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VALLESAURUS CENENSIS WILD, 1991, A DREPANOSAURID (REPTILIA, DIAPSIDA) FROM THE LATE TRIASSIC OF NORTHERN ITALY

SILVIO RENESTO [1] & GIORGIO BINELLI [2]

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Abstract. *Vallesaurus cenensis,* a small drepanosaurid reptile from the Norian (Late Triassic) beds of the Calcare di Zorzino (Zorzino Limestone) is described. The holotype and only known specimen represents the first drepanosaurid in which the skull is preserved articulated with the postcranial skeleton. The study of *Vallesaurus* anatomy confirms previous data about arboreal adaptation in all known drepanosaurids and permits more firm hypotheses about the phylogenetic relationships of the Drepanosauridae to be proposed.

Riassunto. Viene descritto *Vallesaurus cenensis*, un piccolo rettile drepanosauride ritrovato nel Calcare di Zorzino, risalente al Norico (Triassico Superiore). L'olotipo, nonché unico esemplare conosciuto, rappresenta il primo drepanosauride in cui si sia ritrovato il cranio in articolazione con il resto dello scheletro. Lo studio di *Vallesaurus* conferma le ipotesi di specializzazione per la vita arboricola nei drepanosauridi e consente di formulare ipotesi più documentate sulle relazioni filogenetiche del gruppo.

Introduction

The family Drepanosauridae was erected by Olsen & Sues (1986) and first diagnosed by Berman & Reisz (1992). Of the taxa now included within the family, *Drepanosaurus* (Pinna, 1980) from the Calcare di Zorzino and *Megalancosaurus* (Calzavara et al. 1980) from the Dolomia di Forni and Calcare di Zorzino from the Norian (Late Triassic) of Northern Italy were the first to be described. Later, *Dolabrosaurus* from the Petrified Forest Formation, Chinle Group, New Mexico (Berman & Reisz 1992) and, most recently, *Hypuronector,* (informally known for many years as the "deep-tailed swimmer" Olsen 1980), from the Newark Supergroup (Colbert & Olsen 2001), were described. While these forms exhibit different sizes and slightly diverse body form, all share some very characteristic features that unequivocally demonstrate their close relationships (Renesto 1994a,b, 2000; Renesto & Fraser 2003). In addition, *Drepanosaurus* and *Megalancosaurus* both possess a curious claw-like terminal element on the tail. Such a feature has been inferred also for *Dolabrosaurus* (Renesto 2000).

On the basis of these detailed descriptions (Renesto 1994a,b, 2000; Colbert & Olsen 2001) of relatively complete drepanosaur specimens, it became possible to recognize isolated drepanosaur elements. As a consequence, Harris & Downs (2002) identified a characteristic drepanosaur shoulder girdle from the famed Ghost Ranch *Coelophysis* Quarry, and, more recently, Renesto & Fraser (2003) and Fraser & Renesto (2005) recognized isolated drepanosaur cervical vertebrae among the disassociated vertebrate assemblages of the Upper Triassic fissure deposits at Cromhall Quarry, England.

A small reptile from the Late Triassic Calcare di Zorzino (Northern Italy) labelled as specimen MCSNB 4751 of the Museo Civico di Scienze Naturali "E. Caffi" Bergamo (Italy), described here for the first time, has been regarded as a drepanosaurid different from *Drepanosaurus* and *Megalancosaurus* (Renesto 2000: fig. 11). It is of great interest because it represents the first drepanosaurid in which a nearly complete skull is preserved in anatomical connection with the entire post-

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[1] Dipartimento di Biologia Strutturale e Funzionale, Università degli Studi dell'Insubria, via Dunant 3, 21100 Varese, Italy.
E-mail: silvio.renesto@uninsubria.it;

[2] Dipartimento di Biotecnologie e Scienze Molecolari, Università degli Studi dell'Insubria, via Dunant 3, 21100 Varese, Italy.
E-mail: giorgio.binelli@uninsubria.it.

cranial skeleton, in fact the holotype of *Megalancosaurus* (Renesto & Dalla Vecchia 2005) has the skull preserved but lacks of most of the postcranial skeleton.

Systematic palaeontology

Reptilia

Diapsida Osborn, 1903

Drepanosauridae Olsen & Sues, 1986

Vallesaurus Wild, 1991

Vallesaurus cenensis Wild, 1991

Fig. 1, Pl. 1

Vallesaurus cenesis Wild, 1991; Pinna, 1993, p. 113

Nomenclatural issues. Specimen MCSNB 4751 was collected in 1975 by the staff of the Museo di Scienze Naturali of Bergamo. Just after preliminary preparation it was immediately obvious that it represented a new genus and species and was given to Rupert Wild for study with the agreement that the genus was to be named *Vallesaurus* in honour of the former director of the Museum, the late prof. Valle. The species had to be named *cenensis* after the small town of Cene (Val Seriana, Bergamo Italy), close to the locality in which the specimen was collected, also famed for having yielded pterosaurs (Wild 1978) and protorosaurs (Renesto 1994c).

Wild never published a description of specimen MCSNB 4751, only quoting the generic name *Vallesaurus* in a paper (Wild 1991), without giving any clue for identification of the specimen he was referring. Later, Pinna (1993) in a survey on Norian reptiles of Northern Italy, mentioned *Vallesaurus cenensis*, giving a catalogue number, thus allowing a firm identification of the specimen (Pinna 1993 p.113), and cited Wild as the author of the taxon. Subsequently, the name *Vallesaurus cenensis* was used in the museum postcards that figured specimen MCSNB 4751 and in other popular publications, so that the name become well known. Recently, Wild decided to hand on to others the detailed description of the specimen, and he and the Curator of the Paleontological Section of the Museo Civico di Scienze Naturali of Bergamo allowed us to study it. Since after Pinna (1993) the name *Vallesaurus cenensis* has always been associated to specimen MCSNB 4751 we propose here to keep it for the sake of stability, while leaving the authorship to Rupert Wild.

Fig. 1 - *Vallesaurus cenensis* Wild, 1991, specimen MCSNB 4751, scale bar equals 1 cm.

Holotype. Specimen MCSNB 4751, of the Museo Civico di Scienze Naturali "E. Caffi" Bergamo (Italy). It comprises a nearly complete, yet strongly compressed, articulated skeleton (Fig. 1), exposed on its left side.

Horizon and locality. Upper part of the Calcare di Zorzino (Zorzino Limestone), Norian, Late Triassic, collected in the quarry of Cene, Val Seriana, Bergamo, Lombardy, Italy.

Diagnosis. Small (16 cm total length) drepanosaurid reptile, with digit 4 of the manus as long as the humerus, tarsus with centrale reaching the tibia, modified distal tarsal and metatarsal, hallux clawless and opposable, with one arcuate phalanx. *Vallesaurus* differs from *Megalancosaurus* in the proportionally shorter and higher snout, the stouter and larger maxillary and dentary teeth, the shorter cervical vertebrae, the lack of fenestrated hemapophyses in the caudal vertebrae and the lack of fusion between the neural spines of the second and third dorsal vertebrae, as well as in the absence of elongate carpal and tarsal bones and opposable or modified digits in the manus. *Vallesaurus* differs from *Drepanosaurus* in the lack of the massive claw of the second digit of the manus and differs from *Drepanosaurus*, *Megalancosaurus* and possibly *Dolabrosaurus* in the lack of a terminal spine at the end of the tail. *Vallesaurus* differs from *Hypuronector* in having anteroposteriorly expanded neural spines of the anterior dorsal vertebrae and anterior limbs much shorter than the posterior ones.

Measurements taken on the specimen. Humerus length: 10 mm; radius length: 6 mm; ulna length: 6 mm; femur length: 13 mm; tibia length: 9 mm; third metatarsal length: 3 mm; height of the scapular blade 13 mm; height of the largest dorsal vertebra, 9 mm.

Description

Skull. The skull (Fig. 2, Pl. 1A) is subtriangular and appears quite high in lateral aspect, (but this is partially due to the compression of the specimen), with elongate, semi-elliptical nares, large orbits, a pointed snout region, and a short but wide temporal region. The snout region seems much shorter than in *Megalancosaurus* but this is probably due to the crushing of the anterior tip of the lower jaw and the disarticulation of the premaxillae. The skull has been completely flattened and partially crushed during fossilization, so that the left side of the snout shifted posteriorly with respect to the right and, in addition, the right half of the snout region is nearly completely crushed, while the left side of the skull roof is visible in dorsal aspect. Some bones of the braincase and of the palate are exposed on the lateral surface of the skull, rendering the identification of several skull elements difficult.

Each premaxilla shows a long and narrow medial process that runs dorsally between the nasals. Posteriorly the premaxillae extend as bear an elongate process passing dorsal to the maxilla and forming at least one third of the anteroventral margin of the wide nasal opening. The premaxillary teeth are small and triangular, about one half the height of those borne by the maxilla. Due to crushing of the tip of the snout, it is not possible to establish how many teeth were borne by the premaxilla. The left maxilla is partially preserved; it is a wide, subtriangular bone, with a very high dorsal process and concave anterior and posterior margins. Posteriorly the bone forms a narrow process which runs ventral to the anterior portion of the jugal. At least 12 teeth are present on the ventral margin of the maxilla. The maxillary teeth are large with respect to the overall size of the skull, their dimensions vary along the series, with bigger teeth alternating with smaller ones. They are laterally compressed, triangular in shape, with a wide base and the better preserved ones bear sharply pointed tips and teeth implantation is subthecodont. The nasals are elongate with a narrow anterior portion forming most of the dorsal margin of the nasal opening, and a deep ventral process contacting the anterior margin of the maxilla and surrounding the posterior margin of the nasal openings. The jugal is a narrow, crescent

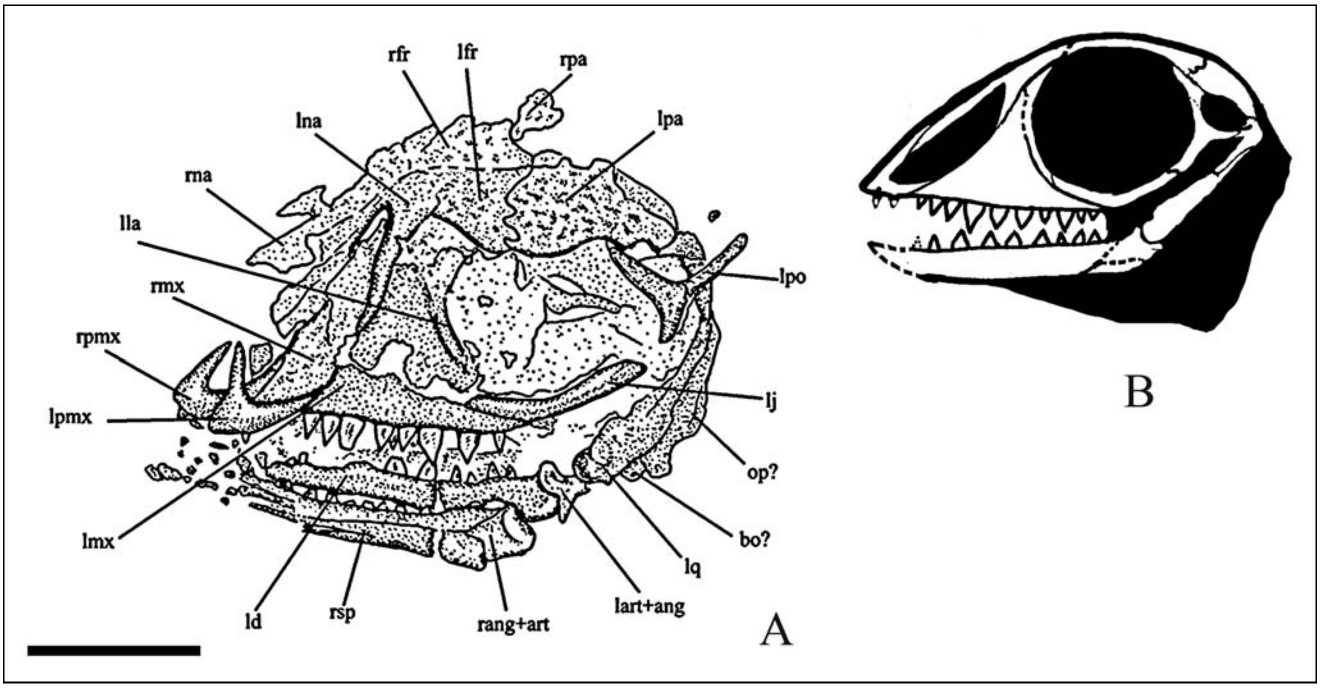

Fig. 2 - *Vallesaurus cenensis* Wild, 1991, specimen MCSNB 4751. Skull A) as preserved, scale bar equals 0.5 cm; B) tentative reconstruction. Abbreviations are: lart+ang) left articular and angular; rart + ang) right articular and angular; bo?) basioccipital?; ld) left dentary; lj) left jugal; lfr) left frontal; rfr) right frontal; op?) opistotic?; lmx) left maxilla; rmx) right maxilla; lna) left nasal; rna) right nasal; lpa) left parietal; rpa) right parietal; lpo) left postorbital; lpmx) left premaxilla; rpmx) right premaxilla; lq) left quadrate; rsp) right splenial.

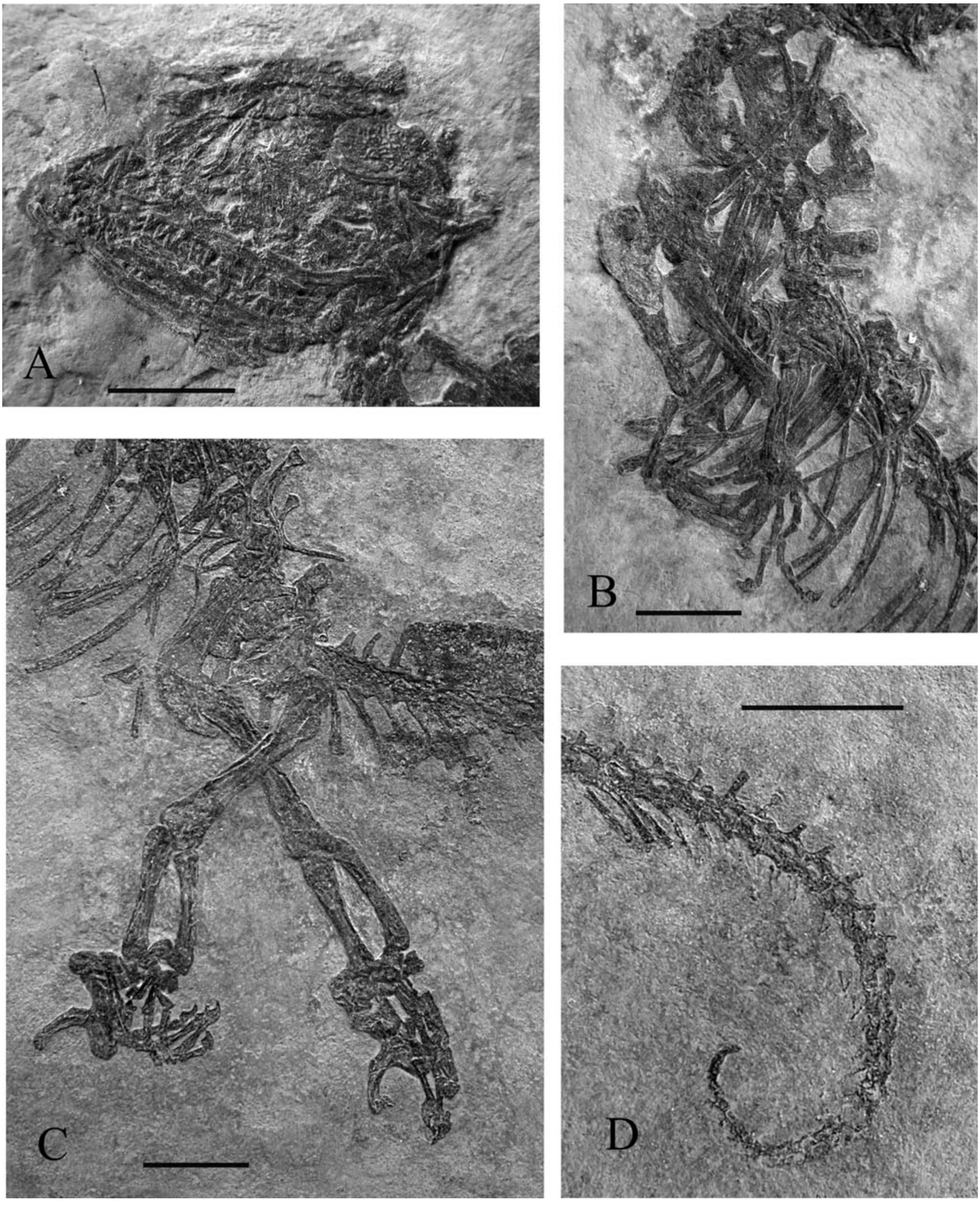

PLATE 1

Vallesaurus cenensis Wild, 1991, specimen MCSNB 4751, holotype A) skull; B) neck anterior trunk region and anterior limb; C) pelvic girdle and posterior limb; D) end of the tail. Scale bars equal 0.5 cm.

shaped bone, that extends well beyond the posterior end of the maxilla forming an elongate, dorsally directed process inclined at about 45°. The posterior margin of the jugal is gently convex, and no traces of a quadratojugal can be detected. However, preservation in this area is poor and there is a hole in the slab just at the posterior corner of the jugal. It is therefore difficult to establish unequivocally if the quadratojugal was absent. The postorbital is triradiate, its ventral process contacts the jugal and its dorsal margin is gently embayed where it borders the upper temporal fenestra. The frontals are deformed and overlapped by nasals in their anterior portion. Their overall shape is subtriangular, with a narrow anterior portion where they form the dorsal margin of the orbits, and becoming much wider posteriorly. The left parietal is well preserved, while only scraps of the right parietal are present. The parietal is a wide, thick and flat bone and its dorsal surface is deeply sculptured by grooves and pits; its anterior margin forms a zigzag suture with the frontal, while the medial articulation with its counterpart is nearly straight, aside from a small notch in the middle that might represent a pineal foramen. More posteriorly the lateral process of the parietal is crushed and partially overlapped by the posterior ramus of the postorbital, thus the suture with the squamosal cannot be detected. Apart from the heavily sculptured surface, the overall shape of the parietal is similar to that reported for *Megalancosaurus* (Renesto 2000; Renesto & Dalla Vecchia 2005). The squamosal is narrow with a well developed ventral process that meets the quadrate. This latter bone is very elongate and narrow, superficially recalling that of pterosaurs. Its posterior margin is straight, lacking the embayment for the tympanum that is present in most lepidosaurs. The articular area for the lower jaw is small and ball-like. Some remains of bones belonging to the palate and braincase are partially visible but poor preservation does not permit a description.

Lower jaw. The anterior tip of the lower jaw is crushed into small splints of bones. The left and right ramii of the lower jaw are disarticulated and the right ramus, exposed on its medial surface, has shifted ventrally with respect to the right one. The dentary is a long and robust bone, but only its middle and posterior thirds are preserved, where it bears triangular, sharp and laterally compressed teeth of unequal sizes. The teeth are slightly smaller than the largest maxillary teeth. Most teeth are broken, so that it is impossible to give a reliable count. On the right ramus of the mandible, a long and thin splenial can be saw. The angular and the surangular are very short, and no coronoid process is present. The articular forms a simple concave articular area for the quadrate, and no retroarticular process is developed.

Vertebral column. The vertebral column consists of 8 cervical, ?16 dorsal, 2 sacral and up to 57 caudal vertebrae. The atlas axis complex cannot be observed in detail. In cervicals 3-8, the centra are longer than high (Fig. 3, Pl. 1B) and bear a long keeled hypapophysis on their caudoventral surface, which extends well beyond the intercentral articulation, reaching the middle of the following centrum. The zygapophyses show distinct necks, with convex and expanded, buffer-like, distal ends that are inclined toward the vertical plane. In the cervical series, the articulation between the pre- and post-zygapophyses lies well forward with respect to the intercentral articulation. As already noticed for other drepanosaurids (Renesto 1994a, 2000; Renesto & Fraser 2003), such an arrangement probably hindered lateral mobility of the neck, while permitting dorsoventral flexion. The neural arch is high and bears a small anteriorly inclined neural spine, which is visible mainly in the anteriormost vertebrae. The morphology of the cervical vertebrae of *Vallesaurus* is very similar to that of *Drepanosaurus* and of the isolated cervical vertebrae found in the Cromhall fissure infillings originally described by Fraser (1988) and now considered to be drepanosaurid (Renesto & Fraser 2003; Fraser & Renesto 2005).

The transition from the cervical to the dorsal series (Fig. 3, Pl. 1B) is marked by an abrupt change of the vertebral morphology. The dorsal vertebrae lack hypapophyses and bear narrower, pointed zygapophyses, high neural arches and very high neural spines. At least 16 dorsal vertebrae can be detected, but due to disarticulation, some vertebrae are either superimposed on others or obscured by other bones, rendering a reliable count difficult. The first dorsal vertebra bears a narrow and high neural spine, and the following 3 vertebrae are highly modified to form a notarium-like structure as seen in *Drepanosaurus, Megalancosaurus* and *Dolabrosaurus*. The neural arch of dorsal vertebrae 2-3 is very high and anteroposteriorly expanded, and the neural spine of the fourth dorsal vertebra shows the same craniocaudally expanded, fan-like outline, but it is smaller than the preceding ones. This notarium-like structure forms a distinct “hump” in the vertebral column. At least one subtriangular "supraneural" bone is present above the expanded neural spines of the second and third dorsal vertebrae: such supraneural elements are known to occur in *Drepanosaurus* and in *Megalancosaurus* (Renesto 2000). Starting from the fifth dorsal vertebra, the neural spines become much narrower anteroposteriorly, but remain more than three times taller than long.

The sacral vertebrae are mostly covered by elements of the pelvic girdle and bear low neural spines as in *Drepanosaurus* (Pinna 1984; Renesto 2000) and *Dolabrosaurus* (Berman & Reisz 1992). Up to 57 caudal

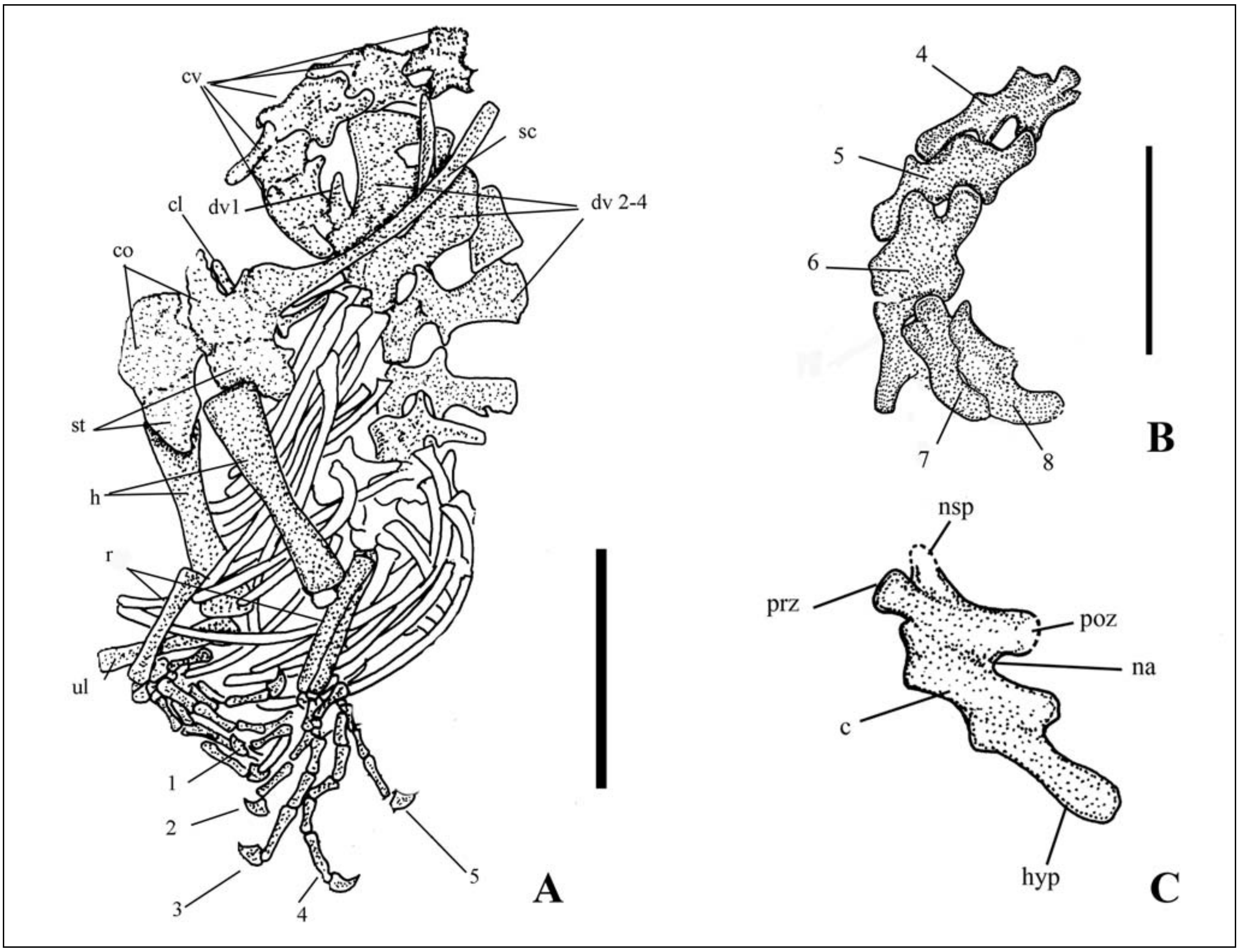

Fig. 3 - *Vallesaurus cenensis* Wild, 1991, holotype. A) Anterior dorsal vertebrae and ribs, shoulder girdle and forelimbs as preserved; B) cervical vertebrae 4-8 as preserved,. C) reconstruction of the fourth cervical vertebra shown on its left side. Scale bar equals 0.5 cm. Abbreviations are: c) centrum; cl) clavicle; co) coracoid; cv) cervical vertebrae; dv) dorsal vertebrae; h) humerus; hyp) hypapophysis; na) neural arch; nsp) neural spine; poz) postzygapophysis; prz) prezygapophysis; r) radius, sc) scapula; st) sternal plates; u) ulna; 1-5) digits 1-5.

vertebrae are visible, but, again, it is difficult to give a precise count because some parts of the tail are covered by patches of fossilized skin and, close to the tip of the tail, a small section of the tail is missing. The caudal centra (Fig. 4) are slightly constricted towards the middle, the zygapophyses are positioned very close to the midline, and the articulation surfaces are oriented close to vertical. Typically the prezygapophyses extend over at least half the length of the centrum of the preceding vertebrae. This pattern gives the vertebrae the appearance of being strongly "inclined" anteriorly as occurs in the isolated Cromhall material (Fraser & Renesto 2005). By contrast, the neural spines of the first three caudal vertebrae are lower than the following ones and inclined posteriorly. Starting from the fourth caudal vertebra, the neural spines become very high and narrow, being at least four times taller than wide, and only slightly expanded at their tip. The height of the neural spines decreases slightly along the caudal series until around the thirtieth vertebra, where the neural spines become abruptly very low and, in the following caudals, they shift more and more posteriorly until they lie just above the bases of the postzygapophyses. The haemal spines are fused with the posterior edge of the centrum; they are narrow and longer than neural spines, being more than four times deeper than wide with only slightly expanded distal tip. The main axis of the haemal spines is deflected backward, which further enhances the angled orientation of the vertebrae so that their ventral ends lie ventral to the succeeding centrum. The overall morphology of the proximal and mid caudal vertebrae resembles that of *Hypuronector* but, according to the description by Colbert & Olsen (2001), in the latter genus the haemapophyses are proportionally much longer and end with narrower tips. The last 17 caudal vertebrae bear very small haemal spines so that the tail becomes cylindrical and the zygapophyses are relatively large and with vertical orientation of the articular surface. The end of the tail is curled ventrally (Fig. 4, Pl. 1D) and, in contrast with *Megalancosaurus* and *Drepa-*

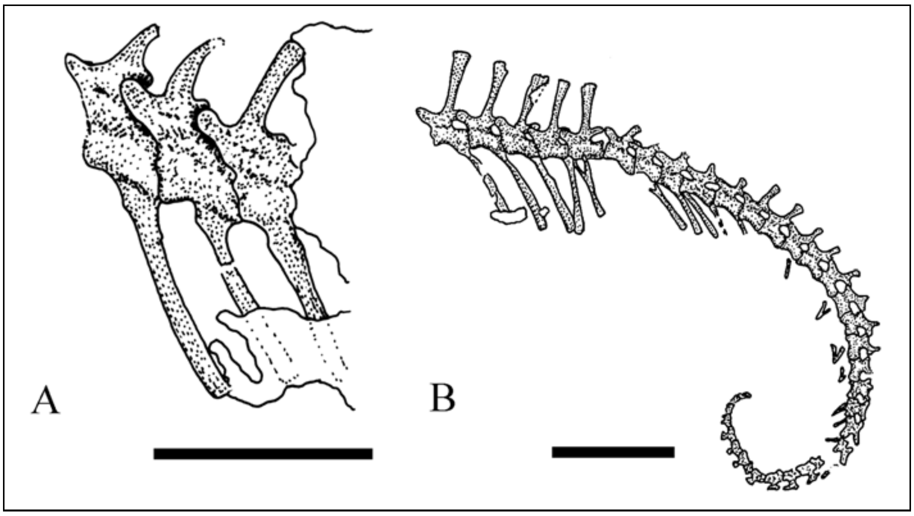

Fig. 4 - *Vallesaurus cenensis* Wild, 1991, holotype. A) proximal caudal vertebrae; B) the tip of the tail. Scale bars equal 0.5 cm.

nosaurus (Pinna 1984; Renesto 2000), no terminal hooked spine is present. The pronounced ventral curling of the distal tail, suggests it may have been prehensile, as in chameleons.

Ribs. Cervical ribs are absent as in other drepanosaurids in which the neck is preserved (Renesto 1994a, 2000). The dorsal ribs are gracile and single headed and their main axis follows a nearly semicircular path so that the trunk had the barrel-shaped appearance of other drepanosaurids. While most ribs are disarticulated, in the last two to three dorsal vertebrae they are still firmly attached to the centra, while in *Megalancosaurus Dolabrosaurus* and *Hypuronector* they are fused to the centra for almost the entire posterior half of the trunk (Renesto 1994a; Berman & Reisz, 1992; Colbert & Olsen 2001). Gastralia are absent, as in other drepanosaurids.

Pectoral girdle. The pattern of the pectoral girdle (Fig. 3, Pl. 1B) is typical for drepanosaurids. The coracoids are thin and flat, the glenoid lies at their posterodorsal end but due to flattening it is impossible to ascertain its orientation. Paired sternal plates are present, fused to the posterior end of the coracoids, as already suggested by Renesto (2000) for *Megalancosaurus* and by Harris & Down (2002) for the isolated pectoral girdle from the Chinle Formation. The scapula shows a small expanded ventral region and a very high and narrow, rod-like, scapular blade that is gently curved medially so that its dorsal tip points anteriorly. No interclavicle is preserved, while a small crescent shaped bony structure just anterior to the coracoids may represent the closely associated, furcula-like clavicles that occur in the isolated drepanosaurid pectoral girdle from the Chinle Formation (Harris & Down 2002).

Anterior limb. The humerus (Fig. 3, Pl. 1B) is a straight bone with a narrow shaft and expanded proximal head. The proximal articular surface is slightly concave, which is consistent with the structure of the glenoid articulation. At its distal head a depression could represent the olecranon notch. No entepicondylar or ectepicondilar foramina are present. The radius and ulna are straight bones lying close to each other. The ulna is

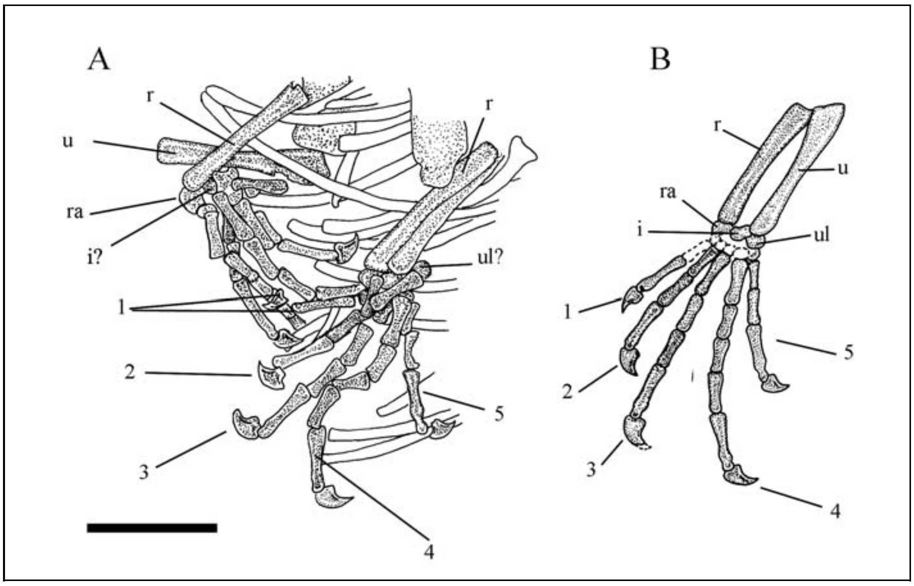

Fig. 5 - *Vallesaurus cenensis* Wild, 1991, holotype. A) Left and right manus as preserved; B) tentative reconstruction. Scale bar equals 0,5 cm. Abbreviations are: i) intermedium, r) radius; ra) radiale; u) ulna; ul) ulnare; 1-5) metacarpals and digits 1-5.

longer than the radius and more robust with an expanded proximal head bearing a small olecranon. It is difficult to reconstruct the pattern of the carpus because the carpal elements are partially disarticulated and obscured by overlapping ribs in both anterior limbs (Fig. 5, Pl. 1B). A small squared element just distal to the right radius is probably the radiale, while a subrectangular element medial to the latter element is identified here as the intermedium. A narrow, rod-like bone close to the lateral margin of the right ulna appears similar to the elongate ulnare of *Megalancosaurus* (Renesto 1994a, 2000), but it could also be a misplaced metacarpal. Some rounded distal carpals are visible in both hands. The metacarpals are moderately elongate, featureless rod-like bones, the fourth being the longest one. The digits are also elongate, the phalangeal formula is: 2, 3 4, 5, ?3. The ungual phalanges have the shape of small, but stout and sharp, claws, which are laterally compressed and bear a well developed ventral process for the insertion of strong flexor muscles. The penultimate phalanx of each digit is at least two times longer than the preceding ones. No opposable digits are present in the manus, while the third and fourth digits are very elongate, the fourth one being as long as the humerus.

Pelvic girdle. The right and left halves of the pelvic girdle are disarticulated (Fig. 6, Pl. 1C), the left half rotated on the horizontal plane so that it is exposed on its medial side and reversed with the pubis facing caudally. The small pubis is closely associated to the subrectangular, posteriorly elongated ischium, forming a broad puboischiadic plate. On the left half of the pelvic girdle a very small opening could represent the thyroid fenestra. The ilium bears a tall iliac blade, which is bent cranially as in all other drepanosaurids. The acetabular region is small and close to the cranial margin of the pelvic girdle as in *Megalancosaurus* and *Drepanosaurus* (Pinna 1984; Renesto 1994a, 2000).

Posterior limb. Due to the disarticulation of the pelvic girdle, the hind limbs are crossed over each other (Fig. 6, Pl. 1C), with the right femur running below the left one. Nevertheles, all the bones of the hind limbs are still in articulation. The femur is nearly twice as long as the humerus; it is a narrow bone with a nearly straight shaft, and a slightly expanded proximal head. The proximal articular surface is gently convex and close to the proximal head of the femur there is a well developed trochanter. The articular area for the tibia is distinctly concave and lies more proximally than that for the fibula, which is much smaller and nearly flat. The two articular surfaces are oriented nearly at a right angle with respect to one another.

The tibia and fibula are approximately one half the length of the femur. The tibia is slightly longer than the fibula and comprises a straight shaft, slightly con-

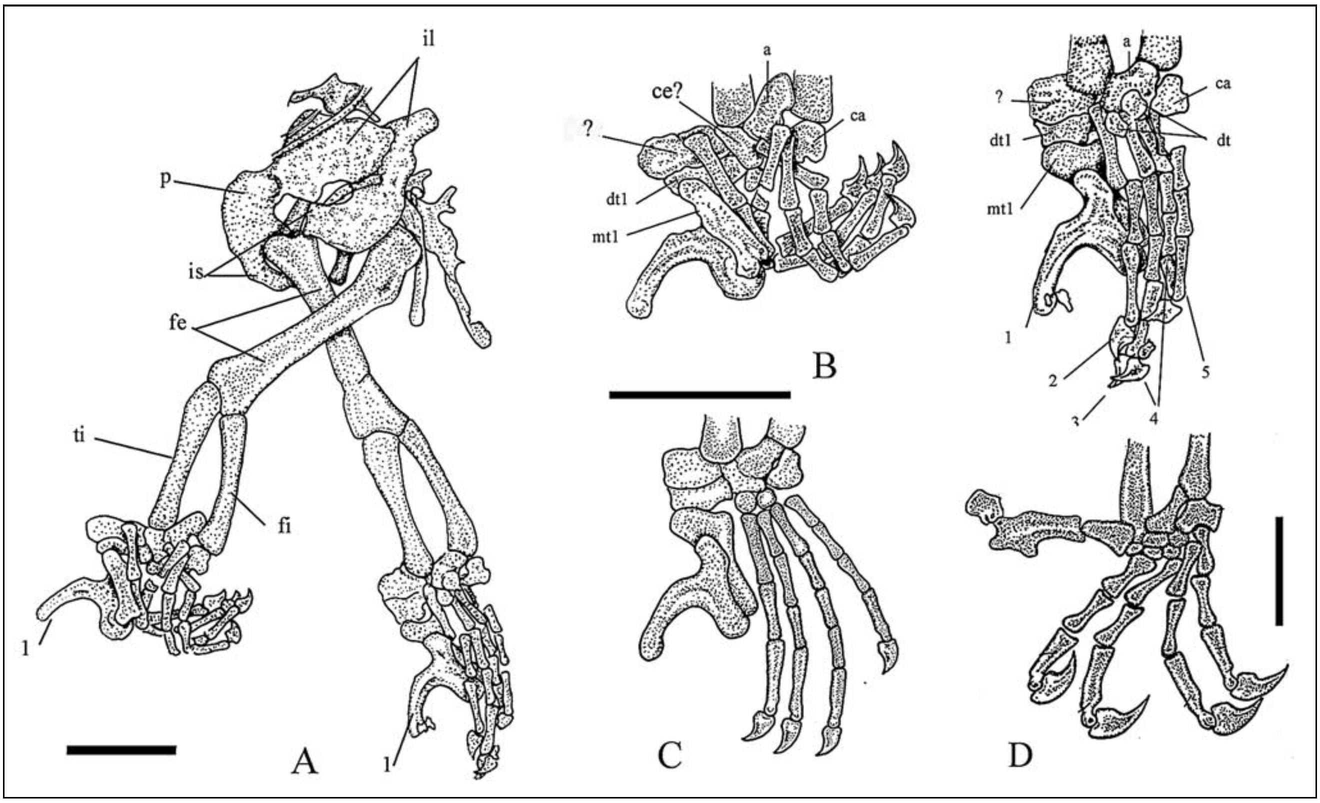

Fig. 6 - *Vallesaurus cenensis* Wild, 1991, holotype. A) Pelvic girdle and posterior limbs as preserved; B) left and right tarsus and pes in dorsal and plantar view, respectively; C) reconstruction of the pattern of the tarsus and pes in plantar view; D) reconstruction of the pattern of the tarsus and pes of *Megalancosaurus*, for comparison. Scale bar equals 0,5 cm. Abbreviations are: a) astragalus; c) calcaneum; ce?) centrale; dt) distal tarsal 1; fe) femur; fi) fibula; il) ilium; is) ischium); p) pubis; ti) tibia; 1) hallux; 1-5) digits 1-5; ?) unidentified bone.

stricted in the middle along with a very convex proximal articular surface and a nearly flat distal one. The fibula is narrow and has an arched outline, because its medial margin is concave while the lateral margin is convex, and both the proximal and distal articular areas are nearly flat. Due to the angled orientation of the articular areas for the femur, the shafts of the tibia and of the fibula diverge in their proximal halves. As a result of the curvature of the shaft of the fibula the two bones converge again distally surrounding a wide spatium interosseum. The left tarsus and pes (Fig. 6B-C) are exposed in dorsal view while the right tarsus and pes are exposed in ventral (plantar) view.

The calcaneum is a small squared bone lying at the laterodistal end of the fibula and the intermedium is more elongate and expanded at its distal end assuming a subtriangular or "L" shaped outline. Distal to the astragalus, a rectangular bone is visible on the left pes and based on topological considerations, it could be regarded as a centrale, that meets the distal head of the tibia, such is the condition in protorosaurs (Benton & Allen 1997). Lateral to the astragalus and the centrale, a wide subrectangular contacts the laterodistal end of the tibia. This bone bulges out from the tibia at a sharp angle and its presence is very probably related to the large and odd hallux, as detailed below, but its identification is problematical. Distal to this latter bone there is another subrectangular element of slightly smaller size, which, as in *Megalancosaurus* (Renesto 2000), could be distal tarsal 1. The pes of *Vallesaurus* seems similar to that of at least two *Megalancosaurus* specimens (Renesto 1994a, 2000; Fig 6 D), both sharing a modified opposable hallux, but the overall shape and structure and the number of the phalanges of the pes in *Vallesaurus,* is different, suggesting that similar features feature may have evolved independently in the two genera.

The hallux, along with the associated metatarsal, is the most peculiar feature of *Vallesaurus.* The first metatarsal is a stout bone, being at least twice the length and more than three times the width of the second and third ones, it is very similar to the one of *Megalancosaurus* (Fig. 6D), but it is not oriented at a square angle with respect to other toes as in the latter genus. Its proximal head is firmly attached to the wide distal tarsal 1 with a suture-like articulation so that little or no movement was allowed, while at its distal end a rounded, convex articular surface is present, forming a mobile joint with the peculiar single phalanx of the hallux. This latter bone has a hooked outline, again like in *Megalancosaurus*, but it also bears a stout dorsal process so that it looks like an asymmetrical "lambda", while in *Megalancosaurus* is present a ventral process (Fig. 6D). In both the right and left pes, the first digit is preserved as hyperextended lying right above the metatarsal, possibly due to the contraction of a very strong ligament, which was inserted in the dorsal process. A tiny patch of skin is present at the distal end of the right hallux, suggesting that no claw sheath was present. The hallux is also opposed to the other four toes, suggesting that its deep modification was very probably a grasping device. In *Megalancosaurus* a further tiny phalanx is also present, while *Vallesaurus* lacks it. Metatarsal and phalanges of toes 2-5 show a more "normal" appearance, being elongate, rod-like bones. Excluding the modified first metatarsal, the third is the longest one, while the longest toe is the fourth one. The phalangeal formula for the pes is 1, 3, 4, 5, 4. As in the manus, the penultimate phalanges are much longer than the preceding ones and the unguals form small, but stout and

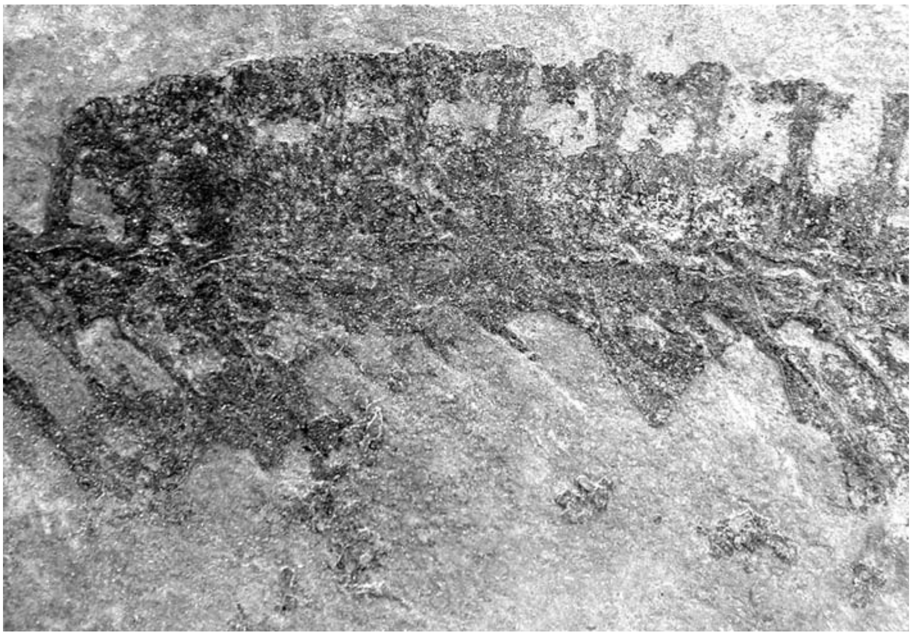

Fig. 7 - *Vallesaurus cenensis* Wild, 1991, holotype. Patches of fossilized skin in the caudal region. Scale bar equals 1 cm.

sharp, laterally compressed claws with well developed ventral processes for the insertion of flexor muscles.

Squamation. Patches of skin are preserved over the skull and especially over the tail (Fig. 7). The scales on the tail are thick with a rounded posterior margin and overlapping each other and rather lizard-like in appearance. The scales on the skull are smaller and apparently more granular. Unfortunately, no scales are preserved in the cervical and dorsal regions nor on the limbs, so that it is impossible to ascertain if any variation of the morphology of the scales occurred in these regions.

Functional adaptations and mode of life

Vallesaurus shares with all other known drepanosaurids a body architecture (Renesto 2000) indicative of a scansorial life-style, in particular, moving on narrow supports such as the twigs of trees. Evidence for arboreal adaptations in drepanosaurids have been detailed elsewhere (Renesto 1994a, b, 2000; Renesto & Paganoni 1995; Renesto & Fraser 2003; Fraser & Renesto 2005; Renesto & Dalla Vecchia 2005) and they will be only briefly summarized here: 1) high neural spines, testifying to the presence of a robust transversospinalis system and stiff trunk (Peterson 1971, 1984; Hildebrand 1974; Cartmill 1985; Tschanz 1986), 2) high and very narrow scapula (Peterson 1971, 1984), 3) modifications in the wrist and/or the ankle to allow rotation of the manus and or the pes (Jenkins & Mc Clearn 1984; Renesto 2000), 4) presence of opposable digits in the manus and/or the pes (Hildebrand 1974; Cartmill 1985; Renesto 2000), 5) penultimate phalanges much longer than preceding ones (Unwin 1987, 1988; Unwin et al. 2000), 6) ungual phalanges forming long, sharp and laterally compressed claws with well developed ventral processes for the insertion of flexor muscles and laterally expanded structures testifying to the presence in life of very long keratinous sheaths (Hildebrand 1974; Cartmill 1985; Bennett 1997; Renesto 2000), 7) high iliac blade anteriorly directed (Peterson 1971, 1984; Hildebrand 1974), 8) tail mobile mostly in the vertical plane but stiff in the lateral plane (Renesto 1994a, 2000; Renesto & Fraser 2003; Fraser & Renesto 2005), 9) presence of prehensile structures at the end of the tail (Cartmill 1985).

Vallesaurus and other drepanosaurids (with the possible exception of *Hypuronector,* Colbert & Olsen 2001) possess a notarium-like structure in the anterior dorsal region and highly modified cervical vertebrae, with adaptations that limited lateral mobility and wide hypapophyses. Both structures indicate the presence of powerful muscles and ligaments for the extension of the neck, possibly suggesting a projectile feeding adaptation (Renesto 2000), in which the head was suddenly launched forward to catch prey and the limited lateral mobility prevented undesired torsions of the neck which could have dislocated the cervical vertebrae during the quick extension. In smaller drepanosaurids like *Megalancosaurus* and *Vallesaurus* such adaptations may be related to an insectivorous diet; the teeth of *Vallesaurus* seem well suited to cut or crush the tough exoskeleton of insects and other arthropods (Fig. 8).

Unlike in *Megalancosaurus*, the manus of *Vallesaurus* has no opposable fingers, however, the shape of the unguals and of the preungual phalanges, along with the length of the fingers, suggest good climbing abilities (Unwin 1987, 1988; Unwin et al. 2000) and the manus of *Vallesaurus* is very similar to that of the enigmatic diapsid *Longisquama insignis*, also considered an arboreal reptile (Sharov 1971; Unwin et al. 2000). Interestingly, the two taxa also share the presence of a fourth digit which is as long as the humerus (see below).

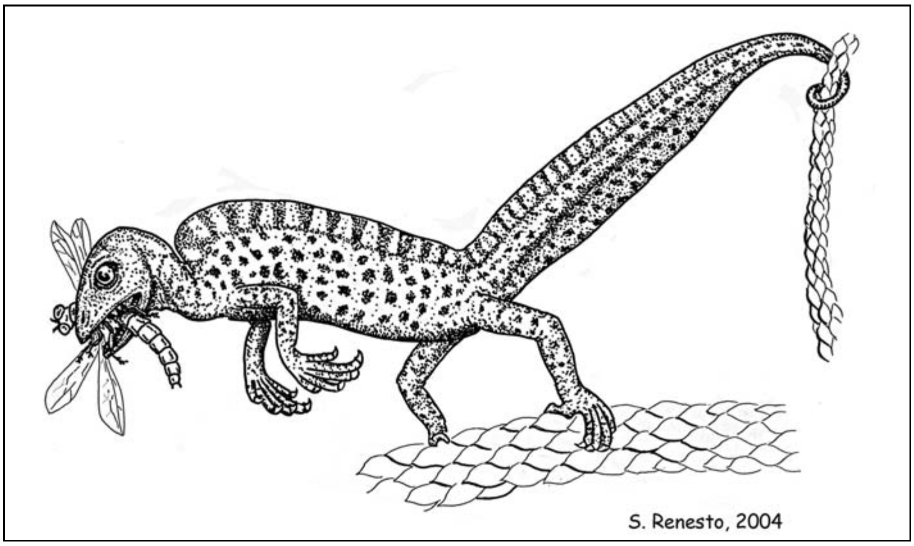

Fig. 8 - *Vallesaurus cenensis* Wild, 1991, hypothetical restoration of life appearance. The reptile is represented while feeding on a small odonate, standing on *Brachyphyllum* twigs, secured by the opposable halluces and by the prehensile tail.

The systematic relationships *of Vallesaurus*

Vallesaurus shares all the synapomorphies of the Drepanosauridae listed by Berman & Reisz, (1992), Renesto (2000), and Colbert & Olsen (2001). These include the very slender rod-like, vertically oriented scapula, dorsal vertebrae with high neural spines (sometimes expanded craniocaudally at their distal ends), exceptionally tall neural and haemal spines on the caudal vertebrae, caudal prezygopophyses considerably overlapping the centrum of the previous vertebra, and zygapophyses lying very close to the midline on the caudal vertebrae. Additional shared characteristics include: a barrel shaped trunk; ribs mostly holocephalous, slender, and triangular in section; gastralia absent; coracoid flat, somewhat expanded caudally; pelvic girdle with a high iliac blade, a rather narrow pubis and an ischium that is elongate caudally; femoral shaft lacking sigmoid curvature; tarsus and carpus modified to allow high mobility of both manus and pes (Renesto 1994a, b, 2000); fifth metatarsal straight and very long, narrow ungual phalanges with well developed flexor processes.

The main differences between *Vallesaurus* and other adequately known drepanosaurids may represent plesiomorphic character states, like the lack of opposable digits in the manus and of the hooked spine at the end of the tail. Of particular interest is the morphology of the ankle joint, with the tibia contacting the centrale, which other than reflecting the primitive condition for drepanosaurids, may be indicative of a close relationship between drepanosaurids and protorosaurs. Indeed, the contact between tibia and centrale is considered a synapomorphy of the latter clade (Benton & Allen 1997). In *Drepanosaurus* and *Megalancosaurus* the centrale is excluded from a contact with the tibia by an increase in size of the distal portion of the astragalus which in *Drepanosaurus* becomes eventually fused with the calcaneum. This trend which is apparently paralleled independently in lepidosaurs. If this interpretation is correct, *Vallesaurus* could be the most primitive drepanosaurid so far known, at least until better preserved specimens of *Hypuronector* become available.

Phylogenetic relationships of the Drepanosauridae

While it is widely accepted that the Drepanosauridae form a clade, their systematic position within diapsids remains uncertain. This is due partially to the highly derived condition of the postcranial skeleton and partialy to poorly preserved cranial material (completely missing in *Drepanosaurus*): Berman & Reisz (1992) considered drepanosaurids as lepidosauromorphs, while Renesto (1994a, b, 2000) suggested archosauromorph affinities. Analyses by Benton & Allen (1997) and Dilkes (1998) lent further support to the hypothesis that drepanosaurids were archosauromorphs, specifically closely related to Protorosauria (Prolacertiformes), an hypothesis also proposed by Rieppel et al. (2003) in their recent revision of this latter clade. More recently, Senter (2004) proposed a new phylogeny for drepanosaurids. He used a dataset including protorosaurs, archosaurs, birds and non-avian dinosaurs (but excluding pterosaurs) in his analysis in order to evaluate the claimed affinities between drepanosaurids and protorosaurs, and between *Megalancosaurus* and birds, these latter already questioned by Renesto (2000). Senter concluded that no avian synapomorphy is present in *Megalancosaurus* nor in any other drepanosaurid (as already suggested by Renesto 2000), but rather that the Drepanosauridae and the enigmatic Late Triassic diapsid *Longisquama insignis* (Sharov, 1971) are both closely related to the Permian Coelurosauravidae (Fig. 9A). Senter (2004) grouped these three taxa in a clade named Avicephala, which forms the sister taxon of Neodiapsida. Within Avicephala, the Simiosauria comprise *Vallesaurus* (cited as MCSNB 4751), *Hypuronector*, plus the Drepanosauridae, this latter taxon consisting of (*Drepanosaurus* (*Dolabrosaurus* + *Megalancosaurus*)). In conclusion, according to Senter's results, the Drepanosauridae should be considered as primitive diapsids, nested before the dichotomy between Archosauromorpha and Lepidosauromorpha.

However, it is our opinion that Senter's (2004) results may stem from uncertainty due to the lack of scoring of many character states for drepanosaurids (especially for the poorly known cranial characters) and, more importantly, from the exclusion of pterosaurs from his analysis. In our opinion, this exclusion from an otherwise large sample of diapsids seems unjustified. For this reason, we re-examined the relationships of the Drepanosauridae by updating and completing the matrix by Senter (2004). Initially, we added the basal pterosaur *Eudimorphodon* to Senter's original matrix (the published one contained some important typographic mistakes).

All datasets described and used for this analysis were resampled by bootstrapping 1000 times. The first analysis was made by the Wagner parsimony method as implemented by MIX of the PHYLIP 3.63 package (Felsenstein 2004). Since MIX does not allow for the coding of multistate characters, character 33 was recoded as suggested by Kluge and Farris (1969) into three two-state characters. In a second phase PARS of the same package was used to analyse all datasets, maintaining character 33 as multistate. Consensus trees were obtained in all cases by CONSENSE and were compared with each against all others by means of the Shimodaira Hasegawa (SH) test (Shimodaira & Hasegawa 1999).

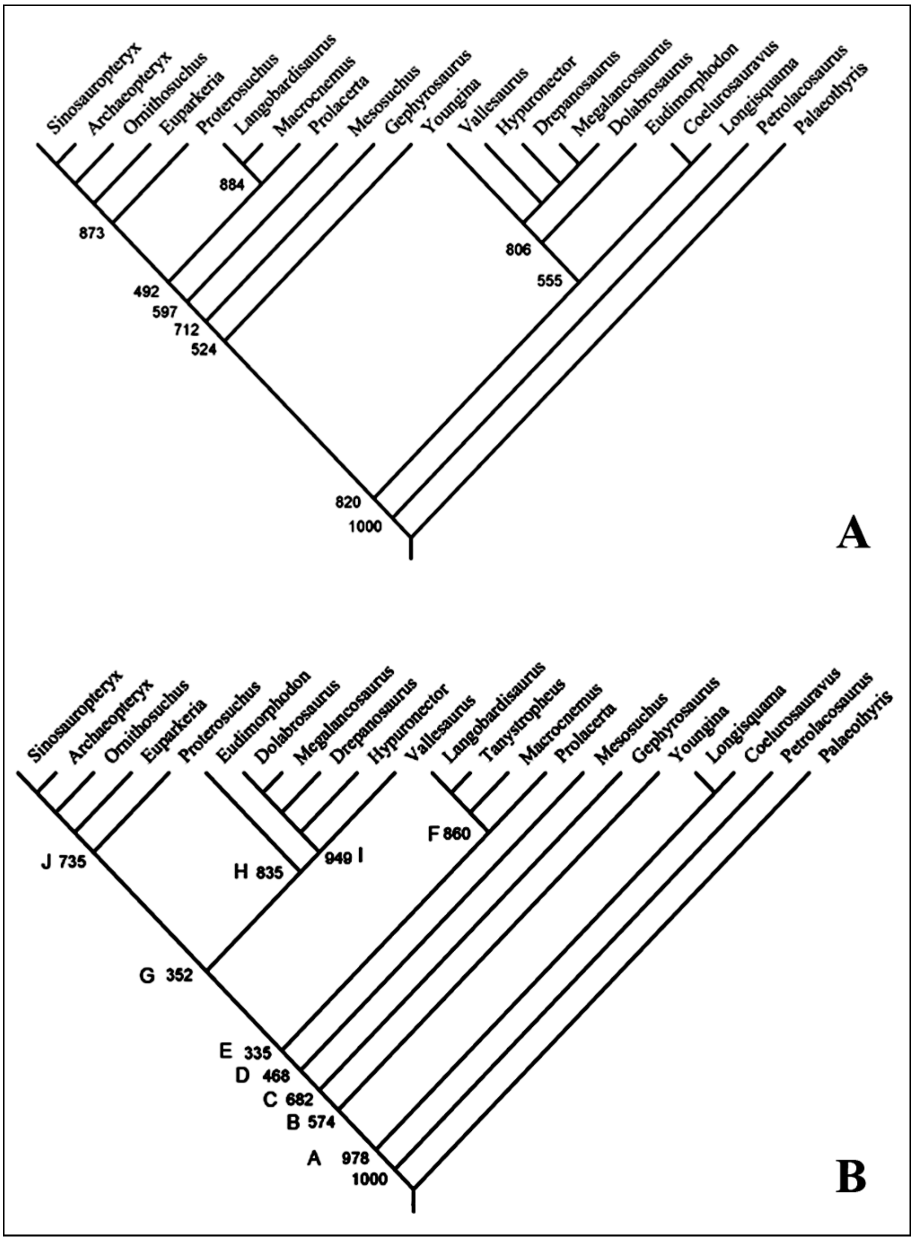

Fig. 9 - A) Results of the inclusion of *Eudimorphodon* in Senter's (2004) cladogram, by using his character set and matrix. B) Relationships of *Drepanosauridae* and *Eudimorphodon* according to the updated character set. Numbers indicate bootstrap values. Main groups are named according to Senter (2004) nomenclature as follows (A) Eosuchia, (B) Neodiapsida, (C) Sauria, (D) Archosauromorpha, (E) unnamed, (F) Protorosauria (Prolacertiformes), (G) unnamed, (H) unnamed, (I) Drepanosauridae, (J) Archosauriformes. See text for further explanation.

The resulting cladogram (Fig. 9A), shows that the addition of *Eudimorphodon* in the original matrix by Senter does not alter the cladogram, but places it outside the Neodiapsida with *Longisquama* and the Drepanosauridae, supported by a bootstrap value of 806.

In a second analysis we used a new matrix with both Senter's data, but giving additional scoring of character states previously reported as unknown, especially on the basis of data from Renesto & Dalla Vecchia (2005) and with the addition of a few other relevant characters (see Appendix 1). The new matrix was analysed by parsimony and yielded a cladogram shown in Fig. 9B. The revised cladogram, supported by high bootstrap values, shows *Eudimorphodon* and Drepanosauridae as sister groups within Neodiapsida, and the clade *Eudimorphodon* + Drepanosauridae (with *Vallesaurus* as the most primitive member) nested between the Protorosauria (Prolacertiformes) and the basal archosaurs. *Longisquama,* however, still remains where Senter's analysis placed it, i.e. excluded from Neodiapsida as the sister group of the coelurosauravids, but it is quite feasible that this is the result of poor knowledge of the genus rather than reflecting a true phylogenetic relationship. The consensus trees obtained by our dataset (either character 33 recoded or left multistate) and by Senter's corrected dataset were not significantly different as shown by the SH test.

Conclusion

The description of *Vallesaurus,* other than increasing knowledge about the diversity of the Drepanosauridae, is important because it permits a clarification of the systematic position of this group. Moreover, being a primitive member of the group, it allows us to predict hypotheses concerning the phylogenetic history of drepanosaurids and their relationships with other diapsids. Our study lends further support to previous studies that considered the Drepanosauridae as diapsids close to protorosaurs (Benton & Allen 1997; Dilkes 1998; Rieppel et al. 2003) and the addition of *Eudimorphodon* to the analysis, which appears to be nested just outside of the drepanosaur/protorosaur dichotomy, suggests that pterosaurs may lie at the base of the archosauriform clade rather than close to the dinosaurs, thereby resurrecting in some way Bennett's (1996) hypothesis concerning pterosaur phylogeny.

A note on Longisquama. As previously reported, both *Vallesaurus* and *Longisquama* show a fourth digit equal in lenght to the humerus, a character considered an autapomorphy of *Longisquama* by Unwin et al. (2000). Judging from recent descriptions and reconstructions of *Longisquama* (e. g. Unwin et al. 2000) further similarities can be found between between *Longisquama* and *Vallesaurus*, some of which are shared by all drepanosaurids. The overall resemblance in the structure of the forelimb and shoulder region may represent a convergence due to the same mode of life (a similar scapula is found also in chameleons and in kueheneosaurids), but other characters may be of more significance, such as the lack of cervical ribs (Unwin et al. 2000), the furcula-like structure and an articulation of the lower jaw positioned well forward with respect to the occiput. Furthermore, some of the putative characters of *Longisquama* that are inconsistent with a close relationship with drepanosaurids (e. g., presence of an antorbital fenestra and acrodont dentition), have been questioned recently (Unwin et al. 2000). Having not examined *Longisquama* first hand, we can neither give a more detailed comparison, nor assess anything about its relationships. However, since the drepanosaurids form such a widespread and diverse group, the hypothesis that *Longisquama* might be a drepanosaurid, should be taken into consideration in further analyses of the Drepanosauridae.

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Appendix 1

Characters and character state descriptions.

1. Tips of premaxilla and dentary, in lateral view: (0) not sharply pointed, (1) sharply pointed forming a strongly acute angle (Senter 2004).
2. Length of skull anterior to orbit: (0) < = length of skull posterior to anterior margin of orbit, (1) > length of skull posterior to anterior margin of orbit (Benton 1985; Evans 1988).
3. Contact between maxilla and external naris: (0) present, (1) absent (Benton 1985; Evans 1988).
4. Antorbital fenestra: (0) absent, (1) present (Benton 1985; Gauthier et al. 1988a).
5. Contact between lacrimal and external naris: (0) present, (1) absent (Benton 1985; Gauthier et al. 1988a).
6. Lower temporal arcade: (0) complete, (1) incomplete (Benton 1985; Dilkes 1998).
7. Inclusion of postfrontal in supratemporal fenestra: (0) absent, (1) present (Benton 1985; Dilkes 1998).
8. Discrete ascending process of quadratojugal, posteriorly bordering infratemporal fenestra: (0) absent, (1) present (Gauthier et al. 1988a).
9. Pineal foramen: (0) open, (1) closed (Gauthier et al. 1988a).
10. Squamosal processes of parietals: (0) not backswept, (1) backswept (Senter 2004).
11. Prefrontal-nasal suture: (0) oriented parasagittally, (1) oriented diagonally in dorsal view (Laurin 1991).
12. Quadratojugal process of jugal: (0) wide and blunt, (1) slender and tapering (Laurin 1991).
13. Slender, ventrally tapering anteroventral process of squamosal: (0) absent, (1) present (Evans 1988).
14. Contact between palatine and ectopterygoid: (0) present, (1) absent (Senter 2004).
15. Teeth: (0) not as in state 1, (1) laterally compressed, pointed, recurved and serrated (Benton 1985; Evans 1988).
16. Ventral displacement of craniomandibular joint below dorsal margin of dentary: (0) absent, (1) present (Maryanska et al. 2003).
17. Craniomandibular joint: (0) posterior to orbit, (1) ventral to posterior extremity of orbit (Fig. 4B) (Senter 2004).
18. Anterior depth of surangular: (0) < 2 × that of angular, (1) > =2 × that of angular (Gauthier 1986).
19. Dorsal overlap of dentary by surangular: (0) absent, (1) present (Senter 2004).
20. Pronounced retroarticular process: (0) absent, (1) present (Benton 1985; Gauthier et al. 1988a).
21. Posterior border of skull: (0) not strongly inclined posteriorly, (1) strongly inclined posteriorly (Senter 2004).

22. Posterior upsweeping of parietals, forming a posterodorsal crest: (0) absent, (1) present (Senter 2004).
23. Ornamentation of parietal rim with pronounced bumps: (0) absent, (1) present (Senter 2004).
24. Lateral mandibular fenestra: (0) absent, (1) present (Benton 1985; Gauthier et al. 1988a).
25. Palatal teeth: (0) present, (1) absent (Benton 1985; Gauthier et al. 1988a).
26. Caniniform teeth in maxilla: (0) present, (1) absent (Benton 1985; Gauthier et al. 1988b).
27. Mid-cervical vertebrae: (0) subequal in length to or shorter than dorsal vertebrae, (1) markedly longer than dorsals (Benton 1985; Evans 1988).
28. Length of mid-cervical centra: (0)<3 × height, (1) >=3 × height (Senter 2004)
29. Posterior face of mid-cervical centra: (0) not convex, (1) convex (Senter 2004
30. Anterior overhang of mid-cervical neural spines: (0) absent, (1) present (Senter 2004).
31. Distal expansion and fusion of anterior dorsal neural anterior dorsal neural spines: (0) absent, (1) present (Dilkes 1998).
32. Dorsal neural spines: (0) low, (1) high and elongate (Benton 1985; Evans 1988).
33. Number of sacral vertebrae: (0) 2, (1) 3, (2) 5 (Gauthier et al. 1988a).
34. Number of sacral vertebrae (0) 3, (1) 4 (new character).
35. Number of sacral vertebrae (0) 3, (1) 5 (Gauthier et al. 1988a)
36. Sacral and anterior caudal neural spines: (0) low, (1) high and elongate (Evans 1988).
37. Mid-caudal neural spines: (0) proximodistally short, (1) proximodistally elongate (height >=4 × anteroposterior length (Senter 2004)).
38. Mid-caudal neural spines: (0) not T-shaped, (1) T shaped (Dilkes 1998).
39. Terminal tail claw: (0) absent, (1) present. (Senter 2004).
40. Cervical ribs: (0) distally blunt, (1) distally tapering (Evans 1988).
41. Posterior trunk ribs: (0) dolichocephalous, (1) holocephalous (Benton 1985; Gauthier et al. 1988b).
42. Length of anterior hemal arches: (0)<3 × length of associated vertebrae, (1) >= 3 × length of associated vertebrae (Senter 2004).
43. Forking and distal closure of mid-caudal hemal arches: (0) absent, (1) present. (Senter 2004).
44. Number of dorsal vertebrae: (0)>= 18, (1) <= 17 (Senter 2004).
45. Scapular blade: (0) short and broad, (1) elongate (Benton 1985; Gauthier 1986).
46. Scapular blade: (0) not inclined anteriorly, (1) anteriorly inclined (leaning forward) (Senter 2004).
47. Clavicles: (0) separate, (1) fused into a furcula (Gauthier 1986).
48. Entepicondylar foramen of humerus: (0) open, (1) closed (Benton 1985; Gauthier et al. 1988a).
49. Width of distal expansion of humerus: (0) >=1/3 × humeral length, (1) < 1/3 × humeral length (Benton 1985; Laurin 1991).
50. Pronounced olecranon process: (0) present, (1) absent (Benton 1985; Evans 1988).
51. Radius: (0) does not extend further distally than ulna, (1) extends further distally than ulna (Benton 1985; Evans 1988).
52. Radiale and intermedium: (0) blocklike, (1) elongate (Senter 2004).
53. Manus length: (0) > humeral length, (1) subequal to or < humeral length (Senter 2004).
54. Metacarpal IV: (0) longer than metacarpal III, (1) not longer than metacarpal III (Evans 1988).
55. Reduction in manual phalangeal count: (0) absent, (1) present (Laurin & Reisz 1995).
56. Long, deep, preacetabular iliac blade: (0) absent, (1) present (Gauthier 1986).
57. Postacetabular iliac blade: (0) posteriorly inclined (leaning posteriorly), (1) vertical (Senter2004).
58. Acetabulum: (0) closed, (1) open (Gauthier 1986).
59. Acetabulum: (0) elongate, (1) round (Benton 1985; Gauthier et al. 1988b).
60. Pubes: (0) not elongate, (1) elongate (Evans 1988).
61. Thyroid fenestra: (0) absent, (1) present (Benton 1985; Evans 1988).
62. Femoral head: (0) not inturned at sub-right angle, (1) inturned at sub-right angle to femoral shaft (Gauthier et al. 1988a).
63. Diameter of femoral shaft: (0) constant or widening distally, (1) distally narrowed. (Senter 2004).
64. Fourth trochanter: (0) absent, (1) present (Benton 1985; Gauthier 1986).
65. Tibial length: (0) > 0.65 femoral length, (1) <= 0.65 femoral length (Senter 2004).
66. Calcaneal tuber: (0) absent, (1) present (Benton 1985; Gauthier et al. 1988a).
67. Length of pes: (0) > femoral length, (1) subequal to or < femoral length (Senter 2004).
68. Reduction in pedal phalangeal count: (0) absent, (1) present (Laurin & Reisz 1995).
69. Metatarsal I: (0) unreduced, (1) reduced to a splint (Gauthier 1986).
70. Metatarsal IV: (0) longer than metatarsal III, (1) not longer than metatarsal III (Senter 2004).
71. Pedal phalanx IV-1: (0) longer than pedal phalanx III-1, (1) not longer than pedal phalanx III-1 (Senter 2004).
72. Tarsal articular surface of metatarsal V: (0) faces proximally, articulates with distal tarsal V, (1) faces inward, articulates with distal tarsal IV (distal tarsal V absent) (Benton 1985; Gauthier *et al.* 1988a).
73. Pedal digit V: (0) functional, (1) vestigial (Benton & Clark 1988).
74. First phalanx of pedal digit V (0)short (1) elongate and metapodial like (Evans 1988)
75. Pedal phalanx V-2: (0) extends further distally than metatarsal IV, (1) does not extend further distally than metatarsal IV. (Senter 2004).
76. Distal tarsal 1: (0) present, (1) absent (Gauthier et al. 1988a).

Appendix 2

Character state data matrix.

taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Palaeothyris	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petrolacosaurus	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	1	?	?	?	0	?	?	?	0	?	?	1	?	?	?	?	?	?	?	?	1	1
Megalancosaurus	1	1	0	0	1	?	1	?	1	0	1	?	1	?	0	1	1	0	0	0	1	0	0	?	?	1	1	1	1	1	1	1	1	0	0	1	1	1
Vallesaurus	1	1	0	0	1	?	1	0	1	0	1	?	1	?	0	1	1	0	0	0	1	0	0	0	?	1	0	0	?	0	1	1	?	0	0	0	1	0
Drepanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	1	1	0	0	0	0	1	0
Dolabrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	1	1
Hypuronector	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	0	?	?	?	0	?	?	1	?	?	?	?	?	?	?	?	1	1	0
Longisquama	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	0	1	0	?	0	1	1	1	0	?	?	0	?	?	0	0	0	?	?	?	?	?	?
Coelurosauravus	1	0	0	0	1	1	1	?	0	1	0	?	0	?	0	0	1	0	0	0	1	1	1	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0
Youngina	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Gephyrosaurus	0	0	0	0	1	1	1	?	0	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	?	0	?	?	?	0	0	0
Mesosuchus	0	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	1	0
Prolacerta	0	1	1	0	1	1	0	1	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Macrocnemus	1	1	?	0	1	?	0	1	0	?	1	?	?	?	0	0	0	0	?	1	0	0	0	0	?	1	1	1	0	1	0	0	0	0	0	0	0	0
Langobardisaurus	1	1	?	0	1	?	0	?	?	?	1	?	?	?	0	1	0	0	?	1	0	0	0	0	?	1	1	1	1	1	0	0	0	0	0	0	0	0
Tanystropheus	1	1	?	0	1	1	0	0	0	?	1	1	?	?	0	0	0	0	?	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Ornithosuchus	0	1	1	1	1	0	0	1	1	1	1	1	1	?	1	0	0	?	?	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0
Proterosuchus	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Euparkeria	0	1	1	1	1	0	0	1	1	1	1	1	1	?	1	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	1	1	0	1	1	0	-	?	1	1	?	?	-	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0
Sinosauropteryx	0	1	1	1	1	0	-	1	1	1	?	1	1	?	1	0	0	1	1	1	0	0	0	1	?	1	0	0	0	0	0	0	1	1	1	0	0	0
Eudimorphodon	0	1	0	0	0	0	1	0	1	0	1	1	1	?	0	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0

taxon	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
Palaeothyris	?	0	0	?	?	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petrolacosaurus	0	0	?	1	1	0	?	1	1	?	1	1	?	0	?	1	1	?	0	1	0	?	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?
Megalancosaurus	1	-	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0
Vallesaurus	0	-	1	1	0	0	1	1	0	1	1	1	0	?	1	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0
Drepanosaurus	1	-	1	1	0	0	1	1	0	1	1	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0
Dolabrosaurus	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	1	?	?	0	1	-	0	0	0	0	0
Hypuronector	0	?	1	1	0	?	1	1	?	1	1	?	0	?	1	1	?	0	1	0	?	0	0	0	0	0	1	?	?	?	?	?	?	?	?	0	?	?
Longisquama	?	?	?	?	?	?	1	0	1	?	1	?	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Coelurosauravus	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	?	?	?	?	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Youngina	0	?	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?	?	0	0	?	0	?	0	0	?
Gephyrosaurus	0	0	1	?	?	?	0	0	0	0	0	?	?	?	?	?	?	0	0	0	1	0	1	0	0	0	0	0	?	?	?	?	?	1	?	0	?	?
Mesosuchus	0	?	1	0	0	?	0	0	0	1	?	1	0	0	?	0	?	0	0	0	1	0	0	0	0	0	0	0	1	?	0	0	0	1	0	0	1	0
Prolacerta	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	1	0
Macrocnemus	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1
Langobardisaurus	0	1	1	0	0	1	?	?	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0
Tanystropheus	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0
Ornithosuchus	0	?	?	0	0	1	1	0	0	?	1	1	0	0	?	1	?	0	0	0	1	1	0	0	0	1	0	1	?	?	0	?	1	?	0	0	1	?
Proterosuchus	0	1	1	0	0	1	0	0	0	1	?	1	0	0	?	0	?	0	0	0	1	0	0	0	0	0	0	1	0	?	0	0	0	1	0	0	1	0
Euparkeria	0	1	1	0	0	1	1	0	0	1	0	1	0	?	?	?	?	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	1
Archaeopteryx	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0	-	1	1	0	1	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	-	1
Sinosauropteryx	0	1	0	0	0	1	1	0	?	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	0	-	1
Eudimorphodon	0	1	1	1	0	1	1	0	0	1	1	1	0	-	0	0	1	1	0	0	1	0	0	0	1	0	0	-	1	0	0	1	1	1	0	-	0	1