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A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese, N. Italy)

Andrea TINTORI Silvio RENESTO
Dipartimento di Scienze della Terra
Università di Milano

KEY WORDS — *Lariosaurus*, *Reptilia*, *Sauropterygia*, *Nothosauria*, *Taxonomy (new species)*, *Triassic*, *N. Italy*.

ABSTRACT — *Lariosaurus valceresii* sp.n. is described on the basis of a well preserved specimen from the Kalkschieferzone of the locality of Ca' del Frate (Viggiù, VA). The specimen, about 1 m long, is dorso-ventrally flattened. The main character of this new species is the very high anterior/posterior limb length ratio, which differentiates it from the well known *L. balsami* Curioni. Being uppermost Ladinian, *L. valceresii* is the youngest species of the genus. On the basis of vertebrate and invertebrate fauna, an alternance of marine and brackish environments is hypothesized, the former of which yields fish and reptiles, the latter mainly conchostracans.

RIASSUNTO — [Un nuovo *Lariosaurus* dalla Kalkschieferzone (Ladinico sommitale) della Valceresio (Varese, Italia) — Viene descritta una nuova specie di *Lariosaurus*, *L. valceresii* sp.n. sulla base di un esemplare molto ben conservato, rinvenuto nella Kalkschieferzone di Ca' del Frate (Viggiù, VA). L'esemplare è lungo circa un metro e si presenta fossilizzato dorso-ventralmente. La principale caratteristica che distingue la nuova specie dal ben conosciuto *L. balsami* Curioni, è la maggior lunghezza relativa dell'omero rispetto al femore. Considerando le lunghezze totali dell'arto anteriore e di quello posteriore negli esemplari di *L. valceresii* si giunge addirittura alla parità, mentre in quelli attribuiti a *L. balsami* Curioni, la differenza tra gli arti si acuisce e ciò indipendentemente dalle dimensioni degli esemplari considerati. Poiché tali forme nuotavano servendosi essenzialmente degli arti anteriori, una maggior lunghezza relativa degli stessi si ritiene ne abbia favorito le capacità natatorie. *L. valceresii* rappresenta la specie di *Lariosaurus* apparsa più recentemente, al termine del Ladinico, quando ancora *L. balsami* era presente.

Vengono inoltre fatte alcune considerazioni paleoecologiche, utilizzando sia i vertebrati che gli invertebrati presenti a Ca' del Frate. Si giunge alla conclusione che il livello fossilifero rappresenti sia episodi marini, con pesci e rettili, che episodi salmastri, ricchi essenzialmente di conchostraci (esterie).

INTRODUCTION

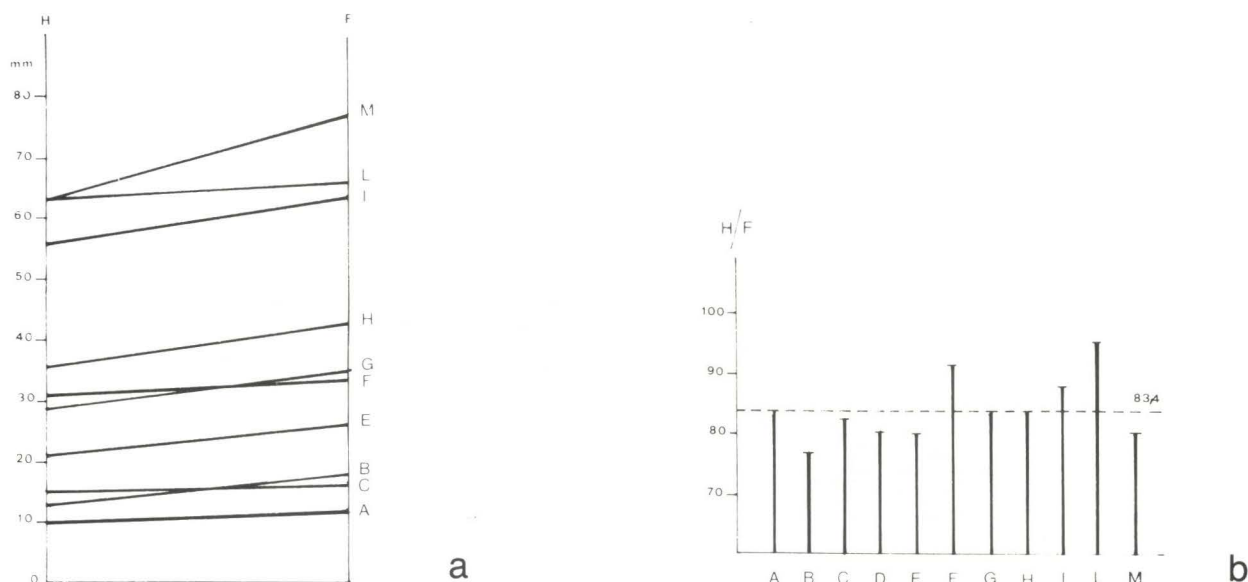
The Kalkschieferzone (Senn, 1924) is the upper member of the Meridekalke and crops out between Valceresio (Varese-Italy) and the Meride area (Canton Ticino - Switzerland). A detailed description of the type section (near Meride) was published by Wirz (1945), who found fish fragments as well as a few invertebrates. More recently Scheuring (1978) studied the microflora of this member, ascribing it to the uppermost Ladinian age.

With respect to vertebrates from the Kalkschieferzone, a few fish have been collected in Italian outcrops at the beginning of this century (De Alessandri, 1910). However, these fishes were not distinguished from those found in the Scisti Ittiolitici di Besano («Grenz-bitumenzone» of Swiss Authors) which have been proved to be a little older (Tintori *et al.*, 1985). The Kalkschieferzone type-section has yielded a small reptile, first described by Kuhn-Schnyder (1974) as *Lariosaurus balsami* Curioni. Recently, the same author (Kuhn-Schnyder, 1987), after a more detailed study

of the same specimen, created for it the new species *Lariosaurus lavizzarii*.

Fossil collection has been random until a few years ago, when a promising outcrop was discovered near Ca' del Frate (Viggiù, Varese); in that occasion a joint project was set up by the Museo Civico di Intrauno Olona and the Dipartimento di Scienze della Terra dell'Università degli Studi di Milano (Tintori *et al.*, 1985).

So far, several hundred fishes have been found, mostly belonging to the very small *Probalecites porroi* (Bellotti) species (Tintori, 1990). A preliminary study of the other material, made by one of us (A.T.), provides a good correlation with the vertebrate fauna found in the Calcare di Perledo-Varenna and described by De Alessandri (1910). In fact, *Probalecites porroi* (Bellotti), *Perleidus altolepis* (Deecke), *Furo trottii* (Balsamo-Crivelli), *Heterolepidotus taramellii* De Alessandri and a new *Peltolepidus* species are known from both localities, while *Legnonotus obtusus* (Tintori & Renesto, 1983) and *Dipteronotus*, have been found only at Ca' del Frate.



Text-fig. 1 - *Lariosaurus* spp. a) Absolute sizes of the humerus compared with those of the femur. b) Humerus/femur length ratio (in percent).

A = *L. balsami*. Perledo, Mariani collection; Museo Civico «E. Caffi» Bergamo (after Mariani, 1923).

B = *L. balsami*. Val Mara; Paläontologisches Museum der Universität Zürich (after Kuhn-Schnyder, 1987).

C = *L. balsami*. Olcio (CO); Musei Civici Lecco n. 663 (pers. obs.).

D = *L. balsami*. (ex *Micromerosaurus* and ex *L. balsami* var. *plinii*). Perledo; Servizio Geologico Italiano, Roma (pers. obs.).

E = *L. balsami*. Perledo; Natur-Museum Senckenberg, Frankfurt am Main (after Peyer, 1933/34).

F = *L. valceresii* n.sp. Estada; Museo Nacional de Ciencias de Madrid (after Sanz, 1976).

G = *L. balsami*. Lierna (CO); Musei Civici Lecco n. 202 (pers. obs.).

H = *L. balsami*. Perledo, Mariani collection; Museo Civico di Storia Naturale Milano (after Peyer, 1933/34).

I = *L. balsami*. Perledo, Curioni collection; Servizio Geologico Italiano, Roma (pers. obs.).

L = *L. valceresii* n.sp. The holotype from Ca' del Frate. Museo Civico di Scienze Naturali Induno Olona.

M = *L. balsami*. Perledo; Bayerische Staatssammlung für Palaeontologie u. historische Geologie, München (after Peyer, 1933/34).

Invertebrates are fairly rare at Ca' del Frate; and mostly represented by the conchostracan crustacean *Palaeolimnadia* (Tintori, in press) as well as a few ostracods and malacostracans.

During the preliminary field work at Ca' del Frate, a well preserved reptile was recovered: the description of this specimen, which at present is the only reptile found at this locality, is the aim of the present paper.

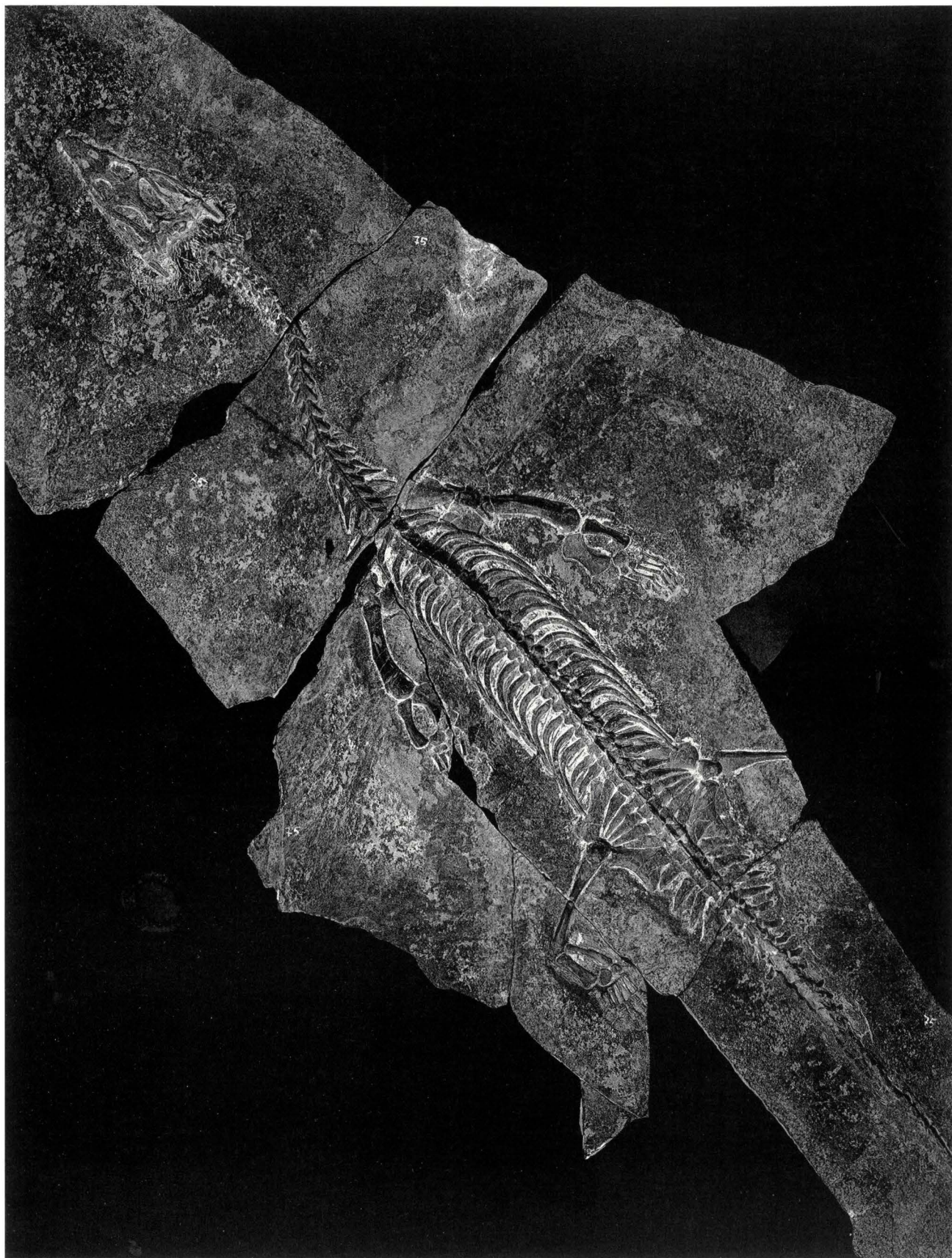
DISCUSSION

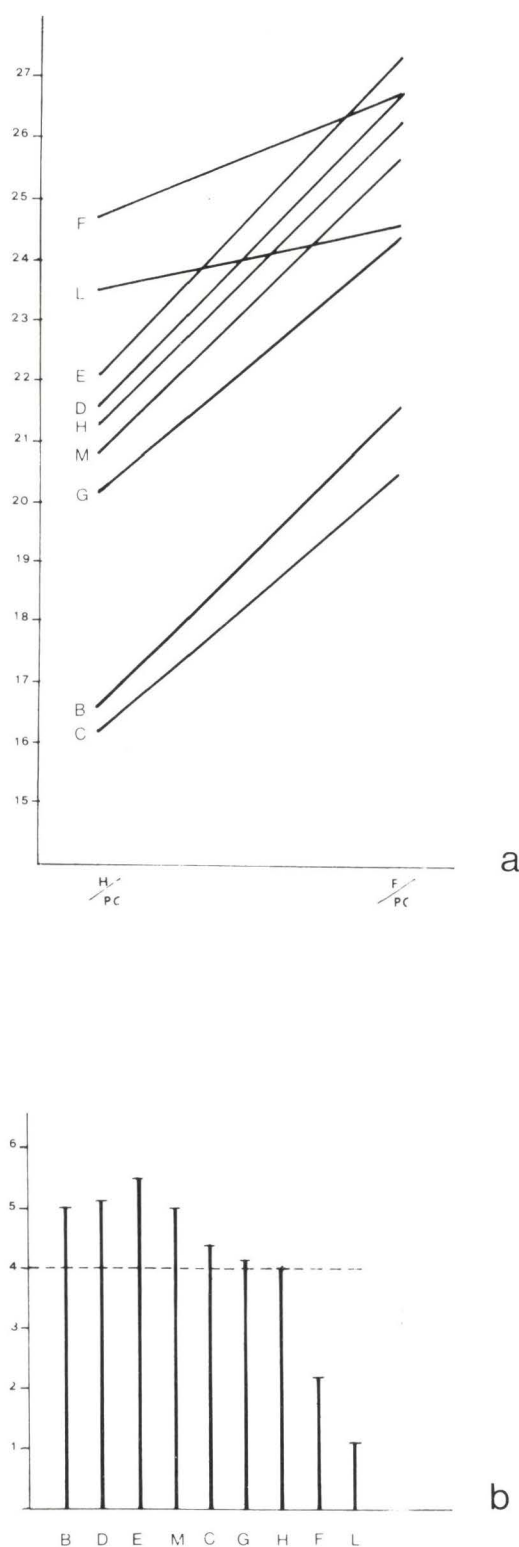
The features of our specimen, including the number of dorsal and cervical vertebrae, are within the standard of the genus *Lariosaurus*. According to Romer (1956) and Sanz (1976), in fact, the number of vertebrae in reptiles can normally vary as much as observed in *Lariosaurus*.

Regarding the species, nearly all the specimens of *Lariosaurus* which were studied have been ascribed to *L. balsami* Curioni 1847. Most of them have been collected in the Perledo area along the Eastern coast of the Como Lake and are referred to with the name of the town in which they are preserved. All the known *Lariosaurus* specimen, except for the holotype of *L. buzzii* Tschanz, are Ladinian. This latter species was erected only recently by Tschanz (1989) on the basis of a single specimen from the uppermost Anisian of Monte San Giorgio. However, there are some very important differences between *L. buzzii* and the other *Lariosaurus* specimens, mainly with respect to the outline and the pattern of the skull. Furthermore, the ulna is not so characteristically flattened and enlarged as in the genus *Lariosaurus* itself, forwarding doubts on the true

EXPLANATION OF PLATE 1

Lariosaurus valceresii n.sp.. Holotype from the Kalkschieferzone di Ca' del Frate (VA) (specimen P500 of the Museo Civico di Scienze Naturali di Induno Olona-VA). Total length: 900 mm.





Text-fig. 2 - *Lariosaurus* spp. a) The ratios between the anterior and posterior stylopodium length toward the precaudal vertebral column length (in percent). b) Differences (in percent) between the two ratios in a). Specimens as in Text-fig. 1.

generic attribution. Kuhn-Schnyder (1987) too described a new species, *L. lavizzarii*, on the basis of the specimen found at the Kalkschieferzone type-section near Meride (Canton Ticino-CH). However, the differences between *L. balsami* and this latter species are very small. According to Kuhn-Schnyder, *L. lavizzarii* is distinguished by a sharper skull outline and by fore-limbs which are remarkably shorter than hind limbs. However, these characters may be due to the early growth stage of the specimen, and we prefer to consider the holotype of *L. lavizzarii* as a juvenile specimen of *L. balsami* (see also Tschanz, 1989, p. 157).

Actually, we found differences in the relative length of limbs in a few other specimens, first of all in the Ca' del Frate *Lariosaurus*, in which the anterior limbs approach the posterior ones in length, while usually the posterior limbs are longer than the anterior ones. That this character is not simply due to allometry in different growth stages is proved by its occurrence in specimens of very different size.

In Text-fig. 1a the absolute values of humerus and femur is compared: three specimens (Ca' del Frate, Estada, Lecco 663) clearly differ from all the other specimens in that they possess a humerus with a size similar to that of the femur. Though the Ca' del Frate specimen is smaller than the München specimen, and has therefore a shorter femur, their humeri are of comparable size. Consequently the Ca' del Frate specimen has a relatively longer humerus than the Monaco one.

The same consideration can be applied to the comparison among the Estada, Lecco 202 and Frankfurt specimens, whose sizes are similar.

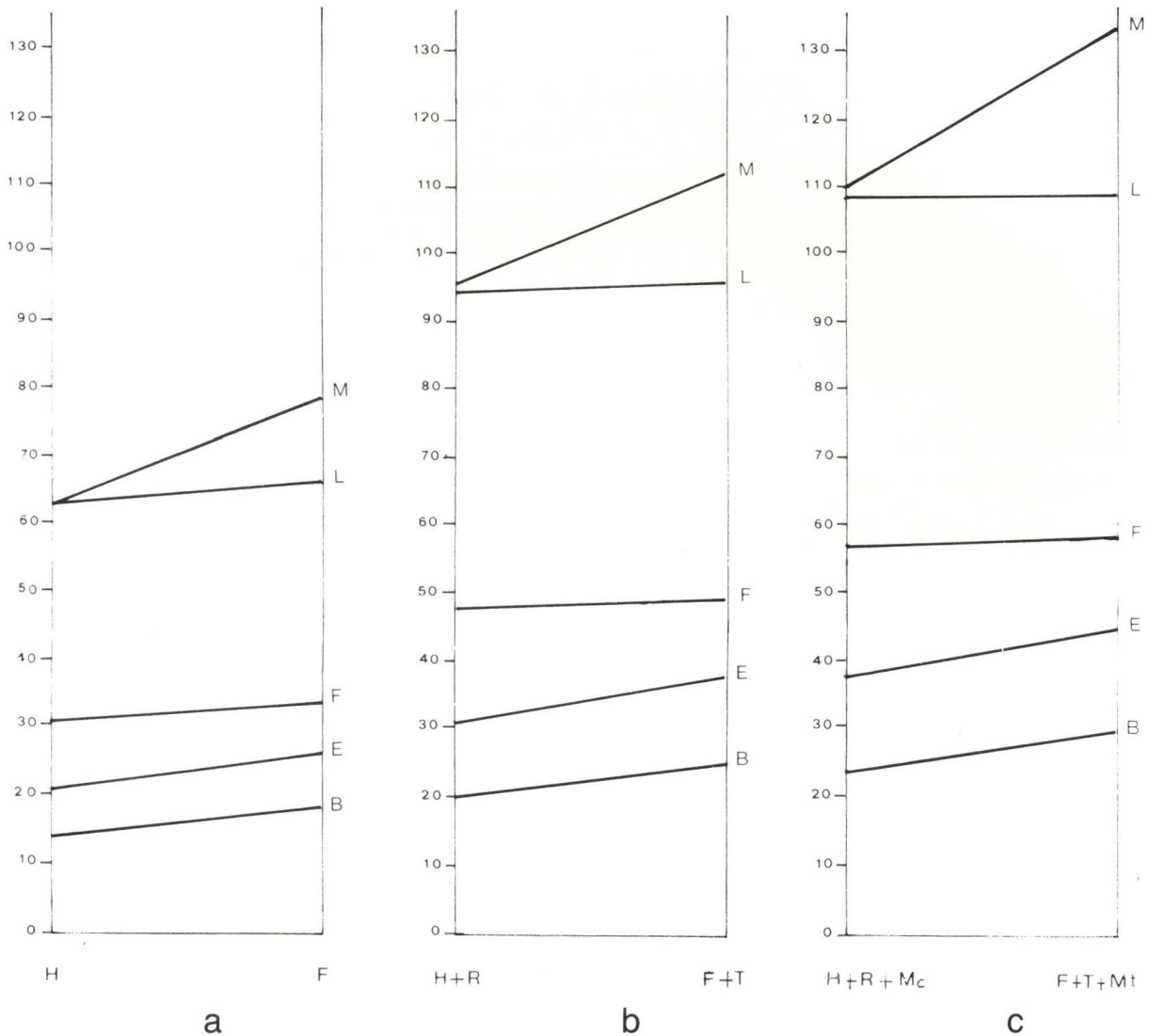
Text-fig. 1b confirms that the specimens from Ca' del Frate and Estada have very high humerus/femur length ratio, whereas the specimen from Val Mara (Kuhn-Schnyder, 1987) has the lowest one.

In Text-fig. 2a the ratios between each humerus and the precaudal vertebral column length are plotted: again, the Ca' del Frate and Estada specimens show a very close affinity. The same result is obtained by calculating the numerical differences between the two ratios, as can be seen in Text-fig. 2b.

In Text-fig. 3 it is possible to observe that, as we add the different limb sections, in Ca' del Frate and Estada specimens the anterior and posterior limbs gradually reach the same size. In all the other specimens, on the contrary, the posterior limbs become proportionally longer than the anterior ones.

Following Sanz (1976), we have used his multivariate analysis, including the measurements of our specimen. As already shown by Sanz (1976), there seem to be no remarkable difference among all the known *Lariosaurus* specimens (excluding *L. buzzii* for the reason above shown).

However, we consider the results obtained by comparing limb lengths, (especially if referred to vertebral



Text-fig. 3 - *Lariosaurus* spp.. a) Comparison between the absolute sizes of humerus and femur. b) Comparison between absolute sizes of humerus + radius and femur + tibia. c) Comparison between absolute sizes of humerus + radius + third metacarpal and femur + tibia + third metatarsal. Specimens as in Text-fig. 1.

column measurements, see Currie & Carroll, 1984) to be much more indicative. Therefore we erect a new *Lariosaurus* species, *L. valceresii* sp.n., based on both the Ca' del Frate and the Estada (*L. balsami* in Sanz, 1976; *L. lavizzarii* in Kuhn-Schneider, 1987) specimens.

The major differences among the three species of *Lariosaurus* (namely uppermost Anisian *L. buzzii*, provided that it really belongs to this genus, the Upper Ladinian *L. balsami*, and the uppermost Ladinian *L. valceresii* sp.n.), are in the orbit length/temporal opening length ratio and in the humerus/femur length ratio. For this latter character, a trend from a relatively short humerus (*L. buzzii*) to a humerus only slightly

shorter than the femur (*L. valceresii*) has been evidenced. As already pointed out by Sanz (1976, 1980) and Kuhn-Schneider (1987), *Lariosaurus* swam in the water mainly by rowing with the anterior limbs. The fact that the anterior limbs themselves became progressively longer with the time could be interpreted as a gradual improvement of the swimming capability.

SYSTEMATIC PALEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
 Suborder NOTHOSAURIA Seeley, 1882
 Family NOTHOSAURIDAE Baur, 1889
 Genus LARIOSAURUS Curioni, 1847

LARIOSAURUS VALCERESII sp.n.
Pl. 1, 2; Text-figs. 4-7

1976 *Lariosaurus balsami* Curioni - SANZ, pp. 547-567, fig. 2.
1987 *Lariosaurus lavizzarii* p.p. - KUHN-SCHNYDER, pp. 18-19.

Diagnosis — *Lariosaurus* with the length of anterior limb of almost the same as that of the posterior one; humerus long and stout, with well developed entepicondylar foramen and supinator process.

Holotype — Almost complete specimen, 900 mm long, Museo Civico di Scienze Naturali di Induno Olona P500 (Italian Government number: 59781).

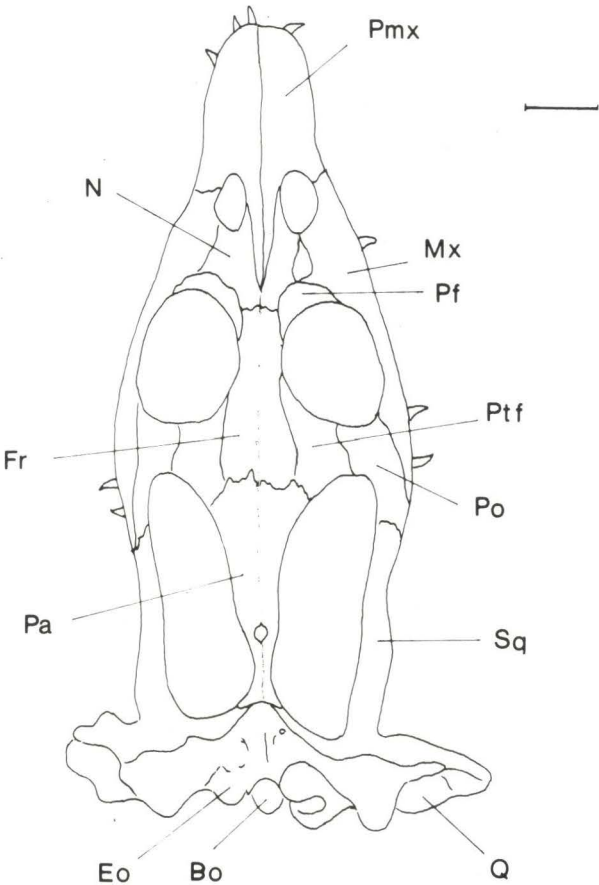
Type locality — Ca' del Frate (Viggiú, Varese, Italy).

Horizons and distribution — The holotype was collected in the Lower part of the Kalkschieferzone (Meride Limestone), uppermost Ladinian. The species is known also from the Muschelkalk of Estada (Spain).

Etimology — Named after the valley (Valceresio) where the type locality lies.

Total length	900
Snout-occipital condyle length	94
Width at nostril level	16
Width at orbit level	31
Orbits length	16 - 16
Orbits width	11 - 8.5
Temporal openings length	30 - 31
Temporal openings width	9 - 11
Right humerus length	63
Right radius length	31
Right ulna length	32
Right metacarpal III	15
Left femur length	66
Left tibia length	30
Left fibula length	30
Left metatarsal III	13

Tab. 1 - *Lariosaurus valceresii* n.sp.. Holotype; measurements (in mm). Double measurements are for the left (first) and the right (second) elements.



Text-fig. 4 - *Lariosaurus valceresii* n.sp.. Holotype. Schematic sketch of the skull in dorsal view. Bo = basioccipital, Eo = exoccipital, Fr = frontal, Mx = maxilla, N = nasal, Pa = parietal, Pf = praefrontal, Pmx = praemaxilla, Po = postorbital, Pt f = postfrontal, Q = quadrate, Sq = squamosal. Scale bar equal to 1 cm.

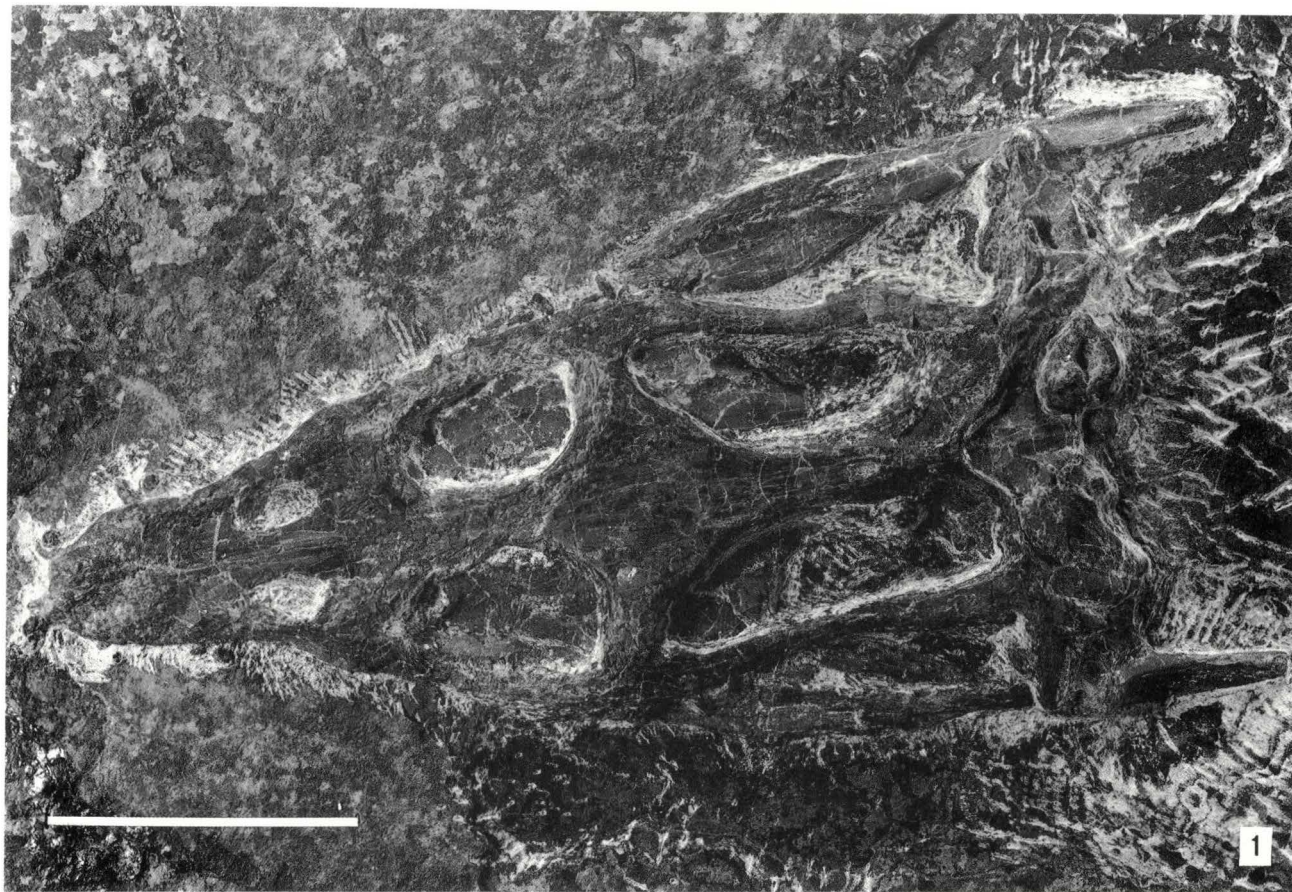
DESCRIPTION

SKULL

The skull is complete (Pl. 2, fig. 1; Text-fig. 4), but the bones, mainly at the orbit level, are crushed or seriously damaged, so that it is difficult to give their detailed description. The pattern of the skull is typical for the genus *Lariosaurus*, though its outline is nar-

EXPLANATION OF PLATE 2

Figs. 1-2 - *Lariosaurus valceresii* n.sp.. Holotype from the Kalkschieferzone of Ca' del Frate (VA) (specimen P500 of the Museo Civico di Scienze Naturali di Induno Olona-VA). 1) The head in dorsal view. 2) The anterior right limb. Scale bar equal to 3 cm.



rower and more triangular in shape than that of *L. balsami*. The temporal openings are about twice as long as the orbits; the latter, as well as the external nares ($L/l = 1.75$), are elliptical ($L/l = 1.45$) rather than sub-circular as in the type species.

The premaxillae are narrow and elongated, bearing few long, pointed teeth. Their posterior border is elongated proximally and builds the anterior part of the naris. The maxillae are large, well expanded in front of the orbits. Lateral to the latter they narrow sharply, while their posterior part tapers gradually and meets the distal border of the postorbitals, ending at the first third of the temporal fossae.

The frontals seem to be fused, however certainty is hindered by poor preservation of the area. They are elongated and a little expanded in the posterior region. Traces of an interorbital canal can be seen at the left orbit level. The parietals are surely fused: the resulting unpaired bone is narrower than in the type species, at least in its anterior part, so that the constriction posterior to the pineal foramen is here less evident.

The nasals are trapezoidal and form the posterior border of the nostrils; they meet only at their posterior end. The praefrontals are small, curved bones, with a concavity directed backward which forms the anterior margin of the orbits. The postfrontals are trapezoidal and their suture with the parietal is very irregular.

The squamosals are long and narrow in their anterior part, when lining the temporal fossae; they greatly enlarge in the posterior region, partially overlapping the quadrate.

In the occipital region only a few features are detectable: the rounded stout basioccipital, the left exoccipital and a small triangular supraoccipital, bearing traces of the upper posttemporal fenestra.

Few teeth are preserved: six on each premaxilla, five on each maxilla. The former are larger, measuring somewhat more than four mm. All the teeth are subcircular in cross-section and show on their surface several longitudinal ridges.

In the lower jaw, only the posterior region is visible. The retroarticular process is long and stout; anterior to the latter, the glenoid fossa is well developed and perpendicular to the body axis. The small exposed area of the dentary bears a few, gently curved teeth.

VERTEBRAL COLUMN

At least 84 vertebrae are visible (Pl. 1); their preservation is generally good, apart from the neural arches and spines. Though the shape of the vertebrae is typical of the genus (Peyer, 1933, 1934; Mazin, 1985; Kuhn-Schnyder, 1987), their number only partially agrees. In fact, there are: 22 cervicals (usually only 21)

and 20 dorsals (usually 22); five sacrals and at least 39 caudals.

The first five cervical vertebrae lie in lateral view, allowing their amphicoelus centra to be observed. All the other vertebrae expose their dorsal side, showing the well developed prae- and postzygapophyses. The dorsal part of the vertebral column consist of 18 trunk and two lumbar vertebrae, the latter being smaller and bearing very short and stout ribs. The five sacrals are about the same size as the lumbar, and bear low neural spines. The caudals decrease gradually in size and their neural spines seem to be rather low.

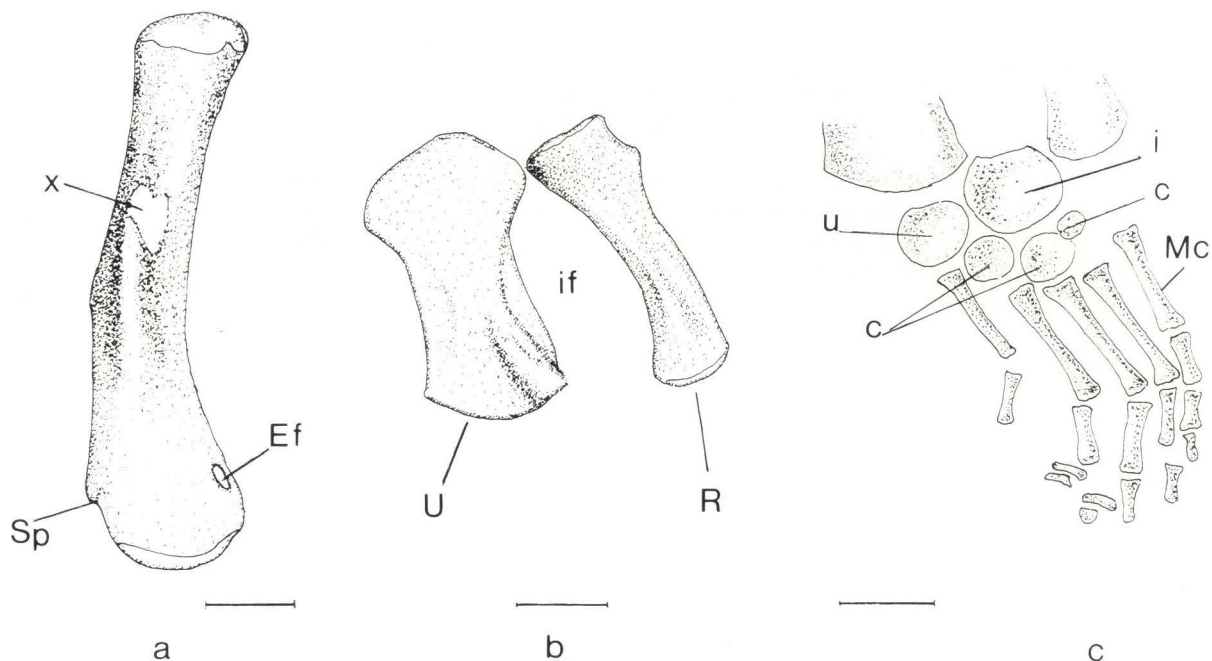
Short and stout cervical ribs are present, except for the atlas axis complex. At about the 15th cervical, ribs change from a stout triangular, to a more elongated and pointed shape. The last cervical ribs are well exposed, showing their double headed articular surface. Posterior to that vertebra, ribs with single articular head appear. The dorsal ribs are stout and bent downward at about one third of their length. The two lumbar ribs are short and straight; they closely resemble the five sacral ribs. The first pair of caudal ribs is blunt and forward directed; the following are slender and backward directed, the longest pair being the third one.

APPENDICULAR SKELETON

A small portion of the shoulder region can be seen. The short and stout scapula bears a strong process which overlaps the glenoid fossa. The coracoid is visible only in its distal part, where it meets the scapula to form the glenoid process.

The humerus (Pl. 2, fig. 2; Text-fig. 5a) is a long and stout bone, gently bent posteriorly, very thick at its proximal end and more flattened at its distal one. The proximal articular surface is oval and strongly convex and it is much more developed than in the other known *Lariosaurus* specimens. At the distal end a single, broad articular area seems to be present for both radius and ulna. Near the posterior margin of the distal end a well developed entepicondilar foramen shows a drop-like outline. On the opposite side, about six mm from the articular surface, the bone outline makes a little embayment, followed by a stout supinator process. This latter seems to be present only in a *Lariosaurus* sp. (Sanz, 1976, fig. 5). The insertion area for the scapulo-humeralis muscle as well as the deltoid muscles are larger than those for the subscapularis and the latissimus dorsi muscles. Furthermore, they are separated by a low ridge.

The radius and the ulna (Pl. 2, fig. 2; Text-fig. 5b) are approximately one half of the humerus length. The articular surfaces of the radius are slightly convex. The ulna displays the shape which is peculiar of the genus:



Text-fig. 5 - *Lariosaurus valceresii* n.sp.. Holotype. a) The left humerus in dorsal view. b) The right radius and ulna. c) The right manus in dorsal view. Ef = entepicondylar foramen; Mc = metacarpals; R = radius; Sp = supinator process; U = ulna; X = broken area; c = distal carpals; i = intermedium; if = spatium interosseum; u = ulnare. Scale bars equal to 1 cm.

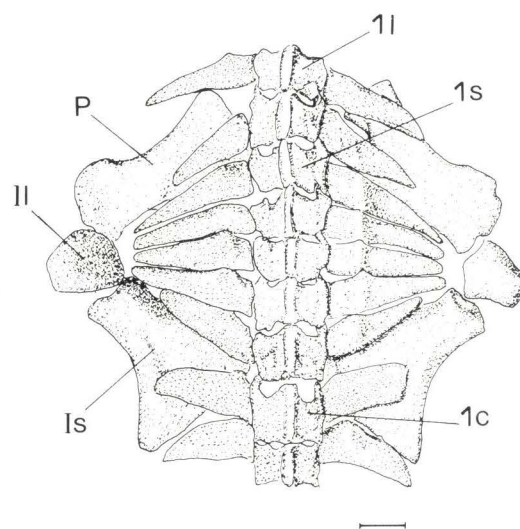
broad, flattened, with a ridge in the distal part ending near the articular surface for the intermedium. The two embayed medial borders of radius and ulna, along with the upper margin of the intermedium, define a large spatium interosseum.

The carpus (Pl. 2, fig. 2; Text-fig. 5c) consists of a large intermedium (about 12 mm wide), articulating both with the radius and the ulna, and of a smaller subcircular ulnare (about 7 mm wide), which articulates directly with the fifth metacarpal. Three distal carpals are visible; two are approximately the same size, the third is quite smaller. Five long and slender metacarpals are observed on the right limb. Only the first phalanx of each finger is well preserved, the other phalanges are disarticulated.

The pelvic girdle (Text-fig. 6) consists of a small ilium and large plate-like ischium and pubis, the latter two showing similar features. Actually, both ischium and pubis are thick near the acetabular area and then flatten distally. Their ventral region is very large and flattened. The posterior edge of the ischium is gently embayed, apparently like the anterior margin of the pubis.

The femur (Text-fig. 7) is much slender than the humerus. Traces of the insertion of the iliofemoralis muscle and of the puboischiofemoralis muscle occur

just below the proximal articular head. The distal articular area has a gently convex outline.



Text-fig. 6 - *Lariosaurus valceresii* n.sp.. Holotype. Pelvic girdle in dorsal view. Il = ilium; Is = ischium; P = pubis; 1c = first caudal vertebra; 1l = first lumbar vertebra; 1s = first sacral vertebra. Scale bar equal to 1 cm.

The tibia and the fibula are stout bones. The former is somewhat shorter and broader than the latter, as well as flattened dorsoventrally and expanded on both ends. On the distal end of the tibia two articular areas can be seen, the one for the intermedium being well developed. The fibula displays a gently curved shape; its concave median edge defines a rather large spatium interosseum. The distal end of the fibula is flattened.

The tarsus consists of a well developed intermedium and a slightly smaller fibulare. No distal tarsals are preserved. The five metatarsals are long and slender, with expanded ends. Only the phalanges of the first two toes are preserved. These are short with a flat and discoidal last one.

COPROLITES

In the Ca' del Frate fossiliferous level several coprolites have been found. Except for one, which is still inside a *Probalecites*, all the others are not related to

any fossil. However, their large size, is indicative of large animals. In our fauna the only species reaching a remarkable size is *L. valceresii*, the largest fishes being no more than 12 cm long. A few of these coprolites exhibit fish parts such as scales, skull bones, teeth. In one case a lower jaw, with well preserved teeth, certainly belongs to *Perleidus altolepis*, perhaps the most common fish after *Probalecites porroi*. As a consequence, it is possible that *L. valceresii* preyed on fishes rather than on small reptiles as in the case of *L. buzzii* (Tschanz, 1989).

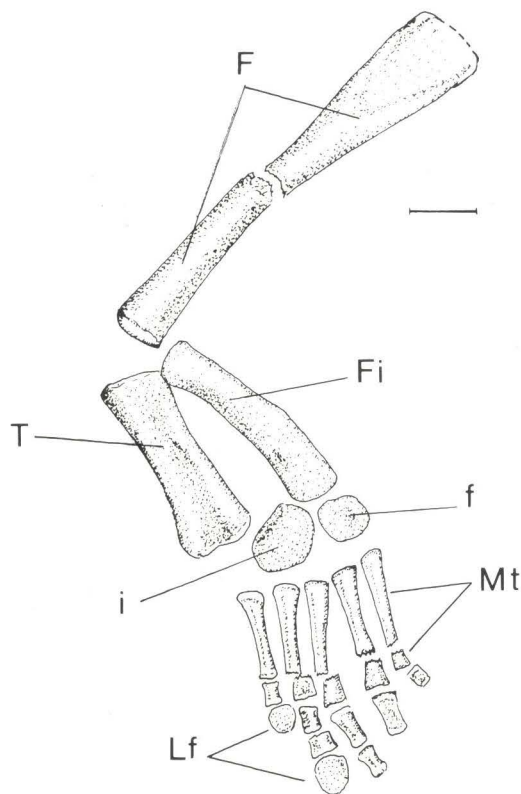
PALEOENVIRONMENTAL REMARKS

Up to now the Kalkschieferzone has always been thought to have sedimented totally in a marine environment, if not in a hyperhaline one. In fact, it lies between the Calcare di Meride s.s. (Meridekalke of the Swiss authors) (yielding *Daonella* and *Protrachyceras*) and the overlying Marne del Pizzella (Raibler Schichten) which include evaporite lenses (Wirz, 1945). However, no exclusively marine fossils have been found while, on the other hand, the invertebrate fauna is very poor. Nevertheless, some fresh water (or at least, brackish water) organisms are present. The study of the fauna from Ca' del Frate, which is considered to be entirely allochthonous (Tintori, in press), allows to exclude hyperhaline waters. As a matter of fact, a great amount of conchostracans (fresh water dwellers) have been found, which indicate the proximity of land, with abundant superficial fresh water. In case of heavy rain, floods brought conchostracans into the basin, possibly reducing the water salinity.

A similar environment is suggested by some of the fish from Ca' del Frate. For instance, the genus *Perleidus*, widespread during the Lower and Middle Triassic, is found in Madagascar both in marine and brackish deposits (Beltan, 1988). Martin (1982) recorded *Perleidus* together with *Dipteronotus* from the Moroccan Atlas in a brackish (or marine?) intercalation inside a continental series (Dutuit & Heyler, 1983). *Dipteronotus* used to live in marine environment with strong continental influence, as in the Upper Buntsandstein of the Elsass and Baden (Gall *et al.*, 1974). It is also found at Ca' del Frate in layers which also yield conchostracans (Tintori, in prep.).

Sanz (1976, 1983) concluded that the fauna from Montreal-Alcover, including *Lariosaurus*, was a typical coastal taphocoenosis, mostly on the basis of the other fossil content. Cephalopods, corals, echinoderms indicate a marine environment, well comparable to the basin where the Calcare di Perledo-Varenna was deposited.

The remarkable correspondence among the vertebrate fauna of Ca' del Frate, Perledo and, though in a lesser degree, Montreal-Alcover, would support the



Text-fig. 7 - *Lariosaurus valceresii* n.sp., Holotype. Left posterior limb in dorsal view. F = femur; Fi = fibula; Lf = last phalanx; Mt = metatarsals; T = tibia; f = fibulare; i = intermedium. Scale bar equal to 1 cm.

hypothesis that the layers of the Kalkschieferzone yielding vertebrates were deposited in a marine environment.

In the course of field work at Ca' del Frate, one of us (A.T.) observed that layers which are rich of conchostracans are fairly poor of fish, while in the main vertebrate level conchostracans are almost absent. Consequently we infer that salinity in the Kalkschieferzone basin was relatively variable. Brackish waters would compel most of the fish, and also *Lariosaurus*, to migrate in search of a strictly marine environment, which they would probably find in the adjoining basin of the Calcare di Perledo-Varenna.

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Andrea TINTORI

Silvio RENESTO

Dipartimento di Scienze della Terra
Via Mangiagalli 34, 20133 Milano, Italia