third pedal digit in *M. preonensis* (15.6 mm) reaches approximately 90% the length of the tibia (Fig. 9C), while in *M. endennae* the length of third metatarsal and pedal digit (19 mm) is greater than that of the tibia (14.5 mm), reaching the 130% of the length of the tibia. Thus *M. endennae* had a proportionally longer pes and a shorter crus than *M. preonensis* (Fig. 9C, D), and could have been able to lower its center and this along with better grasping abilities than *M. preonensis* rendered this species better suited for bridging between tree twigs.

The stout process on the ventral margin of the first phalanx of the hallux in *M. endennae* may have housed the insertion of a strong flexor hallucis longus ensuring a very strong grip on narrow supports. This muscle originates from the posterior surface of the fibula and usually ends on the ventral margin of the last phalanx of the hallux, however in marsupials with opposable clawless halluces, the terminal phalanx may be greatly reduced (e. g. Black et al. 2012), and the flexor hallucis longus is inserted more proximally on the metatarsal

(Haughton 1864), it may therefore be hypothesized that also in *M. endennae* the muscle insertion was not on the reduced terminal phalanx but on the stouter first one. Studies on small arboreal mammals (Byron et al. 2011; Youlatos et al. 2018) show that prehensile hallucal grasping assured by an opposable hallux represents a significant advantage for agile locomotion on small narrow twigs with different orientations by providing an effective clamp that creates strong frictional resistance and torsional forces that can counterbalance the torque due to possible shift of the center of mass out of the substrate axis. This frictional resistance exerted by the hallux is extremely effective to counter the effects of gravity while clinging with a claw it is less useful, and this could explain the loss of the claw on the hallux, replaced by a nail, which occurs in arboreal marsupials like sugar gliders such as *Petaurus* (Fig. 10C) or *Acrobates* and also in some primates like marmosets (Haines 1958). For instance the small marsupial *Acrobates pygmaeus*, whose size (70-80 mm of body length, with a tail approximately as long as the body) is smaller than that of *M. endennae* (about the same size of *Vallesaurus*), employed mainly hallucal grasping when moving on small substrates with different orientation (Youlatos et al. 2018). The same model of locomotion may be hypothesized for *M. endennae*.

Locomotion on large and vertical substrate are seldom performed or even avoided by *Acrobates*, but if the animal has to move on similar substrates, as for other arboreal marsupials with the same pes structure, it performs usually an “abducted grasping” (Fig. 10D) that is grasping by abduction and extension of toes and hallux, and clinging mainly with the claws.

The post-mortem contraction of the hallux resulting in a strong dorsal hyperextension in both *M. endennae* specimens may suggest the presence of a robust extensor digit 1 muscle (*sensu* Diogo & Molnar 2014) that may have enabled *M. endennae* to apply a similar “abducted grasping” pattern on large substrates, avoiding the interference of the rather stiff, sickle-shaped hallux by keeping it extended while clinging with the sharp and recurved claws of toes 2-5.

The stouter and more recurved fibula of *M. endennae* with respect to *M. preonensis* may indicate that the iliofibularis and peroneus brevis muscles had to be more developed in *M. endennae*.

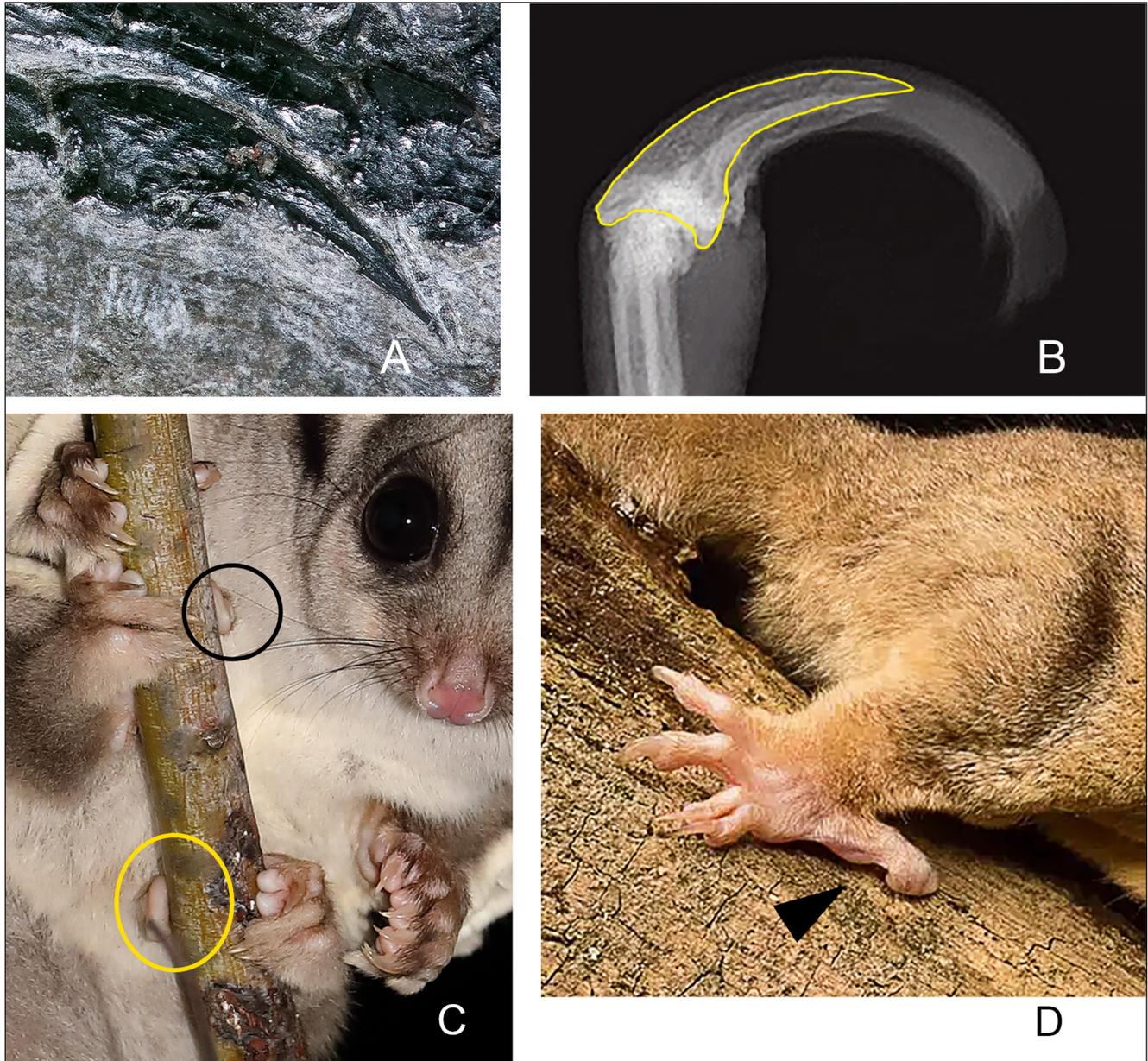


Fig. 10 - A) Ungual phalanx of the pes of *M. preonensis* MPUM 8437; B) unguis phalanx of the manus of *Choloepus didactylus* (outlined in yellow) from a X ray photo showing also the keratinous sheath. Figures not to scale. C, D) Details of the feet of extant specimens belonging to the genus *Petaurus* grasping on narrow substrate (C), and performing abducted hallucal grasping on larger substrate (D). The ellipses in C and the triangle in D indicate the opposable hallux bearing a flat nail instead of a claw. B, modified from Gough-Palmer et al. (2008); C, modified from a photo of Patrick Kavanagh (CC Creative Commons free use) D, modified from Australian Geographic. Figures not to scale.

The iliofibularis is a knee flexor and the peroneus brevis is an ankle extensor that helps to maintain stability and balance when grasping different narrow twigs with spread limbs (Foster & Higham 2012); Foster & Higham (2012) reported that in the lizard ecomorphs that move usually on very small diameter surfaces like narrow twigs, the knee joint performs a quicker flexion that requires a stronger iliofibularis muscle than in lizards that walk on larger substrates.

Indeed, in Cuban anoles the muscles involved in knee flexion (*m. flexor tibialis internus posterior* and *m. iliofibularis*) are more developed in arboreal species (Anzai et al. 2014). The flexor tibialis internus posterior is inserted on the medial side of the proximal head of the tibia which is more expanded in *M. endennae* (Fig. 11B) than in *M. preonensis* which has a distinctly narrower proximal head of the tibia (Fig. 11A).

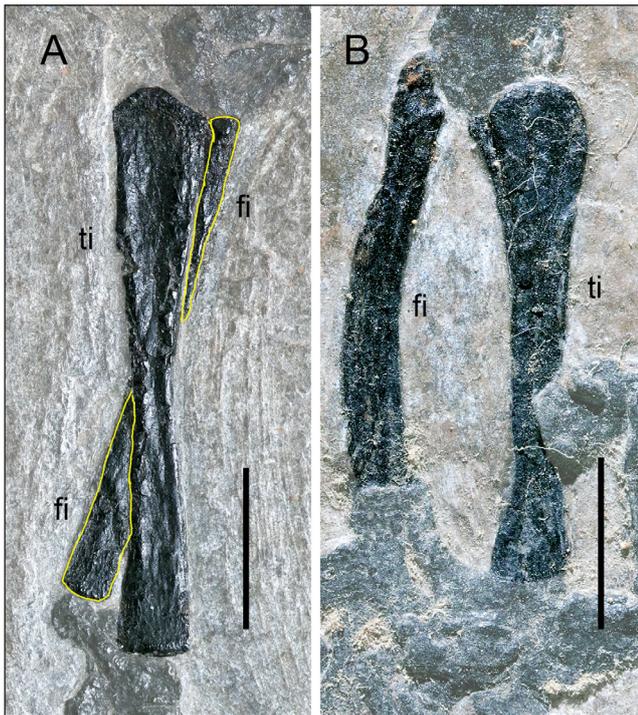


Fig. 11- Comparison between the tibia (ti) and fibula (fi) of *Megalancosaurus preonensis* MPUM 8437 (A), and of *Megalancosaurus endennae* MBSN 25 (B). The exposed portions of the fibula of *M. preonensis* has been outlined in yellow. Contrast on other bones has been digitally reduced for clarity. Scale bars equal 5 mm.

CONCLUSION

The difference in the anatomy of the hindlimb skeleton above described for *M. preonensis* and *M. endennae* supports the hypothesis that the two species may have exploited different microhabitats in the arboreal environment. *M. endennae*, thanks to its stronger hindlimb musculature and to the presence of an opposable clawless hallux may have been better adapted to locomotion among intricate narrow twigs, being also able to exploit a wider variety of microhabitats (Lemelin 1999) It is thus feasible that, like in several small arboreal mammals, the grip provided by an opposable clawless hallux allowed *M. endennae* to apply an effective torque to keep its center of mass aligned to the substrate during locomotion on narrow supports ensuring also the required stability for bridging or manipulate items with the hands. In addition, the recurved claws of the other four pedal digits represent an adaptation to cling effectively, increasing the actual central angle for a wider support surface (Cartmill 1985).

M. endennae may have been also able to walk more effectively on a wide variety of substrates,

using abducted grasping on larger substrates, and a strong grip on narrower supports like terminal branches (Fig. 12), thus *M. endennae* may have been a more active forager than *M. preonensis*.

M. preonensis instead may have preferred, or was mainly confined to, larger supports where the long, but less curved, pedal claws that are less effective for interlocking in small irregularities or crevices of small substrates, may have been effective for clinging or as hooks, even hanging upside-down like in sloths or dermopterans. *M. preonensis* may eventually have assumed a stable head-down posture by clinging with the claws with a reversed hind foot posture, further stabilized by clinging also with the hook at the end of the prehensile tail: the stiffness of the tail and the robust stiff “hook” formed by the terminal spine (functionally identical to a claw) may even have allowed in both species hanging by the tail with less muscular effort than in chameleons or other vertebrates with less stiff and hook-less prehensile tails, such as New world primates that can use the tail as a fifth limb to secure themselves (Xu & Gray 2017). In such a tripod stance *M. preonensis* could have freed the prehensile hands to catch small invertebrates with a snapping motion, (Castiello et al. 2015) in a praying mantis like fashion (Fig. 12). Praying mantises capture their preys with a “strike” (Roeder 1959), that is a rapid grasping movement of their specialized fore-legs.

Catching the prey by a fast striking of a portion of the body, requires a precise estimate of its distance and position, thus a three dimensional vision and eye-limb coordination is required. Chameleons can move each eye independently and use monocular vision to check the environment and locate potential prey. Once the prey is approached, both eyes focus independently on the prey and eye accommodation is coupled just before projecting the tongue (Harkness 1977; Ott et. al 1998; Ott 2001).

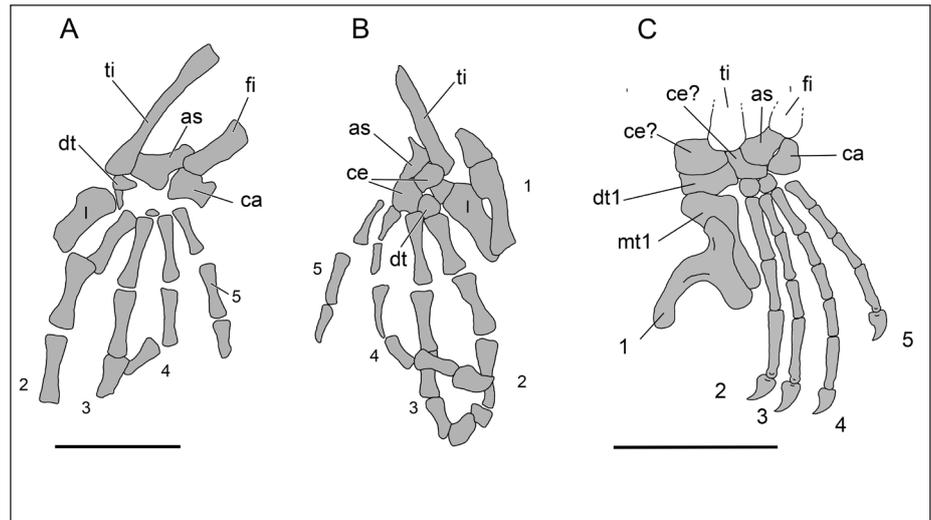
Even in the praying mantis, which compound eyes are fixed, the exact position and distance of a prey is estimated with quick saccades of the whole head (Mittelstaedt 1957; Lea & Mueller 1977; Rossel 1980) that allow a sort of binocular triangulation (Rossel 1986). *Megalancosaurus* had proportionally very large eyes that, as in chameleons could have been protruding laterally and also oriented forward, eventually allowing binocular vision, unimpeded by the very narrow, pointed snout (Renesto & Dalla Vecchia 2005). Ob-



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Fig. 12 - Left, *Megalanosaurus proemius* reconstructed with a dragonfly seized by the anterior limbs while clinging upside down to the tree bark with its claws and with the terminal hook of the tail. Right, *Megalanosaurus endimae* reconstructed in tripod stance grasping the twigs and secured also by the hooked tail.

Fig. 13 - A-B) drawing of the tarsus and pes as preserved in *Dolabrosaurus aquatilis* holotype, specimen CM 28589; A, left pes, B, right pes, both in dorsal view (bones identification according to Renesto et al 2010); C) Drawing of the pes of *Vallesaurus cenensis* holotype specimen MCSNB 4751, as reconstructed in Renesto & Binelli (2006). Abbreviations are as, astragalus; ca, calcaneum; ce, centrale; dt, distal tarsals; fi, fibula; ti, tibia; I metatarsal; 1-5 pedal digits. Scale bar equals 1 cm in A, B and 5 mm in C.



viously it cannot be ascertained if *Megalancosaurus* had an independent chameleon-like eye accommodation ability or instead had a true stereoscopic vision, but the inflated, almost bird-like, postorbital region of the skull is suggestive of a developed brain area for vision and eye-limb coordination, that may have enabled precise spotting and capture of the prey by grasping “strikes” of the pincer-like forelimbs.

It is also worth to notice that the morphology of the preserved elements of the hindlimb of the similarly sized drepanosauromorph *Dolabrosaurus aquatilis* Berman & Reisz, 1992, as redescribed by Renesto (1994) and Renesto et al. (2010), are nearly identical to that of *M. endennae*, in particular the similarities in the tarsus and pes are striking (Fig. 13A, B). *Dolabrosaurus* shares with both *M. endennae* and *M. preonensis* a L-shaped astragalus and calcaneum with pronounced lateral tuber, and with *M. endennae* it shares also a recurved shaft of the fibula with a wide spatium interosseum, along with a virtually identical opposable hallux with an elongate first phalanx and a much smaller, clawless terminal one (but the first metatarsal of *Dolabrosaurus* appears to be much larger than that of *M. endennae*). The hallux of *Dolabrosaurus* is also preserved in the same strongly hyper-extended position, suggesting a similar arrangement of flexor and extensor muscles allowing both a firm grip on narrow substrates and abducted grasping on larger ones.

Vallesaurus cenensis (Fig. 13C) is a very small drepanosauromorph with a clawless and opposable hallux in the pes (Renesto & Binelli 2006), that may have played a similar functional role; however, *Vallesaurus* hallux differs from those of *Megalancosaurus* and *Dolabrosaurus* in having only one elongate,

sickle-shaped phalanx, and also the morphology of the tarsus and pes is different from those of the former genera. The calcaneum of *Vallesaurus* lacks a distinct lateral process, distal tarsal I is enormous, larger than the calcaneum the first metatarsal is parallel to the others, it is elongate but much stouter than metatarsals 2-5, the first and only phalanx of the first pedal digit is strongly curved, with a distinctly concave ventral margin, while the dorsal margin bears a prominent process for extensor muscles (Fig. 13C). Ultimately, it can be concluded that the overall architecture of small drepanosauromorphs results to be strikingly similar to that of some small arboreal mammals (phalangeriids metatherians, small primates and extinct plesiadapiforms, Szalay & Dagosto 1988; Meng et al. 2017; Youlatos et al. 2018), and the name Simiosauria once proposed by Senter (2004) for the drepanosauromorph clade indeed reflected an actual adaptive convergence.

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