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A NEW PROLACERTIFORM REPTILE FROM THE LATE TRIASSIC OF NORTHERN ITALY

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Key-words: *Langobardisaurus pandolfii*, New Genus, Reptilia, Diapsida, Late Triassic, Description, Palaeoecology.

Riassunto. Vengono descritti due esemplari di Rettili fossili raccolti a Cene (Val Seriana, Bergamo), nel Calcare di Zorzino (Norico Medio, Triassico Superiore). I due esemplari provengono dal medesimo strato e presentano caratteri scheletrici pressochè identici, per cui possono essere considerati conspecifici con ragionevole certezza. Possono inoltre essere classificati come appartenenti all' ordine dei Prolacertiformi. I confronti con i taxa già noti, consentono di ritenerli come appartenenti ad un genere ed una specie nuovi per la scienza: *Langobardisaurus pandolfii*. Le caratteristiche dello scheletro suggeriscono infine che *Langobardisaurus* fosse un rettile terrestre e si nutrisse prevalentemente di insetti.

Abstract. A new diapsid reptile is described from the locality of Cene (Seriana Valley, near Bergamo, Lombardy, Northern Italy) from an outcrop of the Calcare di Zorzino (Zorzino Limestone) Formation (Middle Norian, Late Triassic). It is based on virtually identical specimens, differing only in size. Analysis of available diagnostic characters allows it to be included in the Prolacertiformes, representing a new genus and species, *Langobardisaurus pandolfii* probably related to *Macrocnemus*, possibly to *Cosesaurus*, and to the Tanystropheidae. It is assumed here that *Langobardisaurus pandolfii* was adapted to a terrestrial mode of life and probably to an insectivorous diet.

Introduction.

The Norian (Late Triassic) vertebrate localities from the Bergamo Prealps (Lombardy, Northern Italy) are of worldwide interest for the diversity and importance of their faunas. The main fossiliferous unit is the Calcare di Zorzino (Zorzino Limestone), which was deposited in intraplatform basins surrounded by the huge Dolomia Principale carbonate platform (Tintori et al., 1985; Tintori, 1991, 1992). These basins were deep and several kilometers large (Jadoul, Berra & Frisia, 1992). The fossils consist mainly of fishes (Tintori et al., 1985; Tintori, 1991, 1992; Tintori & Sassi, 1992) but reptiles are also well represented, with at least ten different genera, often unknown from other localities. Despite the depositional environment, terrestrial reptiles

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are more frequently found than marine ones, suggesting the existence of emergent areas surrounding the basins in which the Calcare di Zorzino was deposited. Aquatic reptiles are represented by the armoured placodont *Psephoderma* (Pinna, 1979; Pinna & Nosotti, 1989) and by the thalattosaur *Endennasaurus* (Renesto, 1984, 1992). Among the non-marine reptiles are included the oldest pterosaurs so far described (Wild, 1978; Renesto, 1993) and remains of many terrestrial reptiles. Fragments of the armour of the thecodont *Aetosaurus* (Wild, 1991), an isolated skull of a gavial-like phytosaur ascribed to the genus *Mystriosuchus* (Pinna, 1987) have been collected, along with complete or partial skeletons of strange diapsids like the arboreal archosauromorph *Megalancosaurus* (Renesto, 1994) and the problematic diapsid *Drepanosaurus* (Pinna, 1980, 1984) also of probable arboreal habits (Renesto, in press).

Additional findings are represented by the two specimens (Pl. 1, 2), here described, that were collected in 1974 by Mr. Mario Pandolfi, preparator of the Museo Civico di Scienze Naturali "E. Caffi", Bergamo (Bergamo Museum of Natural Sciences). Both specimens were found at the same locality (the small quarry of Cene, Seriana Valley, Lombardy, Northern Italy) and come from the same bed, which is only a few centimeters thick. The almost identical structure of their skeletons suggests that the two specimens are conspecific. Analysis of their skeletal characters reveals that these reptiles belong undoubtedly to the Prolacertiformes (as defined by Wild, 1973, 1980a; Olsen, 1979; Benton, 1985; Carroll, 1988; Evans, 1988). This group comprises *Prolacerta*, from the Lower Triassic of South Africa (Parrington, 1935; Gow, 1975), *Macrocnemus*, from the Middle Triassic of Monte San Giorgio, Switzerland (Peyer, 1937; Rieppel, 1989), *Tanystropheus*, from the Middle Triassic of Switzerland and possibly from the Late Triassic of Italy (Peyer, 1931, 1937; Kuhn Schnyder, 1962; Wild 1973, 1980a, b, 1987), *Tanytrachelos*, from the Late Triassic of the U.S.A. (Olsen, 1979), possibly *Cosesaurus*, from the Middle Triassic of Spain (Ellenberger & de Villalta, 1974; Ellenberger, 1977; Olsen, 1979; Sanz & Lopez-Martinez, 1984), along with *Malerisaurus, Trachelosaurus, Prolacertoides, Kadimakara, Protorosaurus*, from many Triassic localities around the world (Benton, 1985; Evans, 1988). The differences between the specimens from Cene and other genera, require the recognition of a new genus and species, related both to *Macrocnemus* and to the tanystropheids (as defined by Olsen, 1979) as detailed in the systematic discussion.

SYSTEMATIC PALAEONTOLOGY

Class **Reptilia**
Diapsida
Superdivision **Neodiapsida** Benton, 1985
Division **Archosauromorpha** Huene, 1946
Plesion *Prolacertiformes* Camp, 1945

Family *incertae sedis*
Genus *Langobardisaurus* gen. n.

Type species: *Langobardisaurus pandolfii* sp. nov.

Derivatio nominis. From "*Langobardi*" (latin, "Long-beard") an ancient German people whose name was inherited by the Italian region (Lombardy) in which the fossils were collected, and *-saurus*, reptile.

Diagnosis. Small prolacertiform reptile with elongated neck and great length disparity between anterior and posterior limbs. Skull triangular with narrow and elongate snout. Pointed premaxilla with elongate posterior process. Maxilla subtriangular, posteriorly elongated; dentary pointed anteriorly, more high and robust posteriorly, ?splenial thin and very long. Dentition thecodont, posterior teeth on the maxilla and on the dentary three cusped; three cusped teeth are retained in the adult. Vertebral column consisting of 9 cervical, 17 dorsal, 2 sacral and up to 45 caudal vertebrae; cervical and dorsal vertebrae procoelous; cervical vertebrae longer and narrower than in *Macrocnemus*, the longest one being slightly more than 2.5 times the length of the mid dorsal ones; neural spines low, somewhat thickened distally, presence of stout horizontally widened pre- and postzygapophyses, absence of lateral foramina on the cervical centra. Dorsal vertebrae with well developed transverse processes, last three dorsal vertebrae bearing fused ribs or elongated transverse processes, directed slightly anteriorly as in tanystropheids; caudal vertebrae elongate with low neural spine and small "Y" shaped chevrons; presence of very long laterally projecting pleurapophyses on the proximal portion of the tail. Detectable elements of the pectoral girdle as in other prolacertiforms. Both anterior and posterior stylopodia longer than related zeugopodia. Humerus slender, straight, distal articular surfaces for the radius and ulna divided by an embayment of the head of the bone forming an entepicondylar groove; radius and ulna straight, forming a very narrow spatium interosseum, phalangeal formula for the manus 2, 3, 4, 5, 3, each digit ending in a small claw. Femur sigmoidal, about 30 per cent longer than the humerus. Tibia and fibula slightly shorter than the femur, forming a narrow spatium interosseum; tarsus comprising a rounded calcaneum, a L shaped astragalus, a large centrale, a tiny third distal tarsal, followed by a wide fourth distal tarsal. First four metatarsals much more elongated than related proximal phalanges and slightly increasing in length from the first to the fourth one; fifth metatarsal short and hooked. Phalangeal formula for the pes 2, 3, 4, 5, 3. First phalanx of the fifth toe elongated and metapodial as in tanystropheids.

Langobardisaurus pandolfii sp. n.

Pl. 1-3, Text-fig. 1-10

Derivatio nominis. The species is dedicated to Mario Pandolfi, the preparator of the Museo Civico di Scienze Naturali "E. Caffi", Bergamo. His finds and his skilled preparation of many specimens provided great aid to scientific research on the fossil vertebrates from the Bergamo region.

Horizon and locality. The uppermost section of the Calcare di Zorzino, Middle Norian, Late Triassic. Type locality: the small quarry near Cene (Val Seriana, Bergamo, Lombardy, Northern Italy).

Holotype. Museo Civico di Scienze Naturali "E. Caffi," Bergamo (Lombardy, Northern Italy), specimen n. MCSNB 2883. Partial skeleton seen in ventral view, lacking the anterior limbs and portions of the vertebral column.

Paratype. Museo Civico di Scienze Naturali "E. Caffi," Bergamo (Lombardy, Northern Italy), specimen n. MCSNB 4860. Complete skeleton of a juvenile individual, seen in ventral view.

Diagnosis. As for the genus.

Description.

The two specimens are both exposed from the ventral side (Pl. 1, 2). Specimen MCSNB 2883, the holotype (Pl. 1) is larger (its femur is about twice the length of the femur of MCSNB 4860); the heads of the long bones and the tarsals are fully ossified. It probably represents an adult or a subadult. The anterior limbs and portions of the dorsal region and of the tail are missing. The neck is bent dorsally, forming a backwards directed ring, so that the skull lies below the shoulder region; very few cranial characters can be seen. Specimen MCSNB 4860 is complete, but its neck was also bent dorsally after death and, along with the skull, it lies below the trunk, where little can be seen. This specimen represents a juvenile stage. For this reason it has been considered more advisable to design specimen MCSNB 2883 as the holotype, despite its incompleteness. However, the generic diagnosis and the following osteological description rely on both specimens, since they are virtually identical, apart for their absolute size (Tab. 1).

Unfortunately it was impossible to prepare the opposite side of the stone slab to allow a more detailed analysis of the skull in either specimens. The fragility of the stone rendered this operation impossible in the case of specimen MCSNB 4860, and specimen MCSNB 2883 was collected as separate fragments, which were fixed with glue to a resin slab before preparation. The kind of sediment and the conditions of preservation rendered also difficult any attempt at X-ray investigation.

Skull. In the holotype (Pl. 1; Fig. 1) the skull is poorly preserved, and only the middle portion of the jaws can be detected, just between the posterior cervical vertebrae and the left coracoid. In the paratype (MCSNB 4860) (Pl. 2, 3) it is partially covered by vertebrae, ribs and gastralia, so that only the anterior region can be observed; in addition the right and left halves of the skull shifted from their original position. The snout is narrow and the premaxilla seems to show a posteriorly elongate process. Only a limited portion of the lower jaw is exposed in the holotype, while nearly all its ventral outline can be observed in the paratype. At the anterior tip of the snout the dentary is pointed and narrow, becoming deeper and more robust posteriorly. Ventral to this bone a very thin, elongated splenial is visible.

The implantation of the teeth is fully thecodont. The teeth of the premaxilla and of the anterior part of the dentary, are lost in the paratype (only impressions on the matrix and on the premaxillae are preserved, suggesting that their number had to

Specimen	MCSNB 2883	MCSNB 4860
skull length	-	(26)
skull height	-	(12)
length of the cervical vertebrae	- - - 20 - 19, 16.5, 13.5	-
average length of the dorsal vertebrae	7.5	-
length of the first caudal vertebra	6.5	2.5
humerus length	-	18 (L), 15 (R)
humerus proximal width	-	3.5 (L)
humerus distal width	-	2.5 (L)
humerus cross section	-	1.5 (L)
radius length	-	10.5 (L), 12 (R)
ulna length	-	12.5 (R)
length of the third metacarpal	-	2.5 (L)
femur length	56 (L), 58 (R)	27 (L)
femur proximal width	8.5 (L), 9 (R)	4 (L)
femur distal width	5 (L)	2.5 (L)
femur cross section	-	2 (L)
tibia length	47 (L)	24 (R)
fibula length	44 (L)	23 (R)
length of the third metatarsal	10.5 (L), 11 (R)	-
Ratios		
humerus/femur	-	0.66
humerus/radius	-	1.5
femur/tibia	1.19	1.16
humerus/metacarpal 3	-	7.2
femur/metatarsal 3	-	3.6

Tab. 1 - Measurements (in mm) and ratios taken on the two examined specimens (L= left; R=right).

be six-seven). The entire snout is covered by cervical vertebrae in the holotype. The teeth on the maxilla and in the middle and posterior portion of the dentary are three-cusped both in the holotype and in the paratype. In this latter, the dentary widens posteriorly and bears on its upper margin at least 25 teeth; on the holotype, the more posterior maxillary tooth that can be detected seems to be multi-cusped and mesiodistally (labio-lingually) enlarged (Fig. 1).

Vertebral column. The neck is bent sharply caudally in both specimens, some vertebrae are incompletely preserved in the holotype, and nearly the entire neck lies below the dorsal region in specimen MCSNB 4860, thus the number of cervical vertebrae cannot be established exactly. However, judging from size and proportions of the visible elements, the neck probably consists of 9 vertebrae; the centra are procoelous as in *Tanytrachelos* (Olsen, 1979). The last six cervical vertebrae are rather well preserved in the holotype (Fig. 2, 3A).

The length of the centra increases from the first toward the sixth-seventh, then it decreases and the last cervical vertebra is much shorter than the preceeding ones. The seventh cervical centrum (Fig. 3A) is slightly more than 2.5 times longer than the dorsal ones. Both pre- and postzygapophyses are well developed and horizontally oriented. The neural spines are very low and somewhat expanded at their dorsal margin. The articular facets for the ribs lie near the anterior end of the ventral margin of each centrum. The cervical vertebrae are followed by 17 dorsal, 2 sacral and about 45 caudal vertebrae. An anterior dorsal vertebra, possibly the first one, is exposed from dorsal view in the holotype (Fig. 1; Fig. 3B), it shows wide pre- and postzygapophyses,

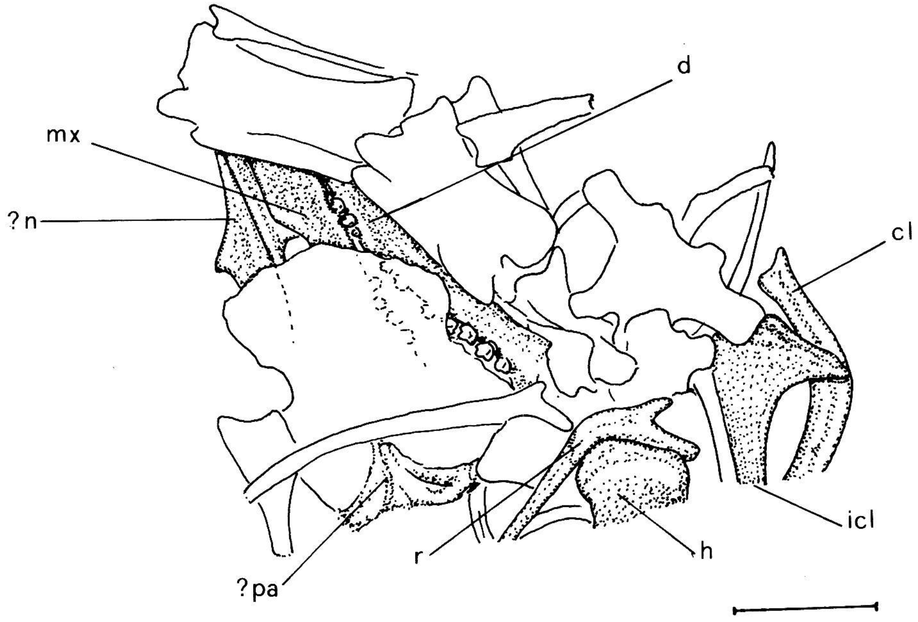

Fig 1 - *Langobardisaurus pandolfii.* Elements of the skull and of the pectoral girdle as preserved in the holotype (stippled). The coracoid and other overlapping bones are unstippled to avoid confusion. Abbreviations are: cl) clavicle; d) dentary; h) humerus; icl) interclavicle; mx) maxilla; ?n) ?nasal; ?pa) ?parietal; r) dorsal rib. Scale bar equals 1 cm.

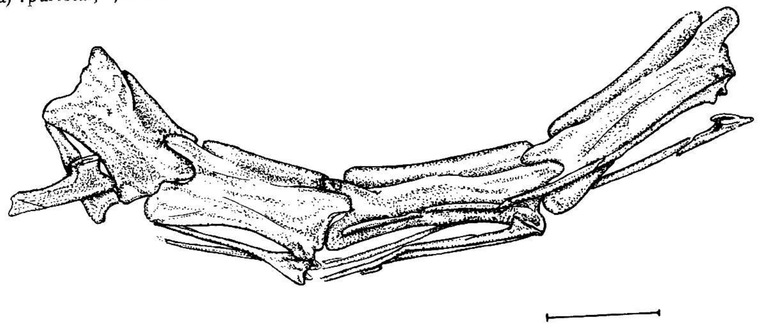

Fig. 2 - *Langobardisaurus pandolfii.* The cervical vertebrae as preserved in the holotype. Scale bar equals 1 cm.

with horizontal articular facets, and a low neural spine. Stout, elongate transverse processes projects laterally. Other dorsal vertebrae are covered by thin, very fragmented gastralia. The more posterior dorsal vertebrae are visible, exposed in ventral view, both in the holotype and in the paratype (Pl. 1 and 3; Fig 4). Their centra are rather elongate and the last four dorsal vertebrae bear very long transverse processes (or short, fused ribs) distally expanded as in *Tanystropheus* and in *Tanytrachelos* (Wild,

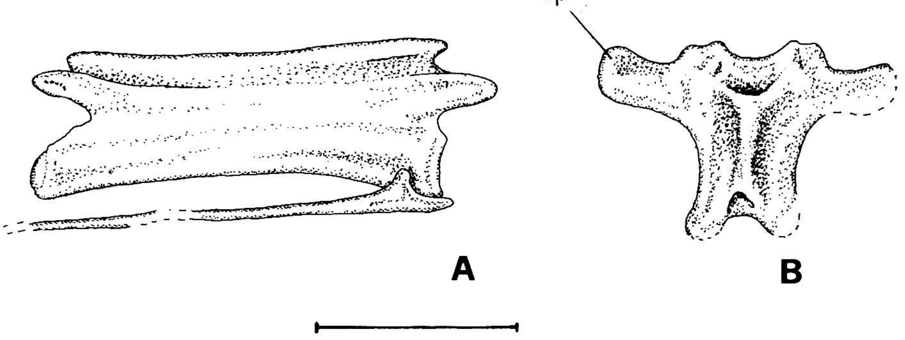

Fig. 3 - *Langobardisaurus pandolfii.* Holotype. A) The seventh cervical vertebra in lateral view; B) the first dorsal vertebra in dorsal view (tp: transverse process). Scale bar equals 1 cm.

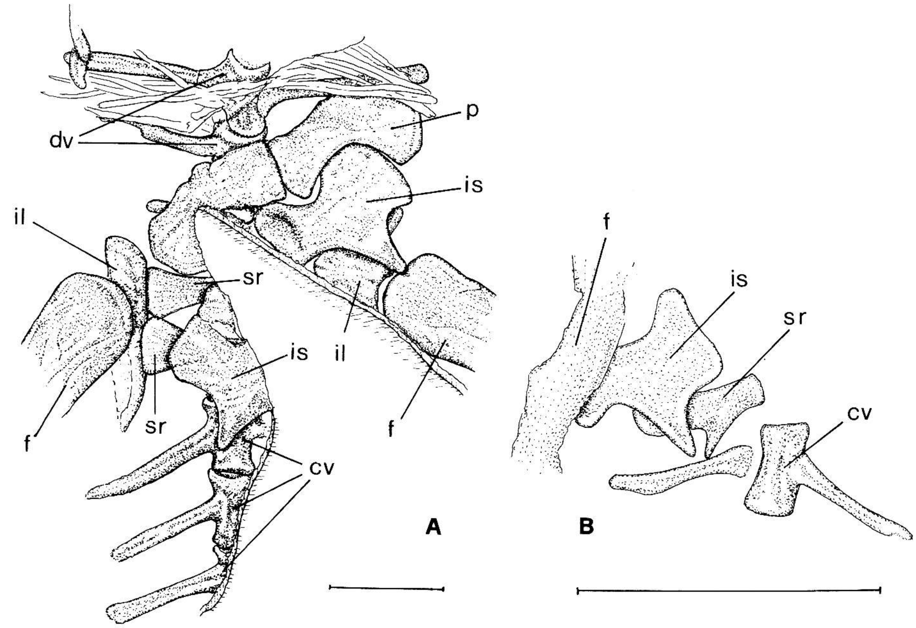

Fig. 4 - *Langobardisaurus pandolfii.* Posterior dorsal, sacral and anterior caudal regions of the vertebral column and pelvic girdle, as preserved in the holotype (MCSNB 2883) (A) and in the paratype (MCSNB 4860) (B). Abbreviations are: cv) caudal vertebrae; dv) dorsal vertebrae; f) femur; il) ilium; is) ischium; p) pubis; sr) sacral ribs. Scale bars equal 1 cm.

1973; Olsen, 1979). The sacral vertebrae are visible only in specimen MCSNB 4860, where they are partially covered by pelvic bones. Their morphology is similar to the more posterior dorsal ones, the centra being somewhat shorter. Caudal vertebrae are elongate, with low neural spines and small "Y"-shaped chevrons at least till the 16th caudal vertebra. The first 12 caudal vertebrae (Fig. 4) bear very long laterally projecting transverse processes, somewhat expanded at their ends and directed caudally. In the paratype, the tail is almost complete, its length being about two times that of the dorsal plus sacral vertebral region.

Ribs. Cervical ribs are elongate and splintlike until the seventh cervical vertebra. The rib head (Fig. 2, 3A) is dicephalous and bears a distinct free anterior process. The ribs of the fifth and sixth cervical vertebrae are about two times longer than the associated centra. The ribs of the eight cervical vertebra are stouter and shorter than the preceeding ones, their morphology resembling slightly the "plowshare" shape (Fig. 2) of the more posterior cervical ribs of *Tanytrachelos* (Olsen, 1979).

The more anterior dorsal ribs can be observed in the holotype (Fig. 1); they are dicephalous but the capitular head is much more developed than the tubercular one. Sacral ribs (Fig. 4) are stout and distally expanded, those of the second sacral vertebra bear a distinct process on their posterior margin as in *Macrocnemus* (Rieppel, 1989). Caudal ribs are absent, and they are replaced by long transverse processes gently bent caudally. The belly region is covered by a large number of very thin gastralia.

Pectoral girdle. The pectoral girdle is poorly ossified in the paratype (possibly owing to the juvenile stage) and only scattered elements are preserved in the holotype (Fig. 1). As in other prolacertiforms the clavicle is narrow and "C"-shaped, the interclavicle shows an expanded rhomboidal anterior portion, followed posteriorly by a narrow stem (only its proximal portion is preserved in the holotype); the coracoid is rounded and wide, with smooth margins. The posterior margin of the left scapula can be observed in the paratype; it shows a deep embayment as in *Tanystropheus* (Wild, 1973).

Anterior limb. The holotype retains only a fragment of the proximal head of the right humerus (Fig. 1), while in specimen MCSNB 4860 (Fig. 5) the anterior limbs are well preserved, with elements in anatomical connection. The humerus is straight and hollow, with narrow shaft and expanded heads. Its proximal articular surface is only weakly convex. If, as assumed here, specimen MCSNB 4860 represents an early ontogenetic stage, it may be hypothesised that the articular surfaces were not fully ossified. The articular areas for the radius and the ulna are gently convex and divided by a distinct groove on the distal margin of the bone. No entepicondylar foramen is visible. Radius and ulna are approximately of the same length and shorter than the humerus; their shaft is straight and both their proximal and distal heads are somewhat expanded. The two bones lie very close to each other forming a very narrow spatium interosseum. The carpus (Fig. 5B) cannot be restored with confidence; two bones (a rounded ?ulnare and a more triangular ?intermedium) lie proximal to a couple of very small rounded bones that can be tentatively considered as distal carpals. Metacarpals

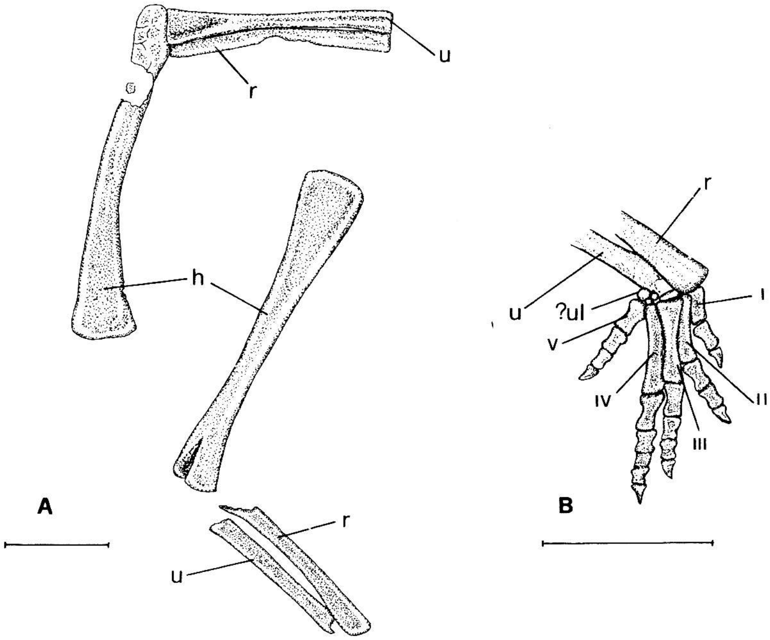

Fig. 5 - *Langobardisaurus pandolfii.* Anterior limbs of specimen MCSNB 4860. A) Left and right humerus (h), radius (r) and ulna (u). B) Left carpus and manus (?ul) ?ulnare; (I-V) metacarpals. Scale bar equals 1 cm.

are rather stout bones, their length increasing from the first to the fourth one, while the fifth metacarpal is very short. The phalangeal formula for the manus is: 2, 3, 4, 5, 3. Each digit ends with a small claw.

Pelvic girdle. The pubis (Fig. 4) is deep and flattened distally; it forms with the ischium a well developed puboischiadic plate. A large thyroid fenestra reaches the symphysis. A thick anterior process can be observed on the anterior margin of the pubis of the holotype. The ischium widens greatly in its distal portion and its posterior margin bears a well developed straight process directed posteriorly. The ilium is covered by the proximal heads of the femora and by other pelvic bones in both specimens, so that its true outline cannot be restored with confidence.

Posterior limb. The femur (Fig. 6) is a very long and narrow bone, with a weakly sigmoidal and hollow shaft. The proximal articular surface is slightly convex in the paratype, while two distinct hemispherical condyles can be seen in the holotype. No patellar (or epiphyseal) ossifications are preserved. The tibia and the fibula are narrow bones with straight shafts, and they are shorter than the femur. Both proximal and distal heads are gently convex and somewhat expanded. They lie in close contact, so that the spatium interosseum is very small. The proximal tarsal elements are very well preserved in the holotype (Fig. 7, 8B). A large, rounded calcaneum meets medially a rather small, "L"-shaped astragalus; distally to them a large centrale is present, it contacts both a tiny third distal tarsal and a wide fourth distal tarsal. This latter bone contacts proximally the astragalus and the calcaneum. The first four metatarsals (Fig. 8) are very long and narrow bones; their length is much greater than that of the related proximal phalanges. The fourth metatarsal is the longest one, and the fifth one is short and hooked, with a ventral process on its lateral margin (Fig. 7). The

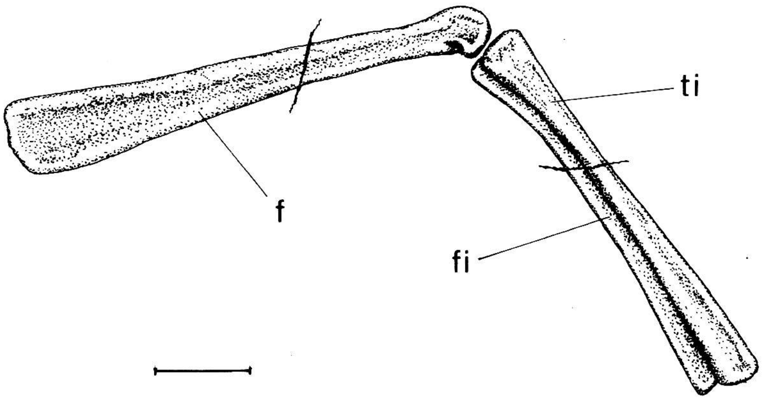

Fig. 6 - *Langobardisaurus pandolfii.* Holotype, right posterior limb. f) Femur; fi) fibula; ti) tibia. Scale bar equals 1 cm.

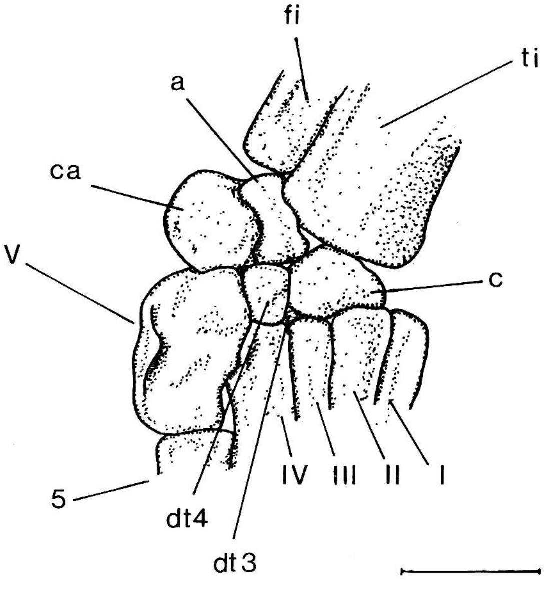

Fig 7 - *Langobardisaurus pandolfii.* Right tarsus, plantar view. a) Astragalus; c) centrale; ca) calcaneum; dt 3-4) distal tarsals; I - V) metatarsals; 5) first phalanx of the fifth toe. Scale bar equals 0.5 cm.

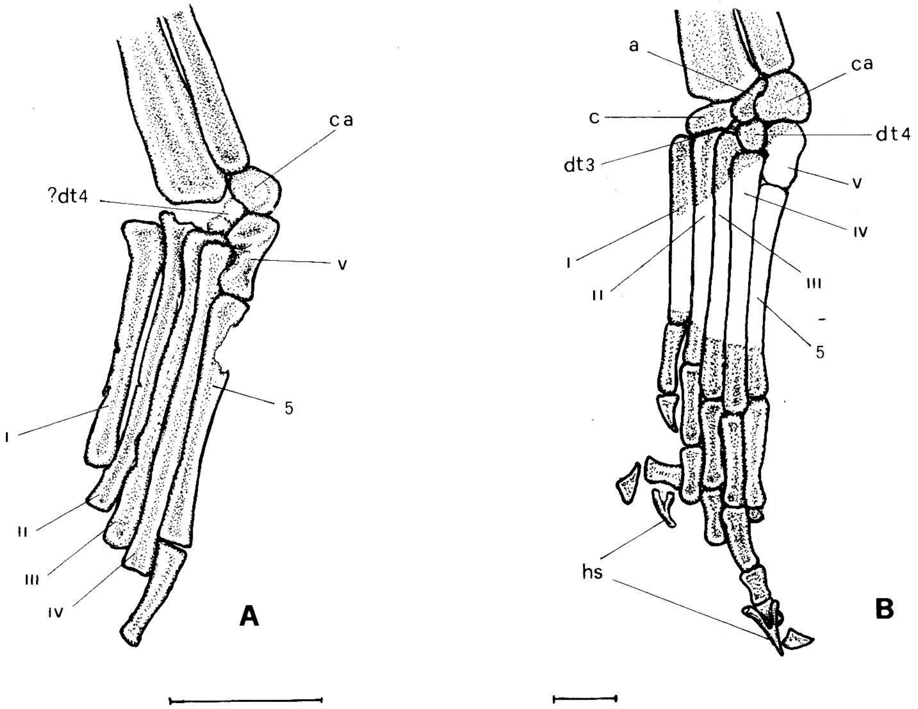

Fig. 8 - *Langobardisaurus pandolfii.* Tarsus and pes of the paratype (MCSNB 4860) (A) and of the holotype (MCSNB 2883) (B), from plantar view. hs) Haemal spines of the caudal vertebrae; other abbreviations as in Fig. 7. Scale bars equal 0.5 cm.

phalangeal formula for the pes is 2, 3, 4, 5, 3. The first phalanx of the fifth toe is very long and its shape is very similar to that of the metatarsals 1-4, as it occurs in tanystropheids (Wild, 1973; Olsen, 1979; Evans, 1988). The metatarsal and the first phalanx of the fifth toe are closely associated each other, probably forming a single functional unit. Each digit ends with a small claw.

Discussion.

Comparison with other Prolacertiformes.

According to Wild (1973, 1980a), Benton (1985), Carroll (1988) and Evans (1988), the main prolacertiform synapomorphies shared by *Langobardisaurus* are the following: neck made up by 8-12 elongate cervical vertebrae, with low neural spines; cervical ribs dicephalous and with a distinct, free anterior process; more posterior dorsal vertebrae with short ribs forming a distinct "lumbar" region; metatarsals I-IV very elongate and fifth metatarsal short and hooked. *Langobardisaurus pandolfii* shows many characters suggesting that it is related to the Triassic prolacertiform genera *Macrocnemus* (Peyer, 1937), *Cosesaurus* (Ellenberger & de Villalta, 1974), *Tanystropheus* (Peyer, 1931; Wild, 1973, 1980a) and *Tanytrachelos* (Olsen, 1979). The phalangeal formula both for the manus and for the pes, the number of cervical vertebrae, the increasing length of the metatarsal from the first to the fourth one, along with the general proportions are similar to those of *Macrocnemus* (Peyer, 1937; Rieppel, 1989) and, possibly of *Cosesaurus* (as redescribed by Sanz & Lopez-Martinez, 1984). On the other hand, the cervical vertebrae are proportionally longer and narrower than in *Macrocnemus*, the sixth and seventh cervical vertebrae are about 2.5 times longer than mid dorsal ones (only two times in *Macrocnemus*, Wild, 1980b); the posterior stylopodia are slightly longer than the related zeugopodia (in *Macrocnemus* they are shorter, or at least subequal; Rieppel, 1989).

These latter characters, along with the presence of an elongated first phalanx of the fifth toe are all considered as synapomorphies of the Tanystropheidae, the family that comprises *Tanystropheus* and *Tanytrachelos* (Olsen, 1979; Evans, 1988). Few elongated vertebrae collected from the Argilliti di Riva di Solto (Norian) in a locality near Bergamo, have been described by Wild (1987) as cervical vertebrae of a new *Tanystropheus* species, *T. fossai* (Wild, 1987). These vertebrae are very different from those of *Langobardisaurus*, because they show a lateral crista near their posterior end (lacking in *Langobardisaurus*), and are amphicoelous, as in other *Tanystropheus* species.

Langobardisaurus pandolfii shows procoelous vertebrae, like *Tanytrachelos* (Olsen, 1979), and three-cusped teeth, like juvenile individuals of *Tanystropheus longobardicus* (Wild, 1973). On the other hand, *Langobardisaurus* does not fit completely the diagnosis for the Tanystropheidae, because these latter are defined also by the presence of 12 cervical vertebrae, of a reduced phalangeal formula for the manus, of a fourth metatarsal shorter than the third one and by the presence of postcloacal bones in some specimens (Wild, 1973; Olsen, 1979; Evans, 1988), representing sexual dimorphism (Wild, 1973). All these characters are lacking in *Langobardisaurus*. A similar condition may be found in *Cosesaurus*. This reptile, known only by one specimen, was considered as a proto-bird (Ellenberger & de Villalta, 1974; Ellenberger, 1977). More recently, however, it was redescribed as a prolacertiform (Sanz & Lopez Martinez, 1984). Judging from the photos and figures from Ellenberger (1977, p. 80, fig. 1; p. 87, fig. 12), *Cosesaurus* shows some similarities with *Langobardisaurus* (general *Macrocnemus*-like proportions, number of cervical vertebrae, presence of elongated first phalanx of the fifth toe), but it has single cusped teeth and rather short cervical vertebrae.

Systematic position of *Langobardisaurus*.

The systematic position of the Prolacertiformes has been debated until recently. Gow (1975), Benton (1985), Carroll (1988) and Evans (1988), considered these reptiles as belonging to the Archosauromorpha, possibly representing the sister group of the archosaurs. On the other hand, Peyer (1931, 1937) and Wild (1973, 1978, 1980a, b, 1987) classified them as early lacertilians. It is beyond the scope of this paper to attempt any revision of the position of the Prolacertiformes as a group and they are considered here as belonging to the archosauromorph lineage, following Carroll (1988) and Evans (1988).

The analysis of the *Langobardisaurus* skeleton, however, may add knowledge to the relationships among prolacertiform reptiles. Two main hypotheses were proposed by previous authors: Gow (1975), Olsen (1979), Wild (1980a) and Benton (1985), considered *Macrocnemus* as the sister group of *Prolacerta*, and *Tanystropheus* as the sister group of *Tanytrachelos*. These two latter genera were grouped in the family Tanystropheidae (Olsen, 1979) representing the sister group of *Prolacerta* plus *Macrocnemus*. Tschanz (1986) and Evans (1988) suggested instead that the similarities between *Macrocnemus* and *Prolacerta* are due to the retention of primitive characters in the former genus, rather than to true synapomorphies. For this reason, Evans (1988) classified *Macrocnemus* as the sister group of the tanystropheids plus *Cosesaurus*. The characters shared by *Langobardisaurus* (and possibly by *Cosesaurus*) with *Macrocnemus* may be interpreted in the same way, as primitive conditions, while the more elongated cervical vertebrae, the elongate first phalanx of the fifth toe (Fig. 9), and the fused "lumbar" ribs may suggest relationships with the Tanystropheidae. *Langobardisaurus*, however, cannot be considered as a tanystropheid, unless the family diagnosis is modified. Too many key characters, especially skull elements, are unknown in *Langobardisaurus*, thus it is not advisable to emend the diagnosis for the Tanystropheidae on these bases. On the other hand, available data suggest that *Langobardisaurus* is the closest relative of the Tanystropheidae. *Cosesaurus* might be the sister group of *Langobardisaurus* plus the Tanystropheidae. This assessment, if confirmed, will give further support to the phylogenetic model proposed by Evans (1988).

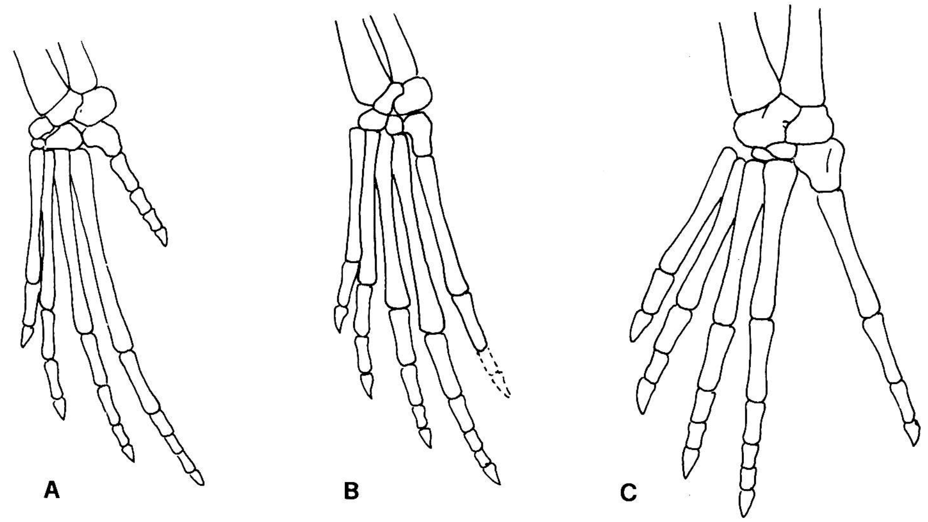

Fig 9 - Comparison among the tarsi and feet of *Macrocnemus* (A), *Langobardisaurus* (B), and *Tanystropheus* (C). A and C redrawn after Wild (1973). A) Modified according to Rieppel (1989). Drawings not to scale.

A note on "*Tanystropheus*" *antiquus*.

"*Tanystropheus*" *antiquus* (Huene, 1908; Wild, 1980b) is a small-to-medium sized prolacertiform from the Lower Muschelkalk and Upper Buntsandstein (Anisian, Middle Triassic) of Germany, which was considered by Wild (1980b, 1987) as a possible ancestor of *Tanystropheus longobardicus*. However, as already noted by Evans (1988) and by Wild himself (1987), "*Tanystropheus*" *antiquus* does not fit the diagnosis for the genus, nor that for the family Tanystropheidae, since it retains only nine cervical vertebrae (in other *Tanystropheus* species and in *Tanytrachelos* there are twelve cervical vertebrae). In addition, juvenile "*Tanystropheus*" *antiquus* have only single-cusped teeth. It should be advisable to give a new generic name to this taxon. Noteworthy, according to the description by Wild (1980b), "*Tanystropheus*" *antiquus* shows some resemblances with *Langobardisaurus* specimens. It might be hypothesised that "*Tanystropheus*" *antiquus* may have been related to *Langobardisaurus* rather than to other *Tanystropheus* species.

Mode of life.

Both known specimens of *Langobardisaurus pandolfii* were collected in a marine deposit, but many skeletal characters, speak against adaptation to an aquatic environment. The general proportions of *Langobardisaurus pandolfii* (Fig. 10) closely resemble those of *Macrocnemus*, and probably its mode of life was similar. *Macrocnemus* has recently been considered a terrestrial lizard-like reptile (Rieppel, 1989). The same skeletal characters supporting terrestrial habits in *Macrocnemus* can be found also in *Langobardisaurus*: the skeleton is very lighty built with hollow bones, whereas in most aquatic reptiles (e. g. "pachypleurosaurs") the skeleton is more massive, to act as ballast, and pachyostosis is frequently found (Carroll, 1985). The tail of *Langobardisaurus*, like that of *Macrocnemus*, is long but not deep or laterally compressed, as in those reptiles that use the tail for propulsion in water. Both neural spines and chevrons are low, while transverse processes on the proximal caudal vertebrae are very long, preventing lateral undulation of the anterior portion of the tail. As noted by Rieppel (1989) these long processes may be related to the insertion of very strong caudifemoralis muscles for powerful retraction of the femur. This latter movement is useful mainly for walking and running, and such a specialization would make little sense in an aquatic animal (Rieppel, 1989). Again, the presence of a posterior process on the second sacral vertebra has been related to terrestrial locomotion (Rieppel, 1989). The fifth metatarsal is hooked, and a well developed lateral process (implied in ventroflexion of the foot during walking) is present on its ventral margin, supporting the hypothesis of adaptation toward terrestrial locomotion. The first four metatarsals and the modified phalanx of the first toe, are elongate and closely associated, forming probably a single functional unit, possibly a device to increase the propulsive force produced by plantarflexion as suggested for *Macrocnemus* (Rieppel, 1989).

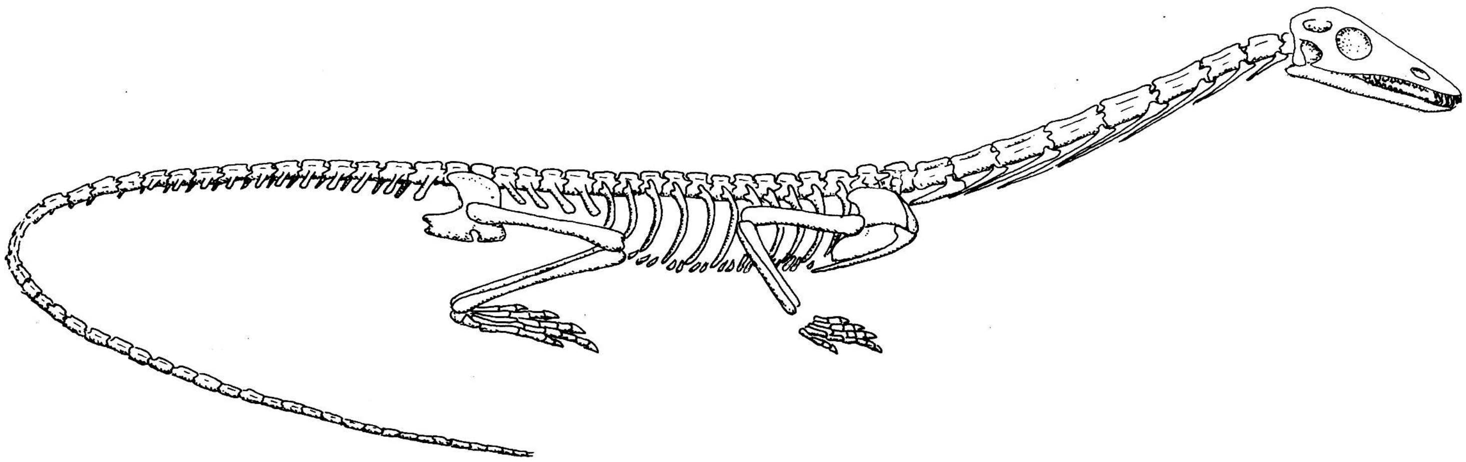

Fig. 10 - *Langobardisaurus pandolfii*. Restoration of the skeleton. The reconstructions of the skull and of the anterior portion of the neck are tentative.

The dentition suggests a terrestrial environment: three-cusped teeth are widespread among a great variety of extant insectivorous reptiles (Edmund, 1969), and the same diet was suggested for juvenile specimens of *Tanystropheus longobardicus* (Wild, 1973). According to Bramble & Wake (1985), Hiiemae & Crompton (1985) and Hildebrand (1978) insects can be considered as liquid-filled tubes and the main difference consists in the thickness and rigidity of the walls of the tube, that is, of the exoskeleton. Larvae are soft and they can be crushed in a "mortar and pestle" system, while the exoskeletons of coleopterans are managed better with shearing cusps. For this reason, the dentition of many insectivorous mammals, have both crushing and shearing structures. The bulky three-cusped posterior teeth of *Langobardisaurus* may have played both roles, enabling the animal to feed on a wide variety of insects. It cannot be excluded that, at least as an adult, *Langobardisaurus* might have fed also upon small vertebrates, like the tiny lepidosauromorph (MCSNB 4862, pers. obs.) that was collected in the same deposit. Many insects (dragonflies and coleopterans) have been collected from the Argilliti di Riva di Solto (Riva di Solto Shales), also of Norian age (Whalley, 1986). The reptile fauna so far collected from the Argilliti di Riva di Solto is very similar to that of the Calcare di Zorzino (Wild, pers. comm.), possibly reflecting the same terrestrial environment surrounding the basins. The lack of insects in the Calcare di Zorzino reflects probably different modes of fossilization relative to the Argilliti di Riva di Solto, rather than differences in the fauna (Tintori, pers. comm.). In conclusion, it is assumed here that *Langobardisaurus pandolfii* was a terrestrial reptile that probably fed upon insects and other small preys.

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PLATE 1

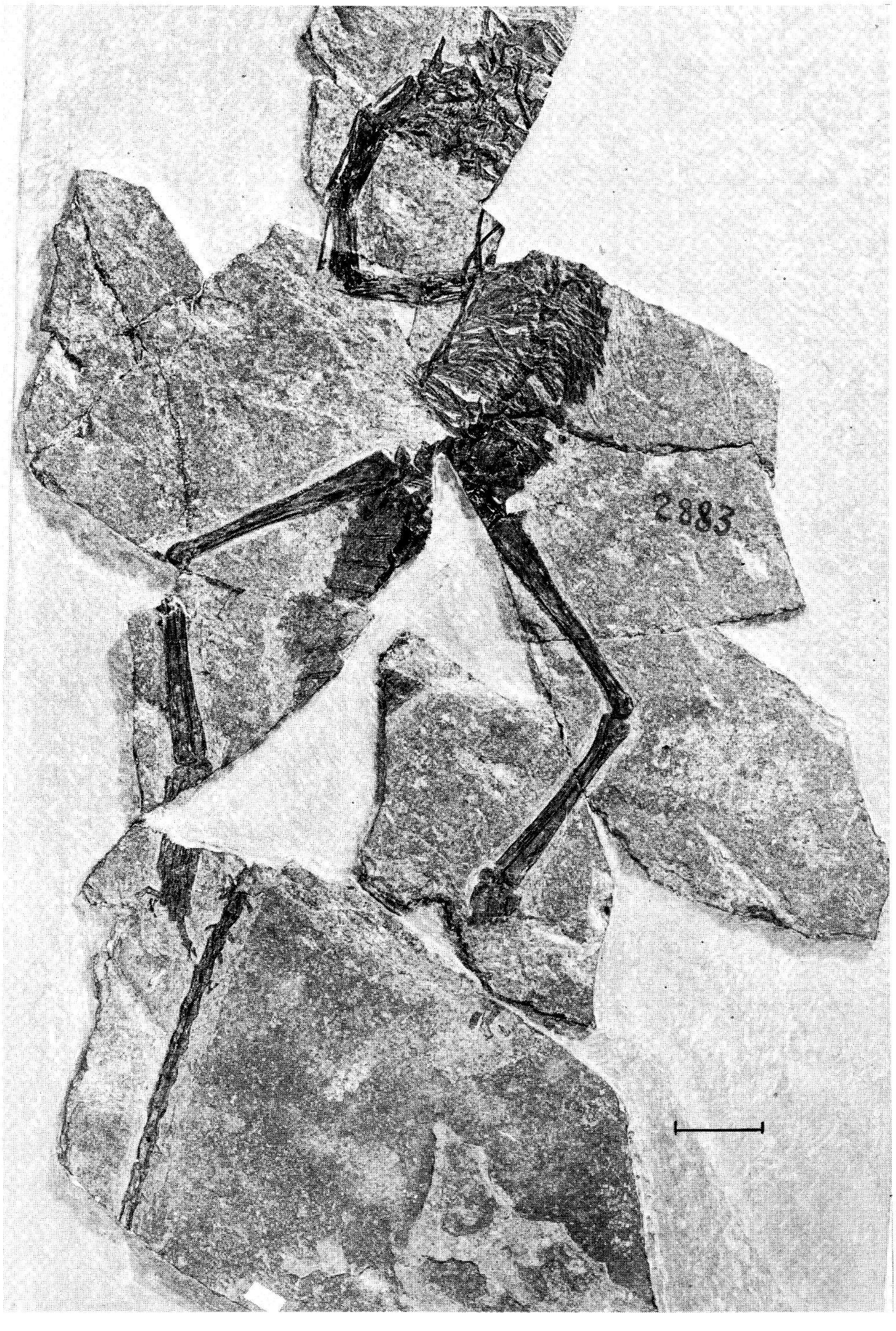
Langobardisaurus pandolfii gen. n., sp. n. Specimen MCSNB 2883, holotype, exposed on ventral side. Scale bar equals 2 cm.

PLATE 2

Langobardisaurus pandolfii gen. n., sp. n. Specimen MCSNB 4860 (paratype) exposed on ventral side. Scale bar equals 2 cm.

PLATE 3

Langobardisaurus pandolfii gen n., sp. n. Specimen MCSNB 4860, the ventral region showing underlying head and neck. Scale bar equals 1 cm.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