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THE ANATOMY AND RELATIONSHIPS OF *ENDENNASAURUS ACUTIROSTRIS* (REPTILIA, NEODIAPSIDA), FROM THE NORIAN (LATE TRIASSIC) OF LOMBARDY

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Key words: Endennasaurus acutirostris, Reptilia, Neodiapsida, Norian, Lombardy (Northern Italy), Description, Systematic discussion.

Riassunto. Una più accurata preparazione dell'olotipo di *Endennasaurus acutirostris*, Renesto 1984, unitamente alla scoperta di un altro esemplare della stessa specie, hanno reso possibile una più completa descrizione dell'osteologia di questo rettile ed una migliore definizione della sua posizione tassonomica. In particolare è stato possibile analizzare parte del tetto cranico dell'olotipo, mentre il nuovo esemplare (paratipo), che conserva l'intera coda, ha potuto fornire indicazioni sulle dimensioni e sulle proporzioni di un esemplare completo. L'analisi dei caratteri ora disponibili indica l'esistenza di affinità tra il genere *Endennasaurus* e un gruppo di Rettili del Triassico: i *Thalattosauria* Merriam.

Abstract. A careful preparation of the holotype of *Endennasaurus acutirostris* Renesto, 1984, that revealed part of the skull roof, along with the finding of a new specimen, allow a more complete descriptiion of the skeletal anatomy of this reptile and a better definition of its taxonomic position. The new specimen (paratype) is partially exposed from dorsal side (the holotype is exposed from the ventral side) and retains almost the entire tail, lacking in the holotype. Analysis of the newly available characters suggests close relationships between *Endennasaurus* and a group of Triassic marine reptiles, the *Thalattosauria* Merriam.

Both *Endennasaurus* specimens were found in the Zorzino Limestone (Norian, Late Triassic), in the small quarry of Endenna, near Zogno, in the Bergamo Prealps (Lombardy, Northern Italy).

Introduction.

A rich vertebrate fauna, among which reptiles are of great importance, lived in the sea and on the carbonatic islands with freshwater reservoirs (Tintori et al., 1985) existing during the deposition of the Zorzino Limestone. Pterosaurs (Wild, 1978), placodonts (Pinna, 1979, 1980) and phytosaur remains have been collected, along with strange diapsids like *Drepanosaurus* Pinna, 1984 and *Endennasaurus* Renesto, 1984.

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Endennasaurus is represented by two specimens, the holotype (5170, Bergamo Museum of Natural Sciences), exposed from the ventral side and lacking the left posterior limb and almost the entire tail, and a second specimen (paratype MBSN 27 in the same collection) exposed from the dorsal side and consisting of few dorsal vertebrae and ribs, part of the pelvic girdle, the right femur and the complete tail.

After the preliminary note (Renesto, 1984), M. Pandolfi of the Bergamo Museum of Natural Sciences, prepared the specimens, exposing part of the skull roof of the holotype, by working on the counterpart of the stone slab.

Analysis of the skeletal features now visible allows a more complete description of the anatomy and mode of life of this unusual reptile, along with a more precise definition of its taxonomic position, suggesting the existence of close relationships between this genus and another group of Triassic marine reptiles, the Thalattosauria Merriam.

Measurements.

To the measurements listed in Tab. 1, can be added an appraisal of the full length of a complete specimen of *Endennasaurus acutirostris*, since the holotype (5170) and paratype (MBSN 27) are almost the same size, the length of the tail of paratype can be added to the length of the precaudal part of the skeleton of the holotype, obtaining a length of about 110 cm, with the tail making up at least three fifths of the entire length.

Palaeontological description

Class Reptilia

Superdivision Neodiapsida Benton, 1985

Family *Endennasauridae* Carroll, 1988

Genus *Endennasaurus* Renesto, 1984

Type-species: *Endennasaurus acutirostris* Renesto, 1984

Generic diagnosis. Skull narrow and elongate, premaxillae long, forming anteriorly a pointed rostrum and posteriorly a well developed process; both upper and lower jaw and palatine bones toothless; frontals long and narrow, forming most of the upper margin of the orbits; occiput lying anteriorly to the quadrate suspension; upper temporal fenestra slit like or closed. Neck rather elongate, vertebrae amphicoelous; 12 cervical, 16 dorsal, 2 sacral and up to 67 caudal vertebrae. In both cervical and dorsal vertebrae the length of the centrum is two times its heigth; intercentral haemal arches in the tail. Pectoral girdle with scapula and coracoid co-ossified; expanded "C" shaped clavicles and an interclavicle with a long posterior stem. Pelvic girdle with small thy-

roid fenestra, ischium with small posterior tubercle; ilium stout with a long horizontal process posteriorly directed. Humerus stout, with expanded and flattened distal head. Femur slender and about twenty per cent longer than the humerus. Sligthly reduced ossification in the carpus and in the tarsus. The carpus is represented by the ulnare, intermedium and centrale (the radiale was retained as cartilage) along with the first four distal carpals. Fifth distal tarsal lost; fifth metatarsal weakly hooked; phalangeal formula of the pes primitive: 2, 3, 4, 5, 4.

	Holotype (5170)	Paratype (MBSN 27)
Skull length from the tip of the snout to the relative quadrate suspension	84	
Skull length from the tip of the snout to the occipital area	77	
Length of the left orbita	11	
Width of the left orbita	8	
Length of the frontal bone	12	
Length of the premaxilla	36	
Length of the fifth cervical vertebra	10	
Length of the 10th cervical vertebra	12	
Length of the fourth dorsal vertebra	11	
Length of the second sacral vertebra	10	9
Length of the first caudal vertebra	10	9
Length of the fifth caudal vertebra	11	10
Length of the humerus	50	
Length of the radius	27	
Length of the ulna	27	
Length of the femur	58	56
Length of the tibia	31	
Length of the fibula	31	

Tab. 1 - Measurements (in mm) of the skeletal elements of the two *Endennasaurus acutirostris* specimens.

Endennasaurus acutirostris Renesto, 1984

Endennasaurus acutirostris Renesto, 1984, p. 165, pl. 11-12, fig. 1-3.

The skull. The skull (Fig. 1, 2) shows a long pointed outline; as described in the preliminary note (Renesto, 1984) the skull of the holotype is transversely broken in the region of the parietals; in addition, the anterior part of the skull had been partially

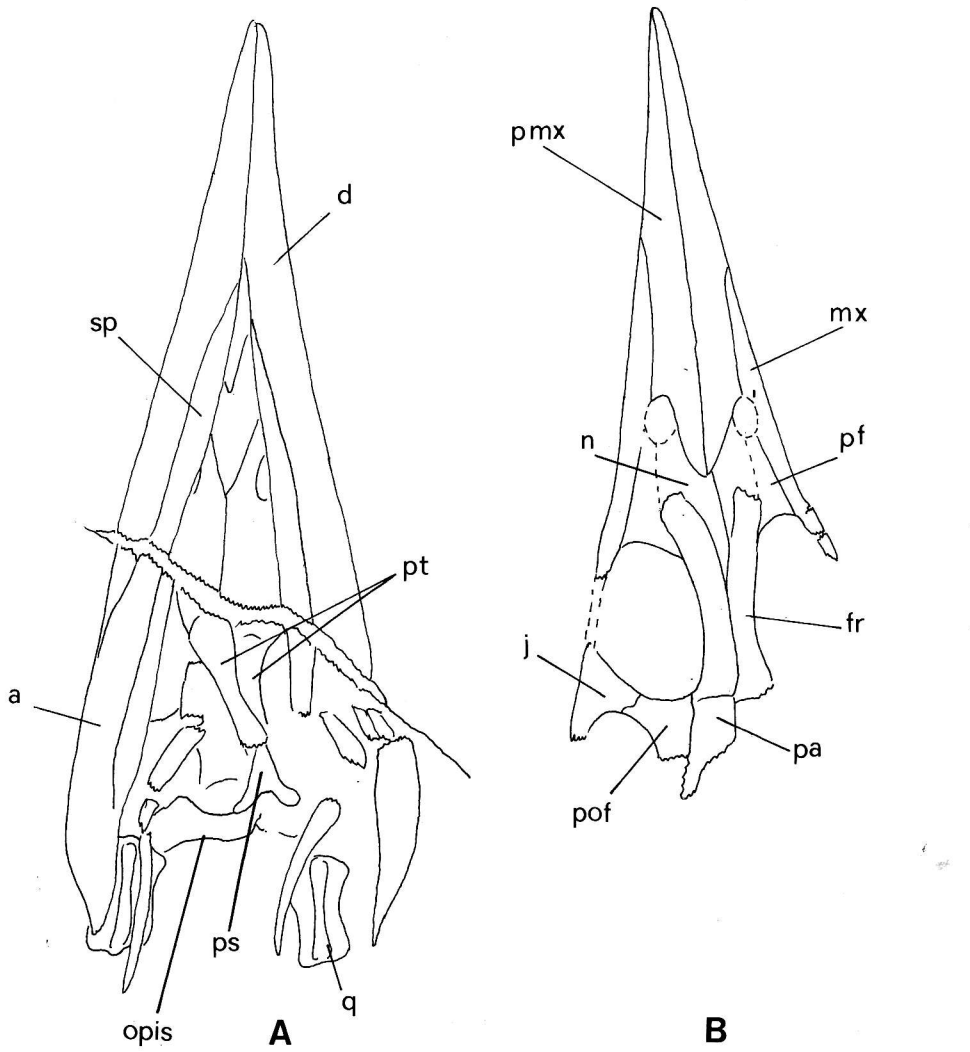

Fig. 1 - *Endennasaurus acutirostris*. Schematic sketch of the ventral (A) and dorsal (B) surfaces of the skull. Scale bar equal to 1 cm.

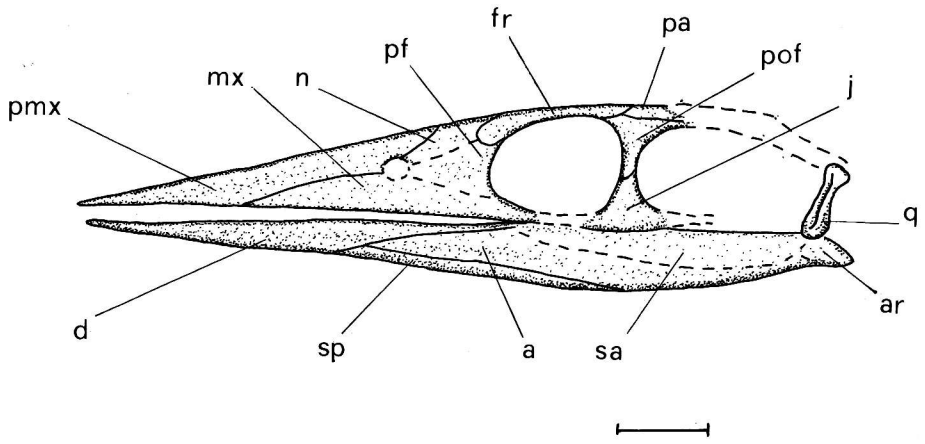

Fig. 2 - *Endennasaurus acutirostris*. Restoration of the skull in lateral view. Scale bar equal to 1 cm.

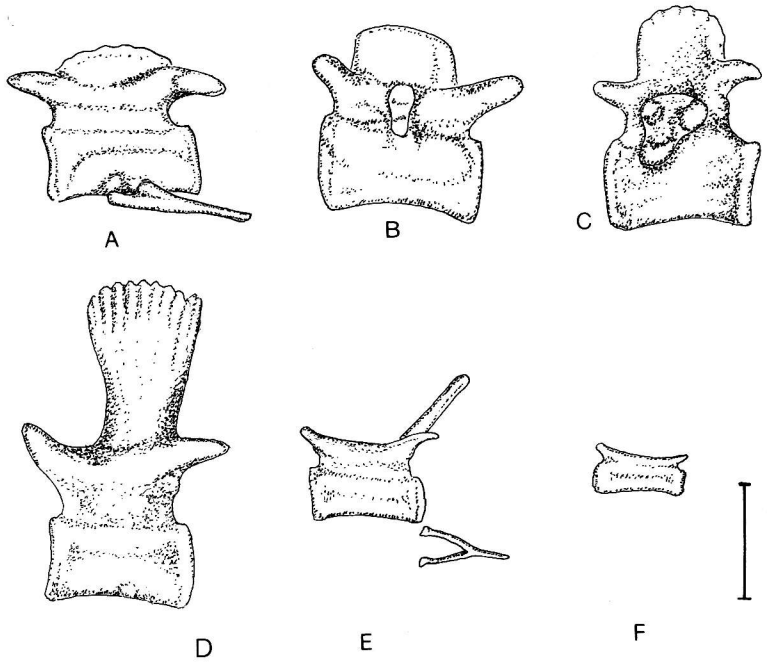

Fig. 3 - *Endennasaurus acutirostris*. A) 9th cervical vertebra; B) 2nd dorsal vertebra; C) 2nd sacral vertebra; D) 5th caudal vertebra; E) 30th caudal vertebra; F) 67th caudal vertebra (A, B, C and D are drawn from the holotype, E and F from MBSN 20). Scale bar equal to 1 cm.

shifted posteriorly, under (looking at the specimen from the ventral side) the posterior part for about half a centimeter length. The whole skull appears to be shorter than its actual length.

In ventral view (Fig. 1A), can be seen the posterior forked end of a thin parasphenoid and the stout left opisthotic with an enlarged distal portion. The pterygoids are stout in their posterior part, becoming thin and expanded anteriorly; this area is smooth and toothless. The palatines and vomers also are toothless. The quadrate is broad and elongate, both medial and lateral margin are concave and a stout anterior ridge is present in the middle of the bone.

The dorsal portion of the skull (Fig. 1B) is here described for the first time. The paired premaxillae are long and form a pointed rostrum; a well developed posterior process is present, but it doesn't reach the frontals. The nares are shifted back far from the tip of the snout, but their true outline is not clearly recognizable, owing to the crushing of the lateral surface of the region, which makes it difficult to establish the pattern of the skeletal elements. The frontals are long and narrow, expanded and diverging anteriorly; these bones form most of the upper margin of the large orbit. As in *Clarazia* (Rieppel, 1987), the area of the postorbital and postfrontal is occupied by a single postorbitofrontal, with a narrow process meeting the jugal. Only the posterior portion of the jugal is preserved; it probably formed most of the lower margin of the orbit. Remains of a thin posterior process can be recognized; it is not possible to see whether the lower temporal arcade was incomplete or closed by a narrow bar. Only small fragments of the bones that form the posterior region of the skull are preserved - mainly the anterior part of the left parietal. This bone is rather large and its lateral margin lies close to the posterior process of the postorbitofrontal; this disposition

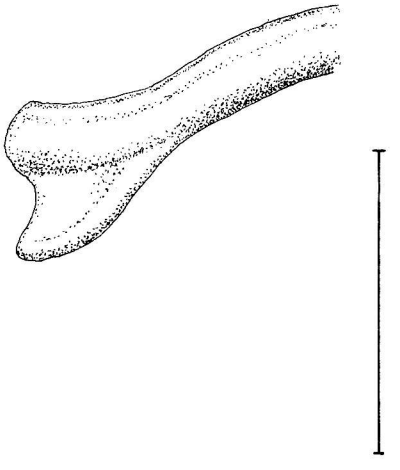

Fig. 4 - *Endennasaurus acutirostris*. Head of the 14th dorsal rib. Scale bar equal to 1 cm.

suggests that the upper temporal fenestra may have been very narrow or closed (Fig. 1B, 2).

Dentition. No teeth are present on the jaws or on the palatine elements (this feature was confirmed also by Xray investigation). The margins of the jaws form a sharp edge that may in life have been covered by a horny beak.

Axial skeleton. The vertebrae (Fig. 3) are amphicoelous. The vertebral column is made up of 30 precaudal (12 cervical, 16 dorsal and 2 sacral) and at least 67 caudal vertebrae. The length of the centra is about two times their heigth both in the dorsal and cervical region; the basis of the neural arch bears stout upward bent prezygapophyses and more horizontal, laterally directed postzigapophyses.

The articulation with the ribs consists of short transverse processes arising from both the neural arch and from the upper part of the centrum (Fig. 3B). This disposition is similar to that described at *Askeptosaurus* Nopcsa (Kühn, 1952; Romer, 1956), and also occurs in pleurosaurs (Carroll, pers. comm.). Neural spines are tall and stout in the caudal portion of the vertebral column. The spines of the first caudal vertebrae (Fig. 3D) are expanded distally and pectinated at their upper margin. The heigth of the neural spines increases from the first to the 30th caudal vertebra, then decreases toward the end of the tail. In the caudal region the spines tend to slant posteriorly from the middle of the neural arch; this slanting increases distally. Intercentral "Y" shaped haemapophyses are present in the tail.

Ribs. Cervical ribs are two headed, subtriangular in shape and almost straight. Dorsal ribs show an holocephalous head with a ventral process (Fig. 4) that contacts a short process arising both from the neural arch and the centrum as described in Romer (1956) for *Askeptosaurus* and *Thalattosaurus* (the same pattern can be found in pleurosaurs; Carroll, pers. comm.). Dorsal ribs change their outline anteroposteriorly: the first dorsal ribs are semicircular in shape, while the posterior ones show a flattened proximal half. The first sacral rib is stout and straight; the second sacral rib is bent anteriorly. In the holotype, a stout pair of caudal ribs is present on the first caudal vertebra.

Gastralia. *Endennasaurus* shows a well developed series of gastralia; at least 30 gastralia are present, each one made up of a straight median element and two stouter lateral elements; these latter are bent upward in their distal portion.

Appendicular skeleton. *Pectoral girdle.* The pectoral girdle (Fig. 5) consists of paired clavicles, coracoids and scapulae and by a long interclavicle.

Clavicles are slender, curved bones; the interclavicle is enlarged anteriorly and posteriorly it ends in a very long and narrow stem. Scapulae and coracoids are broad, with rounded margins; in the coracoid a small foramen can be detected near to the glenoid region. The scapular blade is low.

Anterior limb. The humerus is stout and massive, with expanded and flattened distal end. A well developed ventral process for the insertion of the pectoralis muscle is present.

Radius and ulna are approximately of the same size, about half the length of the humerus (Fig. 6); both these bones show concave lateral margins and expanded heads.

The carpus (Fig. 7) shows a reduced degree of ossification: a large ulnare meets the intermedium and ventrally only the centrale and four distal carpals are present,

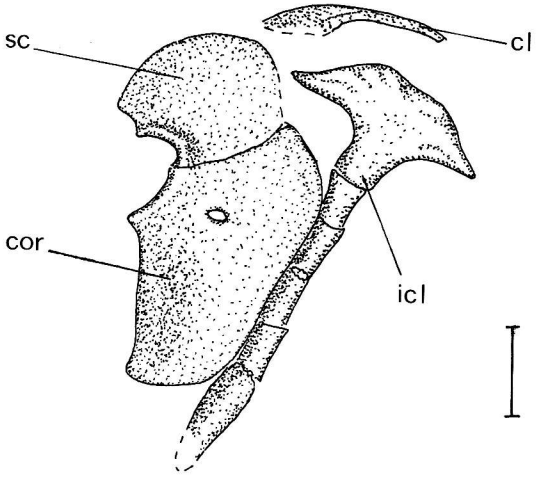

Fig. 5 - *Endennasaurus acutirostris*. Rigth half of the pectoral girdle and the interclavicle. Scale bar equal to 1 cm.

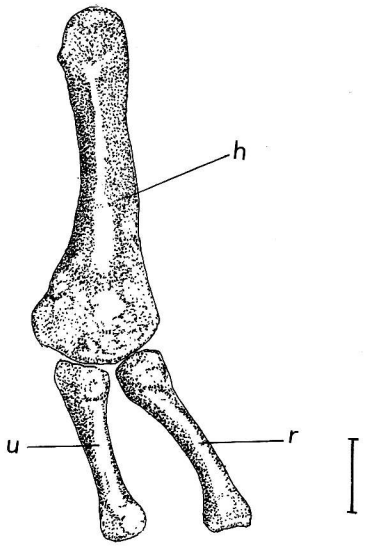

Fig. 6 - *Endennasaurus acutirostris*. Left humerus, radius and ulna in ventral view. Scale bar equal to 1 cm.

the fourth being the largest. The metacarpals are long (the fifth is much stouter than the others), with flat expanded heads. The phalangeal formula for the manus can be stated with confidence only for the first three digits: 2, 3, 4.

Pelvic girdle. The ischium and the pubis are large platelike bones, forming a well developed puboischiadic plate, interrupted by a small thyroid fenestra. A posterior tubercle is present on the ischium. The ilium is stout and long, with a great horizontal process posteriorly directed (Fig. 8, 9); the shape of this bone is almost identical to that one of *Askeptosaurus* (Kühn, 1952). Deep grooves in the medial surface of the horizontal process testify the insertion of powerful tail muscles.

Posterior limb. The femur (Fig. 10) is a slender bone, more gracile than the humerus; its proximal head is flat and shows a gently convex outline; a strong trochanter can be seen on the ventral surface of the bone; at its distal end the femur shows two distinct articular areas separated by a medial concavity.

Tibia and fibula are stout bones, about half the length of the femur. The fibula shows a narrow proximal area for the articulation with the tibia and a large distal head, with a concave outline where it contacts the astragalum, somewhat flatter than that of the articular area for the calcaneum.

The tarsus (Fig. 10, 11) consists of a large astragalum with convex proximal outline, a rounded calcaneum, a single small centrale and four distal tarsals; the second and third distal tarsals seem to be partially fused together; the fourth distal tarsal is the largest and its outline is subtriangular, following the shape of the contacting bones; the astragalum proximally and the upper part of the fifth metatarsal laterally. This latter is short and broad, with a medial embayment that gives it a weakly hooked outline.

The phalangeal formula for the foot is primitive: 2, 3, 4, 5, 4. Each digit ends in a claw.

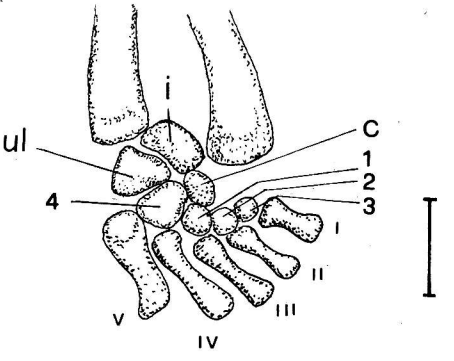

Fig. 7 - *Endennasaurus acutirostris.* Rigth carpus in ventral view. 1-4) Distal carpals; I-V) metacarpals. Scale bar equal to 1 cm.

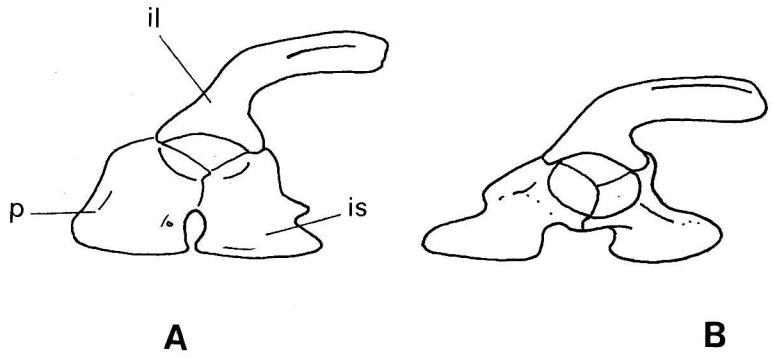

Fig. 8 - Comparison between the pelvic girdles of *Endennasaurus* (A) and *Askeptosaurus* (B). The two drawings are not at the same scale.

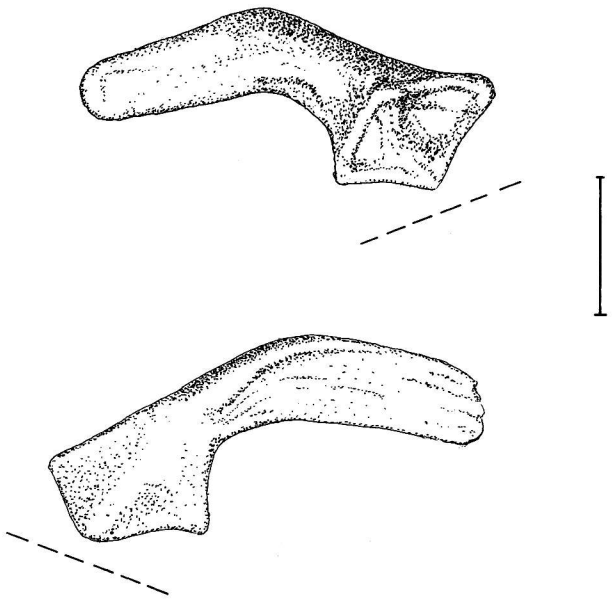

Fig. 9 - Lateral (above) and medial (below) views of the ilium of *Endennasaurus acutirostris*. Scale bar equal to 1 cm.

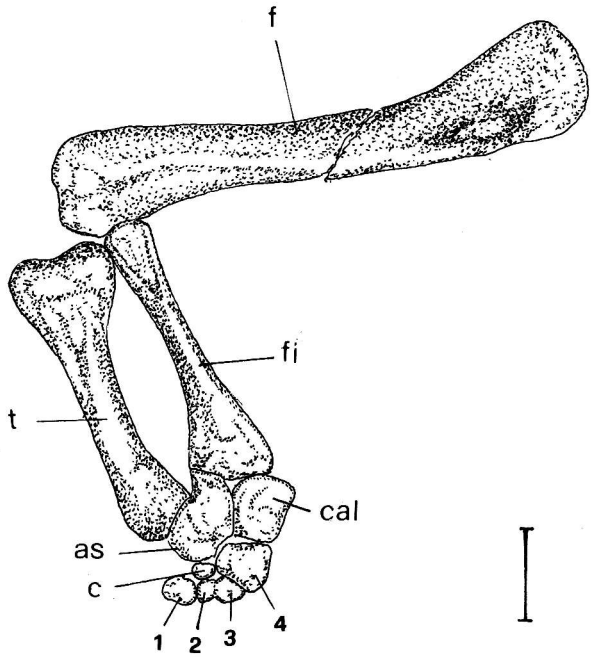

Fig. 10 - *Endennasaurus acutirostris*. Rigth posterior limb in ventral view. 1-4) Distal tarsals. Scale bar equa to 1 cm.

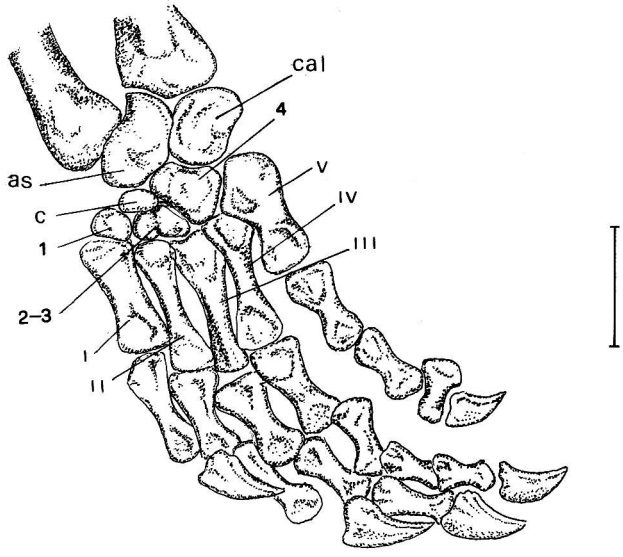

Fig. 11 - *Endennasaurus acutirostris*. Rigth pes in ventral view. 1-4) Distal tarsals; I-V) metatarsals. Scale bar equal to 1 cm.

Systematic discussion.

The combination of characters shown by *Endennasaurus acutirostris*, make its taxonomic position difficult to establish. In the preliminary note (Renesto, 1984) it was classified as an eosuchian, but after the more restrictive definition of this group by Carroll (1988), *Endennasaurus* can't be considered as belonging to this taxon.

Benton (1985), in his cladistic "Classification and phylogeny" of the diapsid reptiles, erected a new taxon, the Superdivision *Neodiapsida*, including all diapsid reptiles, except for *Petrolacosaurus* and few other genera. Many of the synapomorphies shared by the *Neodiapsida* can be detected in *Endennasaurus* testifying its belonging to this group. These are: the absence of teeth on parasphenoid, the absence of a large olecranon, the presence of a rounded acetabulum and of a slender sygmoidal femur, more than 10 per cent longer than the humerus.

Within the Superdivision *Neodiapsida* there is a group of Triassic marine reptiles showing relationships with *Endennasaurus*: the *Thalattosauria* Merriam. Benton (1985) grouped two marine reptiles from the Middle Triassic of Switzerland and North America in the family *Thalattosauridae: Askeptosaurus* Nopcsa and *Thalattosaurus* Merriam. More recently Rieppel (1987) considered two other reptiles from the Middle Triassic of Switzerland, *Clarazia schinzi* Peyer and *Hescheleria rubeli* Peyer, grouped in the family *Claraziidae*, as closely related to *Thalattosaurus*, with *Askeptosaurus* as sister group. According to Rieppel (1987) all these genera form a plesion, the *Thalattosauria* Merriam.

The characters linking the *Thalattosauria* as a monophyletic group are the following ones (Benton, 1985; Rieppel, 1987):

1) premaxillae contacting the frontals; 2) premaxillae elongated, forming a slender rostrum; 3) upper temporal fenestra slit like or closed; 4) lower temporal fenestra open or bounded by a weak bar; 5) occiput lying anteriorly to the relative quadrate suspension; 6) scapula and coracoid short and broad; 7) thyroid fenestra on the pelvis; 8) no posterior process on the ischium; 9) clavicle expanded; 10) no entepicondilar foramen in the humerus; 11) 13-14 cervical vertebrae; 12) thecodont/pleurothecodont recurved teeth; 13) small limbs; 14) reduced ossification both in the carpus and in the tarsus.

Endennasaurus shares with the *Thalattosauria* character 2-10, but not character 1 (the nasals retain their primitive position along the midline of the skull), 11 (*Endennasaurus* has 12 cervical vertebrae), 12 (teeth are absent), 13 (limbs are of normal size) and 14 (the ossification of the carpus and of the tarsus is only sligthly reduced in *Endennasaurus*).

These differences must be considered separately: the dentition is variable among the thalattosaurs: thecodont in *Askeptosaurus* and in *Thalattosaurus*, pleurodont in *Clarazia*. The pattern of the carpus and of the tarsus, along with the greater size of the limbs are probably due to a lower degree of adaptation toward aquatic life. The lack of contact between the premaxillae and the frontals and the primitive phalangeal

formula of the pes (this last feature is present also in *Clarazia*, described by Rieppel, 1987, p. 112, fig. 5d), can be considered as the retention of primitive characters and do not exclude relationships in a large assemblage including *Endennasaurus* and the thalattosaurs. *Endennasaurus* can be considered as the sister group of the *Thalattosauria* (Fig. 12) and following Carroll (1988) it is better to place this genus in a separate family, the *Endennasauridae* Carroll, which diagnosis is given here for the first time:

Family *Endennasauridae* Carroll, 1988

Reptiles of about one meter length; absence of teeth on premaxilla, maxilla and dentary; premaxillae elongated and ending in a pointed rostrum; premaxillae do not reach the frontals;

30 amphicoelous precaudal vertebrae; 2 sacral vertebrae; elongated and laterally compressed tail; interclavicle bearing a long posterior process; pelvic girdle with small thyroid fenestra; humerus shorter but stouter than the femur; carpus lacks ossification of pisiform, fifth distal carpal and radiale; tarsus well ossified, except for the absence

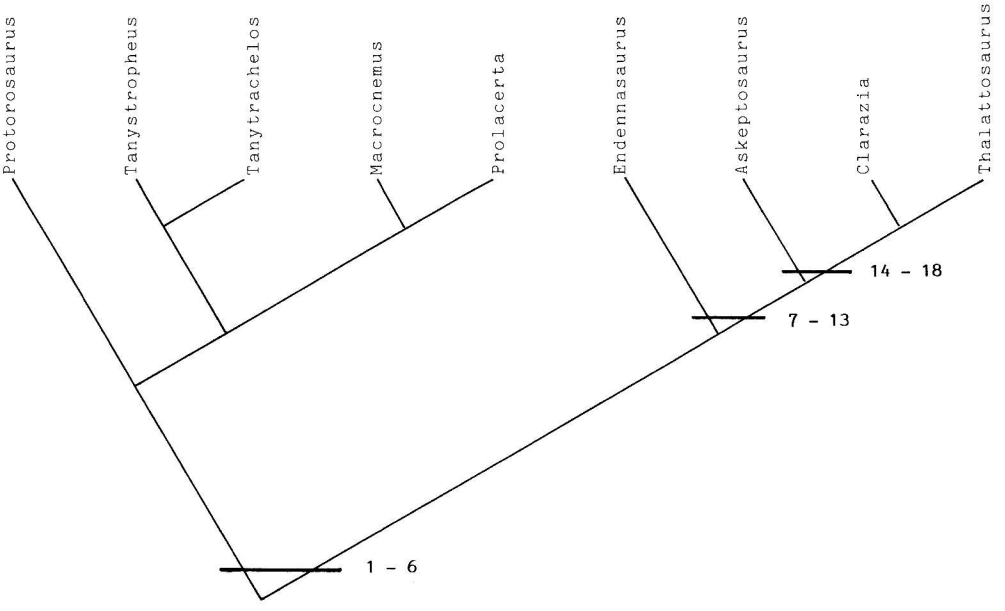

Fig. 12 - Hypotesized relationships occuring among *Endennasarusus*, the *Thalattosauria* and primitive archosauromorph reptiles. Synapomorphies are: 1) vertebrae not nothocordal; 2) no entepicondilar foramen in the humerus; 3) two headed cervical ribs; 4) 8-12 cervical vertebrae; 5) loss of fifth distal tarsal; 6) fifth metatarsal incipiently hooked and articulating with fourth distal tarsal; 7) upper temporal fenestra slit like or closed; 8) lower temporal fenestra open or bounded by a weak bar; 9) premaxillae anteriorly elongated and forming a slender rostrum; 10) occiput lying forward to the relative quadrate suspension; 11) scapula and coracoid short and broad; 12) no posterior process on the ischium; 13) thyroid fenestra on the pelvis; 14) premaxillae contacting the frontals; 15) 13-14 cervical vertebrae; 16) small limbs; 17) reduced ossification both in the carpus and in the tarsus; 18) fifth metatarsal not hooked. Relationships within the Prolacertiformes are from Benton (1985); relationships within the *Thalattosauria* are from Rieppel (1987)

of the fifth distal tarsal; fifth metatarsal incipiently hooked; primitive phalangeal formula in the pes.

The analysis of the skeletal characteristics of *Endennasaurus* may give some indications to define the relationships existing among the *Thalattosauria* and other diapsid reptiles. The taxonomic history of the *Thalattosauria* is indeed rather troubled: they were considered as eosuchians (Romer, 1956), as rhyncocephalians (Kühn, 1969) and recently Kühn-Schnyder (1988) considered the absence of the upper temporal fenestra not as a derived feature, concluding that the *Thalattosauria* are not diapsids.

Many other characters however identify the thalattosaurs as diapsids (Benton, 1985; Carroll, 1988) and following Benton (1985) they share all the synapomorphies of the *Neodiapsida*, while at a lower taxonomic level their position remains uncertain.

Some skeletal characters that can be detected in *Endennasaurus* may suggest relationships between the *Thalattosauria* and primitive archosauromorph reptiles. These elements are: a) the number of cervical vertebrae and their shape; b) the shape of the head of the cervical ribs; c) the vertebrae not nothocordal; d) the lack of entepicondilar foramen in the humerus; e) the absence of ossified sternal plates; f) the lack of the fifth distal carpal and tarsal; g) the incipient hooking of the fifth metatarsal, whose large proximal head articulates with the fourth distal tarsal (as pointed out by Benton, 1985, also the *Thalattosauria* show many archosauromorph features: c, d, e, f of the preceeding list).

The disposition of the bones in the tarsus of *Endennasaurus* is quite similar to that of *Protorosaurus* as figured by Carroll (1988) and of *Prolacerta* as figured by Gow (1975). The existing differences can be due to a reduced ossification of skeletal elements, the beginning of a trend leading to the thalattosaurian reptilian type.

Thus the relationships among *Endennasaurus*, the thalattosaurs and the primitive archosauromorph reptiles may have been as shown by cladogram in Fig. 12, and the hypothesis of Currie (1981) about the existence of relationships between thalattosaurs and prolacertiformes will be reinforced.

Mode of life.

As suggested by the general structure of the skeleton (Fig. 13) *Endennasaurus* shows a certain degree of adaptation toward aquatic life, expressed mainly by the stout, distally enlarged humerus, the massive gastralia and the long, laterally compressed tail. As pointed out before, this adaptation is higher in the thalattosaurs and *Endennasaurus* must be considered as a relict, since much more aquatic thalattosaurs are known from the Middle Triassic, while *Endennasaurus* is only known from the Upper Triassic.

Kühn-Schnyder (1988) suggested that the *Thalattosauria* could have moved also on land and had a durophagous diet, consisting of ammonites, bivalves, gastropods and crustaceans.

Endennasaurus could have moved on land better than the thalattosaurs and this reptile probably lived near the coast preying on small organisms. Its long pointed

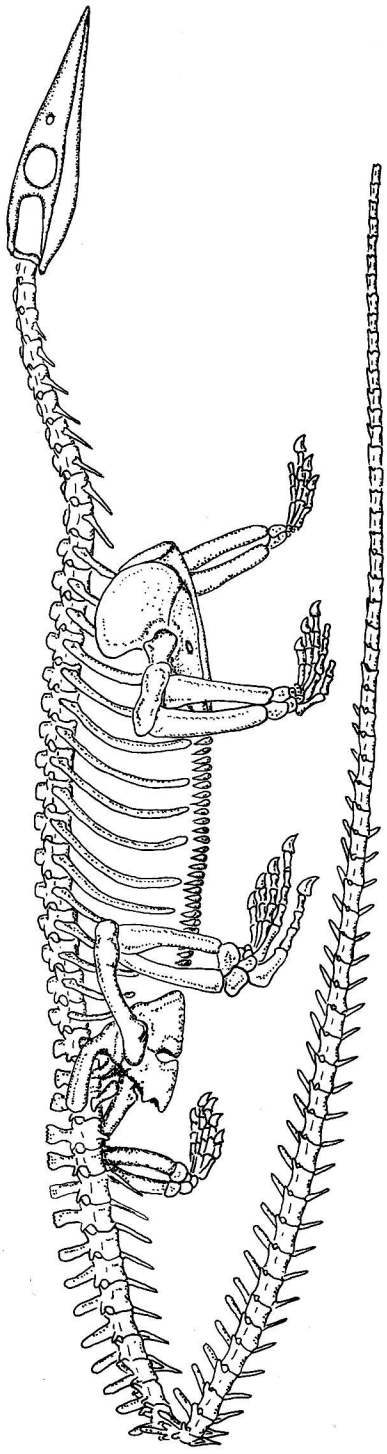

Fig. 13 - *Endennasaurus acutirostris*. Restoration of the entire skeleton.

"beak" does not seem an adaptation to catch fishes or to prey on hard shelled molluscs. *Endennasaurus* preys had to be small animals that did not have a strong shell or exoskeleton, like some crustaceans and small vertebrates.

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List of abbreviations used in figures

a	=	angular	i	=	intermedium	pof	=	postorbitofrontal
ar	=	articular	icl	=	interclavicle	ps	=	parasphenoid
as	=	astragalum	il	=	ilium	pt	=	pterygoid
c	=	centrale	is	=	ischium	q	=	quadrate
cal	=	calcaneum	j	=	jugal	r	=	radius
cl	=	clavicle	mx	=	maxilla	sa	=	surangular
cor	=	coracoid	n	=	nasal	sc	=	scapula
d	=	dentary	opis	=	opisthotic	sp	=	splenial
f	=	femur	p	=	pubis	t	=	tibia
fi	=	fibula	pa	=	parietal	u	=	ulna
fr	=	frontal	pf	=	prefrontal	ul	=	ulnare
h	=	humerus	pmx	=	premaxilla			

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PLATE 32

Endennasaurus acutirostris Renesto, 1984. The holotype 5170. Scale bar equal to 3 cm.

PLATE 33

Endennasaurus acutirostris Renesto, 1984. The holotype 5170. Dorsal view of the skull. Scale bar equal to 1 cm.

PLATE 34

Endennasaurus acutirostris Renesto, 1984. The holotype 5170. Ventral view of the skull. Scale bar equal to 1 cm.

PLATE 35

Endennasaurus acutirostris Renesto, 1984. Paratype MBSN 20. Scale bar equal to 3 cm.

PLATE 36

Endennasaurus acutirostris Renesto, 1984. Paratype MBSN 20. Dorsal and sacral regions in dorsal view. Scale bar equal to 1 cm.


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