

PECULIAR PRESERVATION OF A JUVENILE PACHYPLEUROSAURID FROM BESANO (ITALY)

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Received: February 3rd, 2006; accepted: July 7, 2006

Key words: *Neusticosaurus* (Reptilia Sauropterygia), Besano, Lombardy (Northern Italy), ontogeny, taphonomy.

Abstract. A small pachypleurosaurid collected in the Besano area of Italy, is described. A comparative analysis of size and proportions with other pachypleurosaurids suggests it represents a juvenile specimen of *Neusticosaurus pusillus*. The specimen represents a peculiar taphonomic case: the centra of the dorsal vertebrae are clustered together in the pectoral area while the rest of the trunk is virtually undisturbed, suggesting that disarticulation of dorsal vertebral elements may have occurred before decay of integumental soft parts, possibly before the carcass reached the bottom of the basin.

Riassunto. Viene descritto un piccolo esemplare di pachypleurosauride rinvenuto nell'area di Besano. Un'analisi comparata delle dimensioni assolute e dei rapporti proporzionali rispetto ai pachypleurosauridi conosciuti indica trattarsi di un esemplare giovanile di *Neusticosaurus pusillus*. L'esemplare costituisce un interessante caso di tafonomia in quanto si nota la disarticolazione dei soli corpi vertebrali dorsali, che si sono accumulati nella zona pettorale, mentre il resto del tronco è rimasto indisturbato. Questo fa pensare che tale disarticolazione sia avvenuta all'interno dell'organismo, prima della completa decomposizione delle parti molli ed addirittura prima che l'esemplare raggiungesse il fondo del bacino.

Introduction

The rich vertebrate fauna of Besano-Monte San Giorgio (Lombardy, Italy and Canton Ticino, Switzerland) is among the most important in the world for the Middle Triassic. The first finds were reported by Curioni in 1847, and since then, the vertebrates from the Besano Monte San Giorgio have been studied extensively, with abundant material collected during palaeontological excavations and mining between the end of 19th and the first half of the 20th centuries. Fossils have

been collected from different formations, belonging to four horizons (Zangerl 1935) which age spans from the upper Anisian to the upper Ladinian (Furrer 1995). The marine reptiles comprised ichthyosaurs, thalattosaurs, sauropterygians, while protorosaurs were semi-aquatic (*Tanystropheus*) or lived on land (*Macrocnemus*) along with rauischiids. Pachypleurosaurid nothosaurs are the most abundant reptiles, with two genera and four species so far described (Carroll & Gaskill 1985; Rieppel 1989; Sander 1989), with *Serpianosaurus* as the earliest member from the Anisian/Ladinian boundary (Rieppel 1989) followed by *Neusticosaurus pusillus*, *Neusticosaurus peyeri* (Sander 1989) and *Neusticosaurus (Pachypleurosaurus) edwardsii* (Carroll & Gaskill 1985; Sander 1989). More than 400 specimens have been so far collected, allowing studies about intraspecific variation, sexual dimorphism and ontogeny (Carroll & Gaskill 1985; Rieppel 1987, 1989, 1993; Rieppel & Lin 1995; Sander 1989). In the present paper a new and very small pachypleurosaur specimen collected in the Besano area, is described. The specimen is housed in the paleontological collection of the Museo Civico di Storia Naturale di Milano (Italy) with the catalogue number of BES 273. Unfortunately the collector did not provide adequate informations about the provenance, only stating that it was collected in an outcrops belonging to a level stratigraphically slightly above the Scisti Ittiolitici di Besano (Grenzbitumenzone of Swiss authors). If this information is correct, the specimen should come from the Lower Meride Limestone, possibly from levels corresponding to Cava Inferiore or Cava Superiore horizons which are Lower Ladinian in age. According to Sander (1989) each pachypleurosaur species is confined to each

Age	Formation	fossiliferous levels	pachypleurosaurid taxon
Ladinian	Meride Limestone	Alla Cascina beds	<i>Neusticosaurus edwardsii</i>
		Cava Superiore beds	<i>Neusticosaurus peyeri</i>
		Cava Inferiore beds	<i>Neusticosaurus pusillus</i>
	S. Giorgio Dolomite	Grenzbitumenzone	<i>Serpianosaurus mirigiolensis</i>

Fig. 1 - Correlation between fossiliferous horizons and pachypleurosaur taxa (modified from Sander 1989).

horizon (Fig. 1) so that the attribution of BES 273 to a pachypleurosaur species may represent an indirect clue to check its stratigraphical provenance. The juvenile stage of the specimen rendered difficult detailed morphological and morphometrical comparisons, nonetheless the assignment to a pachypleurosaur taxon was possible by a comparison of size ratios correlated to ontogenetic stage. BES 273 represents also an interesting taphonomic case, testifying the occurrence of a peculiar kind of partial disarticulation which probably occurred

within the body of the animal, probably before the corpse reached the sea bottom.

Systematic Paleontology

Sauropterygia Owen, 1860

Eusauropterygia Rieppel, 1994

Pachypleurosauroidea von Huene, 1956

Pachypleurosauridae Nopcsa, 1928

Neusticosaurus Seeley, 1882

Neusticosaurus pusillus (Fraas, 1881) Seeley, 1882

Type species: *Neusticosaurus pusillus* (Fraas, 1881) Seeley, 1882

1989 *Neusticosaurus pusillus* Sander, p. 576 (cum syn.).

Material. BES 273, a small pachypleurosaur specimen housed in the Museo Civico di Storia Naturale di Milano, exposed in ventral view.

Description

As stated above, specimen BES 273 is almost complete and articulated (Pl. 1A). Only the proximal halves of the right radius and ulna, along with the distal halves of the left radius and ulna with the entire right carpus and manus are missing, but very probably they were lost or destroyed during collection or preparation: the specimen now lies on two slabs which were glued together at the level of the missing portions of the left forearm, whilst the missing portion of the right forearm was probably preserved on another slab which was not collected. Finally, the pelvic girdle is either missing or disarticulated and the pelvic bones scattered among the vertebral centra so that they cannot be individually identified.

Skull. The skull (Pl. 1B, Fig. 2) is exposed in ventral view, however, the palatines are thin and fragmented so that some elements of the dorsal region of the skull can also be described. The premaxillae are subtriangular and extend halfway to the cranial margin of the orbits; their medial processes form the cranial margin of the

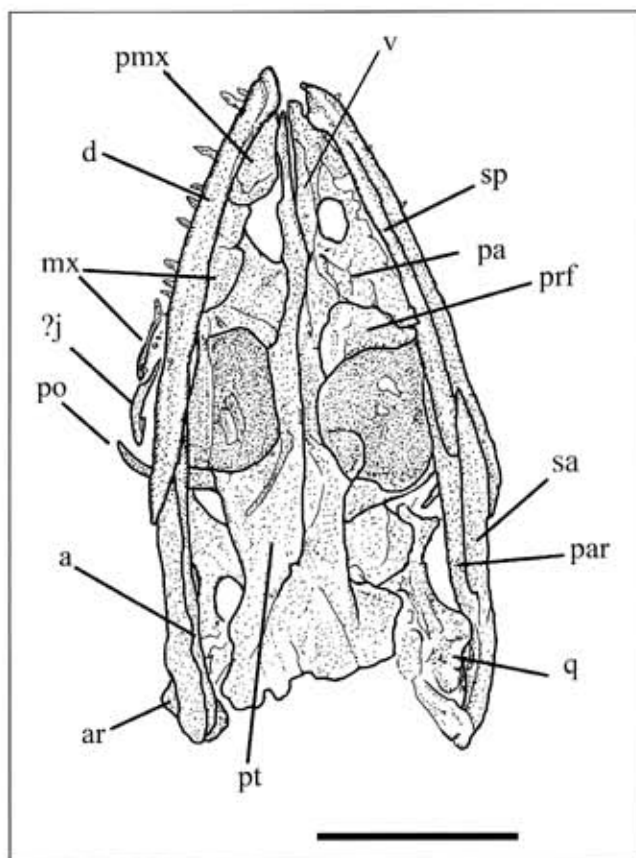


Fig. 2 - BES 273, drawing of the skull in ventral view. Abbreviations: a) angular, ar) articular, d) dentary, ?j) jugal?, mx) maxilla, pa) palatine, par) prearticular, pmx) premaxilla, po) postorbital, prf) prefrontal, pt) pterygoid, q) quadrate, sa) surangular; sp) splenial, v) vomere. Scale bar equals 5 mm.

internal nares. In their caudalmost portion the premaxillae become separated from each other by the cranial portion of the vomers. Caudal to the lateral shelves of the premaxillae, the subtriangular medial shelves of the maxillae are visible along with fragments of the palatines. Just lateral to the right ramus of the lower jaw, fragments of two bones can be observed, one bears a few small teeth and is identified as the right maxilla, the other one may be a splint of bone belonging to the jugal. The prefrontals are curved elements with a thicker caudal margin which forms the anterior margin of the orbits, their outline can be detected owing to the very thin section and partial fragmentation of the overlapping palatines. The orbits are filled with black organic matter, probably remains of the sclera (Sander 1989). The postorbital is triradiate and forms most of the caudal margin of the orbit which is nearly circular in shape and occupies about 28% of the whole skull length (as determined by the length of the lower jaw rami); the ventral process of the postorbital is rather elongate and thin. The caudal portion of the squamosal is visible, its ventral lobe articulates with the quadrate, which forms the caudolateral end of the skull, the caudal margin of the quadrate has a distinct concave outline which can be considered as a tympanic recess, and bears a caudal process which extends beyond the articular surface for the lower jaw. The pterygoids are broad plate-like bones that reach the occipital condyle, they are somewhat constricted in the middle, while they form broad caudolateral processes at their caudal end.

The bones of the lower jaw are slightly disarticulated, allowing observation of their shape and extension. The dentary extends for about two thirds of the length of the lower jaw; its caudal end reaching the level of the postorbital; medially the thin splenial forms the ventromedial portion of the lower jaw, it extends close to the lower jaw symphysis and caudally it extends between the angular and surangular. The angular and prearticular form the posteroventral portion of the lower jaw, while dorsally a well developed surangular is present. The left articular is dissociated from the other bones of the lower jaw, it is a square-shaped bone and a retroarticular process is present.

Axial skeleton. At least 18 cervical vertebrae are visible (Fig. 3): the centra are short and somewhat constricted in the middle, the suture with the neural arches is weak, and the neural spines show a subrectangular shape. Small nubbins of bone lying ventral to the cervical centra can be identified as cervical ribs.

In the dorsal region the centra are deeply amphicoelous, stout and well ossified; rather surprisingly they are disarticulated from the neural arches and are clustered together at the level of the pectoral girdle (Fig. 3), while the neural arches lie undisturbed in anatomical connection to each other (Pl. 1A, C). This disarticula-

tion and overlapping of the centra prevents a reliable count of the dorsal vertebrae, but judging from the size and position of the undisturbed neural arches, up to 16 dorsal vertebrae seem reasonable, suggesting a presacral count of about 32-34 vertebrae.

The sacral vertebrae cannot be identified in this specimen. The caudal portion of the vertebral column is off set from the trunk, but the vertebrae are still in anatomical connection. Up to 52 caudal vertebrae are preserved (Pl. 1D). The first 5-6 vertebrae are curled together, while more distally they follow a roughly straight line until the very end of the tail where the last few vertebrae form a small knot. The caudal centra have been flattened, apart from the thicker articular surfaces that resisted compression. Neural spines appear to be low in the first five-six caudal vertebrae and subsequently are almost invisible. A small subrectangular bone lying among the curled proximal caudal centra is probably a disarticulated sacral or proximal caudal rib.

The gastralia are exposed in the middle and caudal region of the trunk. Their structure comprises a medioventral v-shaped element, and elongate and broad lateral elements. The medioventral element is broader in the middle and bears a blunt cranial process, which decreases in size caudally along the series.

Pectoral girdle and forelimbs. The pectoral girdle is mostly obscured by the overlapping clustered dorsal centra (Fig. 3), only the cranial and parts of the middle of the coracoids are visible, with an elongate shape and median constriction which is typical for pachypleurosaurids (Sander 1989). The caudoventral portions of the broad scapulae can be observed still connected to the coracoids.

The humerus (Fig. 4A) is rather stout, with a gently curving shaft, a concave proximal surface and a slightly convex, nearly flat, distal articular area. The radius and ulna are incompletely preserved, their proximal portions are preserved on the right limb, while in the left limb only their middle and distal portions are present. Both bones show moderately expanded proximal and distal heads, and the ulna seems wider and stouter than the radius, its distal head shows two distinct concave articular areas for the carpal bones. Only the left carpus and manus are preserved. The carpus comprises two rounded elements of about the same size, both are wider than deep and, on topological basis, they can be identified as the ulnare and intermedium. Both carpals are in contact with the ulna and the intermedium also meets the medial side of the distal portion of the radius. The first metacarpal is slightly less than half the length of the second; other metacarpals are simple rod-like bones, the third metacarpal seems to be somewhat longer than the fourth, but this cannot be assessed with confidence due to flattening and slight deformation of the bones. The preserved phalanges are well ossified,

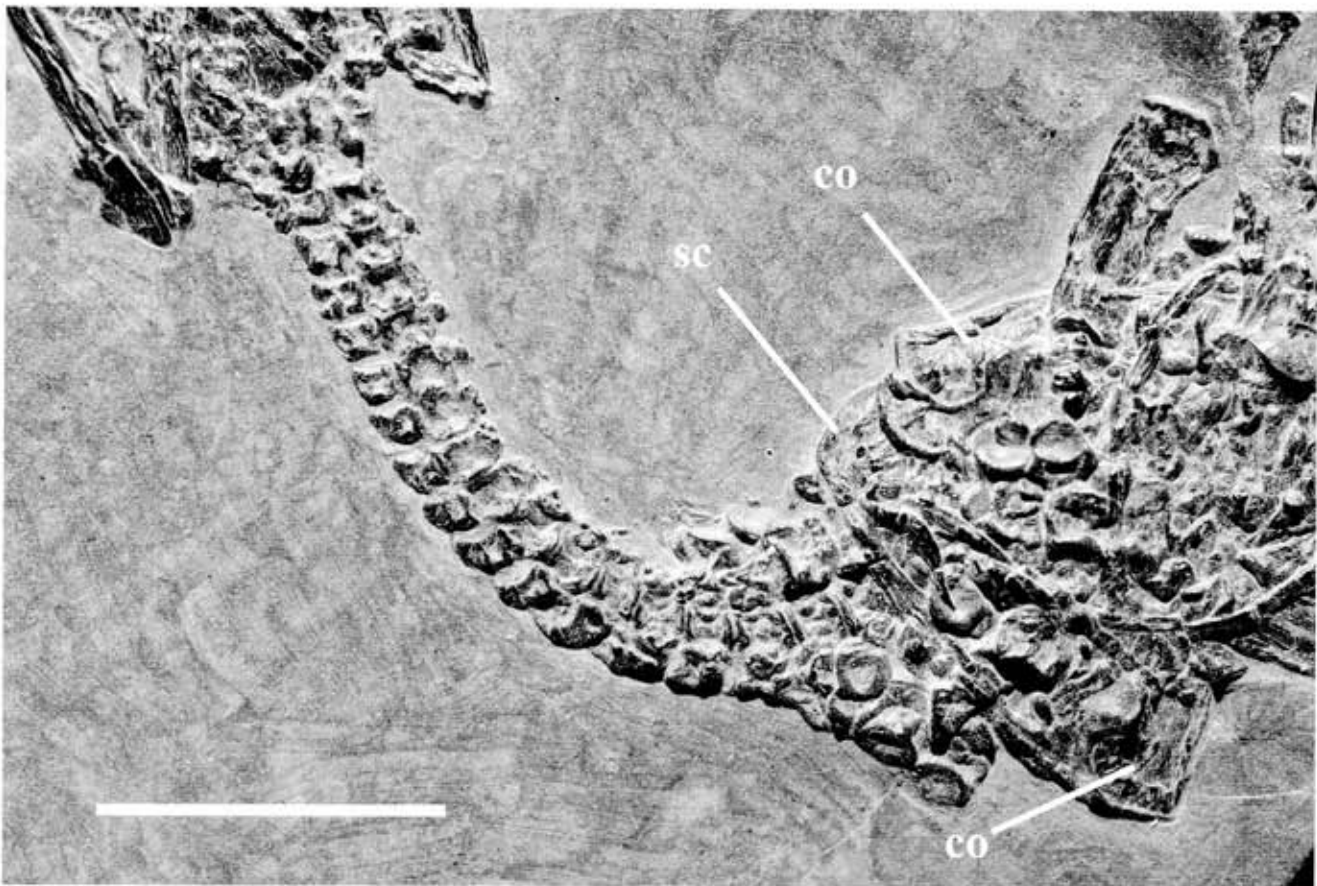


Fig. 3 - BES 273, the neck and anterior dorsal region, showing the clustered dorsal centra. Abbreviations are: co) coracoid, sc) scapula. Scale bar equals 5 mm.

but a phalangeal formula cannot be given because the first digit is truncated by a crack at the middle of the first phalanx. The same crack also damages the second digit at the level of the second phalanx, while the third digit may be complete and bears three phalanges. The fourth digit also bears three phalanges but the distal end of the last preserved phalanx clearly shows a well ossified articular surface indicating that at least another phalanx was present; the same applies to the fifth digit.

Pelvic girdle and hind limb. No element of the pelvic girdle is visible. Perhaps the pelvic bones are obscured by the cluster of disarticulated centra, or they were lost prior to fossilization.

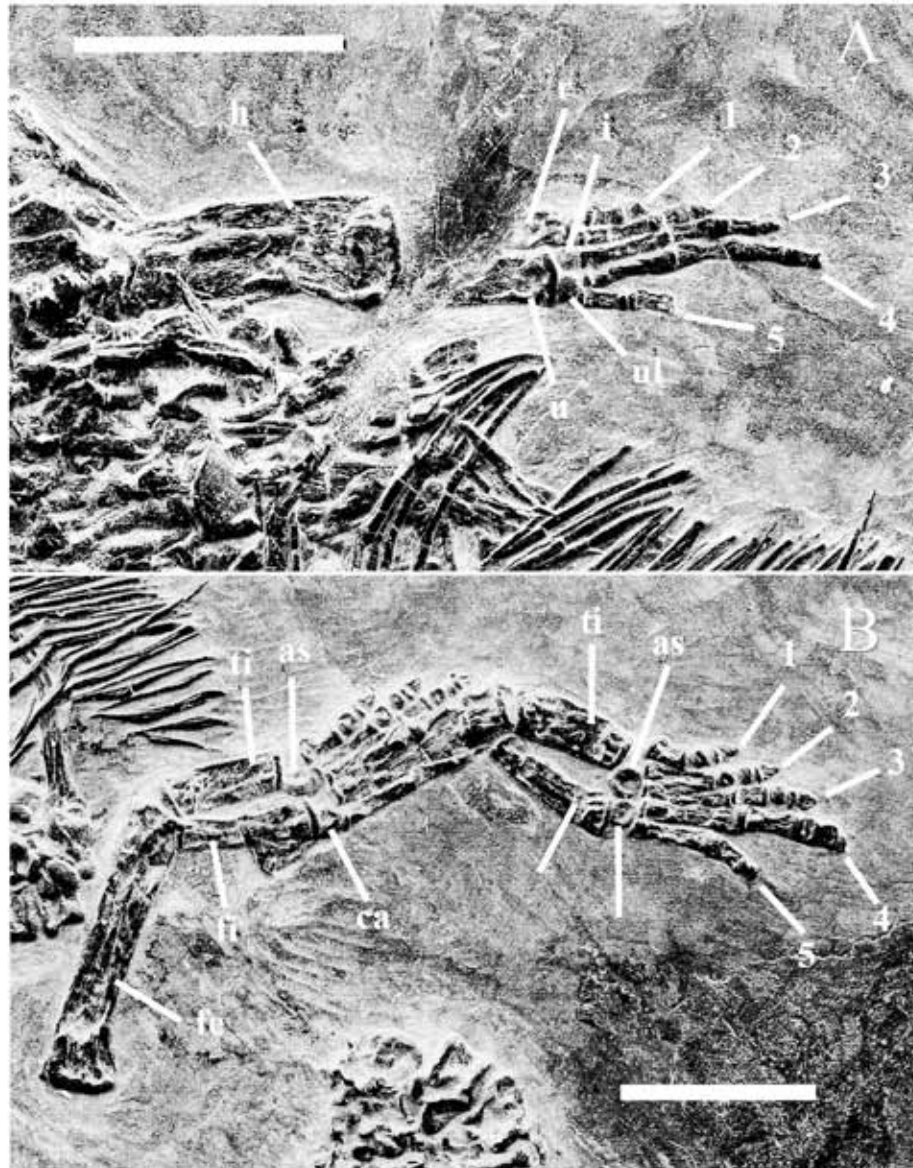
The hind limbs (Fig. 4B) are well preserved; they are disarticulated from the trunk, but each limb element is roughly in anatomical connection with others. The position of the hind limbs recalls pose "R" of Sander (1989) in which both right and left limb are oriented in the same direction with respect to the body axis (in this case both knees point to the left), but the right hind limbs shifted further laterally to the left so that the right crus overlaps the left femur.

The femur is distinctly longer, but narrower, than the humerus; it shows a straight shaft and slightly expanded heads. The proximal head is somewhat inclined

with the shaft and has a gently convex articular surface, while the distal head is in line with the shaft and shows a slightly concave articular surface. The tibia and fibula are of approximately half the length of the femur. The tibia is straight and wider than the ulna which has a curved shaft, thus an elliptical *spatium interosseum* is present between the two bones. Two rounded tarsals, the astragalus and the calcaneum, are ossified, the first metatarsal is short and broad, the other metatarsals are simple rod-like bones, the fourth being the longest. In the first 3 digits, the terminal phalanx is preserved as a narrow triangular element suggesting the presence of a small claw. In the fourth digit, the most distally preserved element is a small discoidal bone, while in the fifth digit the last phalanx is missing, so that the phalangeal formula for the pes can be given as 2, 3, 4, 3(4), 2+.

Discussion. BES 273 can be considered a pachypleurosaurid eusauropterygian as diagnosed by Rieppel (1989, 1994, 2000) and Rieppel & Lin (1995). Within pachypleurosaurs, however, generic assignment is less easy due to the early growth stage, which alters body proportions and also implies some modification of bone morphology. BES 273 shows small size (Tab. 1) and juvenile features that are represented both by skeletal

Fig. 4 - BES 273, A) Left fore limb, abbreviations: h) humerus, i) intermedium, r) radius, u) ulna, ul) ulnare, 1-5) digits of the manus. B) hind limbs, abbreviations: as) astragalus, ca) calcaneum, fe) femur, fi) fibula, ti) tibia, 1-5) digits of the pes. Scale bars equal 5 mm.



morphology and body proportions, mainly in the skull, in the vertebral column and the limbs. The skull is proportionally very large with respect to the trunk and skull bones are loosely articulate. The vertebral column appears compressed, especially in the neck and in the tail regions, where the centra are crushed and flattened apart from the cranial and caudal articular surfaces which remain intact and appear distinctly raised off the substrate. In the trunk, the centra appear more solid, but neurocentral sutures were weak, as testified by the disassociation of the dorsal centra from the corresponding neural arches; only the caudalmost cervical vertebrae bear tiny cervical ribs which, however, are simple nubbins of bone. The absence of the pelvic girdle suggest that it was loosely attached to the vertebral column. The limb bones even the humerus and femur which are always intact in adults are crushed and flattened in BES 273, and only the proximal and distal heads resisted crushing so that the ends of the bones appear raised

with respect to the shafts as described by Sander (1989) for juveniles of *Neusticosaurus*. However an analysis of size and proportions allows precise classification of BES 273.

Absolute size is much smaller than and, more importantly, body proportions fall well outside the range for known specimens of *Neusticosaurus edwardsii*, speaking against the attribution of BES 273 to this taxon. Disassociation and clustering of dorsal centra does not allow a precise count of the dorsal vertebrae, but the number of cervical and caudal vertebrae is consistent both with *Serpianosaurus mirigiolensis* (Rieppel 1989) and with *Neusticosaurus pusillus* (Sander 1989), but not with *N. peyeri*. Again, the trunk length/standard length ratio of BES 273 is consistent with both *Serpianosaurus* and *N. pusillus* but not with that of *N. peyeri* (Tab. 2) which shows somewhat different body proportions (O'Keefe et al. 1999), thus it seems reasonable to make a more detailed com-

	BES 273	<i>N. pusillus</i>	<i>N. peyeri</i>	<i>Serpianosaurus</i>	T 1342
Skull	16	13.8-34.4	11.05-40.6	26.9-80.6	26.9
trunk	21	17.8-84.10	14.5-126.8	41- 187	41
humerus	5	4.7-18.9	2.3-30.6	7.8-44.9	7.8
femur	7	5.7-19.9	3.07-31.92	9.4-40.3	9.4
Standard length	5	4.7-18.2	3.31-34.12	9.7-39.2	9.7
Skull/s. l.	3.7	1.89-2.93-	1.18-3.33	1.94-2.77	2.78
Skull/trunk	0.76	0.34-0.53	0.32-0.56	0.43-0.56	0.65
Skull/humerus	3.2	1.4- 3.2	1.32-4.08	1.6-2.4	3.45
Humerus/trunk	0.23	0.20-0.33	0.20-0.33	0.21-0.36	0.19
Humerus/s. l.	1.13	0.95-1.5	0.75-1.25	1-1.48	0.8
Humerus/fem.	0.72	0.88-1.15	0.9-1.30	0.75-1.24	0.82
Femur/trunk.	0.33	0.22-0.30	0.21-0.25	0.21-0.32	0.22
Femur/std.	1.4	0.97-1.4	0.79-1.06	1.09-1.32	0.96
Trunk/s. l.	4.2	3.78-4.62	4.3-3.71	4.2-4.7	
N. of caudal v.	52+	54-58	42-48	52	
N. of cervical v.	18-	18-20	15-16	14-18	

Tab. 1 - Measurements in mm taken on BES 273 and compared with the size range of *Serpianosaurus*, *N. pusillus* and *N. peyeri*. Data for *Serpianosaurus* and Neusticosaurus taken from Rieppel 1989, Sander 1989 and O'Keefe et al. 1999, sizes and range variations include both sexes where distinguished (Rieppel 1989; Sander 1989), s. l.: standard length.

parative analysis between BES 273 and these former two taxa.

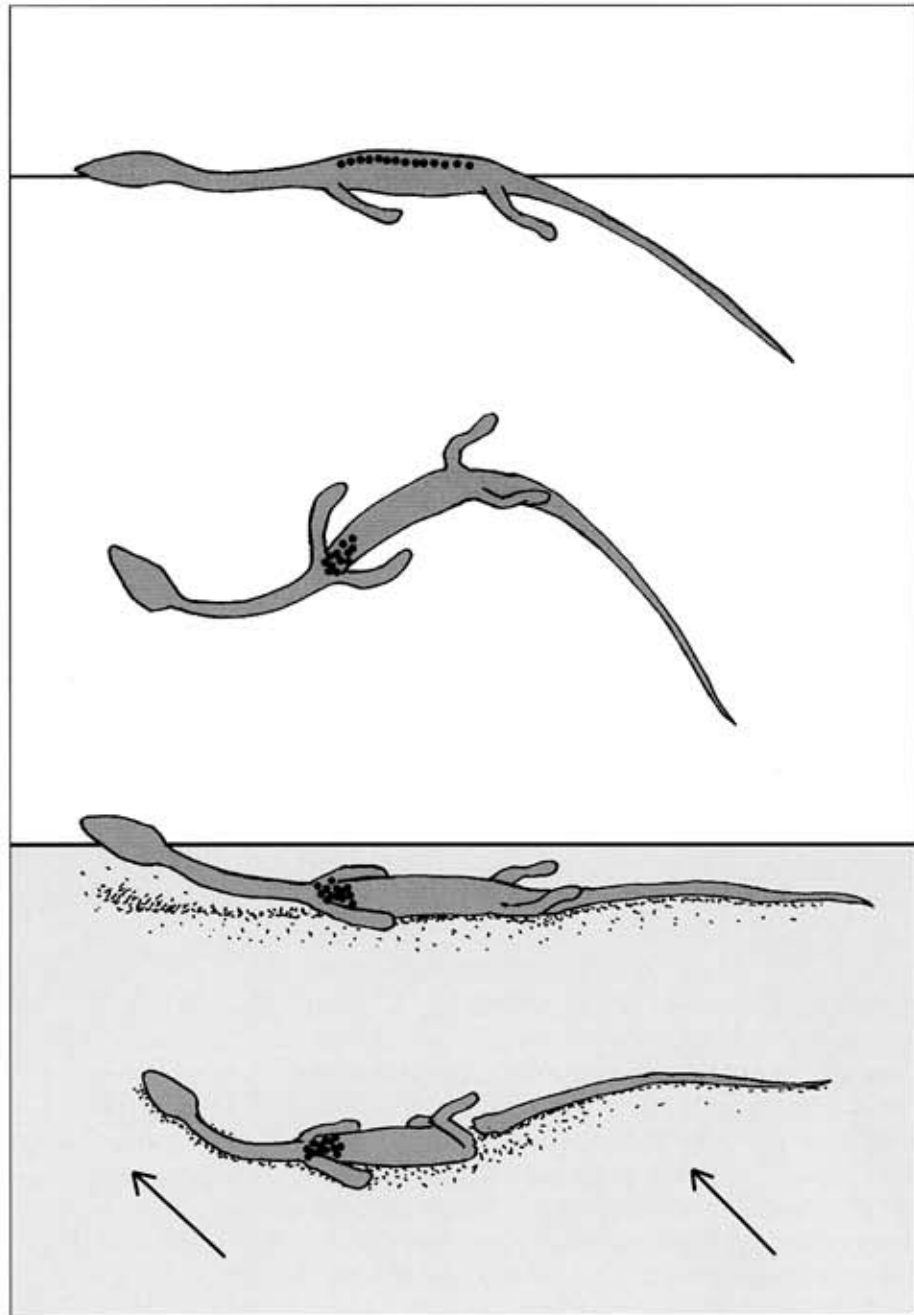
The absolute size of BES 273, while much smaller than the smallest *Serpianosaurus* specimen so far found (T1342, a juvenile, Rieppel 1989, Tab. 1), cannot rule out completely its belonging to *Serpianosaurus*. According to Currie & Carroll (1984), hatchlings of reptiles could reach at least a body length of 29% with respect to adult size, while other studies predict a body size of 31%, for lizards, of 39% for snakes (Andrews 1982; Moffat 1985) and Deeming & Ferguson (1990) report a body length of 46% for crocodiles. By comparison with lizard ratios, trunk length of BES 273 is well below the estimated value for an hatchling of a mean sized adult *Serpianosaurus*, but lies very close to the estimated value for the hatchling of the smallest known sexually mature specimen of the same genus (T3674 Rieppel 1989; O'Keefe et al. 1999) (Tab. 2). Gravid specimens are documented for the Chinese pachypleurosaurid *Keichousaurus* (Cheng, Wu & Ji 2004), and a putative embryo of *Neusticosaurus* (Sander 1988) along with some unquestionable embryos of *Lariosaurus* (Renesto et al. 2003), have been found in the Monte San Giorgio area (but no gravid specimens of any pachypleurosaur genus), suggesting that viviparity occurred among pachypleurosaurs, and newborns may have reached a greater size than hatchlings, BES 273, despite its small size, this specimen cannot be considered neither a newborn of an hatchling of *Serpianosaurus*, as the degree of ossification is more advanced than at birth or hatching stage (Sander 1988, 1989): both carpals and tarsals are fully ossified, phalanges are also well ossified both in the manus and in the

pes, and all caudal vertebrae are ossified. In addition, the tail length/trunk length ratio is close to 200%, while in hatchlings the tail is proportionally shorter (Sander 1989). It is thus feasible that the degree of ossification of BES 273, while testifying a relatively juvenile condition, also indicates that its ontogenetic development was beyond the hatchling stage, suggesting that BES 273 was a small, but immature individual. In this case BES 273 is too small to belong to *Serpianosaurus* while it fits well within the expected size range of juveniles of *Neusticosaurus pusillus*. In conclusion the assignment of BES 273 to *Neusticosaurus pusillus*, is well supported by both skeletal correlates and body ratios. This attribution is consistent with the supposed provenance of the specimen, as *Neusticosaurus pusillus* occurs in the Lower Meride Limestone levels just above the Grenzbitumenzone horizon.

	HL
BES 273	21
<i>N. pusillus</i>	17.8
<i>N. peyeri</i>	16
<i>Serpianosaurus</i> (mean adult size)	31
<i>Serp.</i> (smallest adult T3674)	18

Tab. 2 - Comparison between trunk length (in mm) of Bes 273 and the estimated trunk length at hatchling stage (HL) for different pachypleurosaur taxa: the first value for *Serpianosaurus* is an estimate based on the smallest adult specimen (T 3674) the second number is an estimate based on mean trunk length of adult *Serpianosaurus* (data from Rieppel 1989; Sander 1989; O'Keefe et al 1999).

Fig. 5 - Possible explanation for the disarticulation and clustering of dorsal vertebral bodies in the pectoral region of BES 273. The vertebral bodies collapse in the floating carcass by action of gravity and/or developing gases. After sinking to the bottom, the neck could have swung for a while orienting the head parallel to the direction of the current (arrows), which caused also the drifting of the tail and of the right posterior limb.



Taphonomy. The skeleton of BES 273 is mostly articulated, suggesting that, as for most known pachypleurosaurids, the specimen both suffered little transport in the water column and reached the sea bottom and was buried before decomposition was so advanced as to cause decay of integuments and disarticulation of the skeleton and loss of heavier elements such as the limbs or the skull (Allison 1990). The posture of the skeleton of BES 273 (Pl. 1) follows a clear pattern already described for neusticosaurids (Sander 1989) but presents also a peculiar feature. The neck is bent so that the head is oriented at 90° with respect to the trunk. The position of the limbs corresponds to pose L (fore limbs) and R (rear limbs) of Sander (1989, p. 626, fig. 29). The

tail is slightly set off from the rest of the skeleton, the pelvic girdle is obscured, or lacking, while the limb bones are virtually intact and articulated and, oddly, the centra of the dorsal vertebra are set off from their neural arches and clustered together (perhaps together with pelvic elements) in the pectoral region (Fig. 3) while both gastralia and neural arches have remained roughly in place (Pl. 1C). Most features of the carcass position can be explained with the presence of a mild oscillatory current: after the carcass sank to the bottom, it was initially oriented normal to the current, as for most unanchored elongate objects, however, while the trunk remained in that position, the lighter neck, which had greater buoyancy, (perhaps due to the presence of

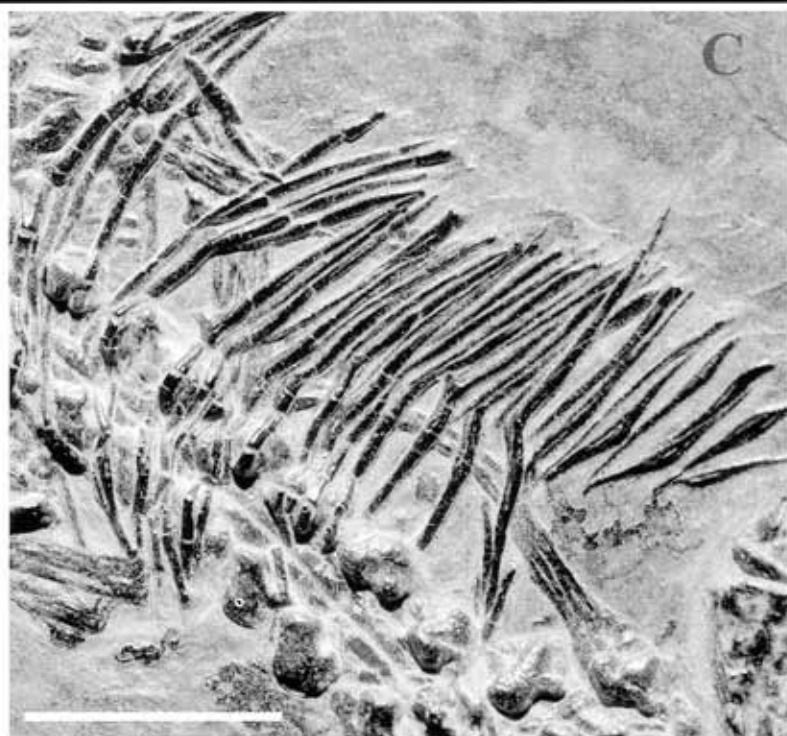
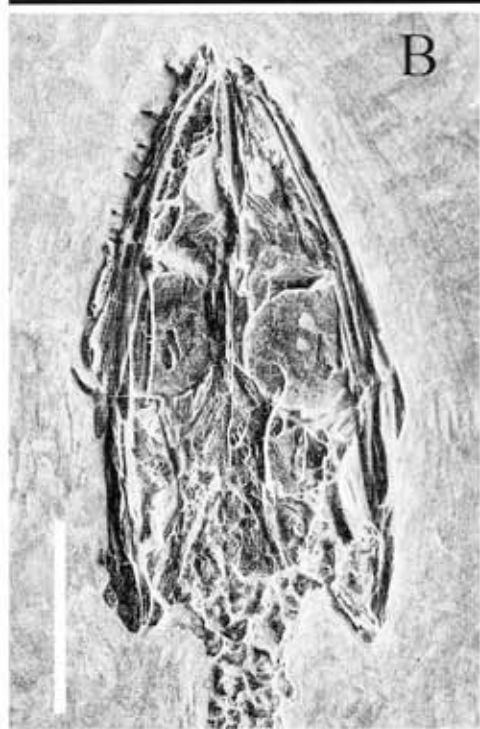
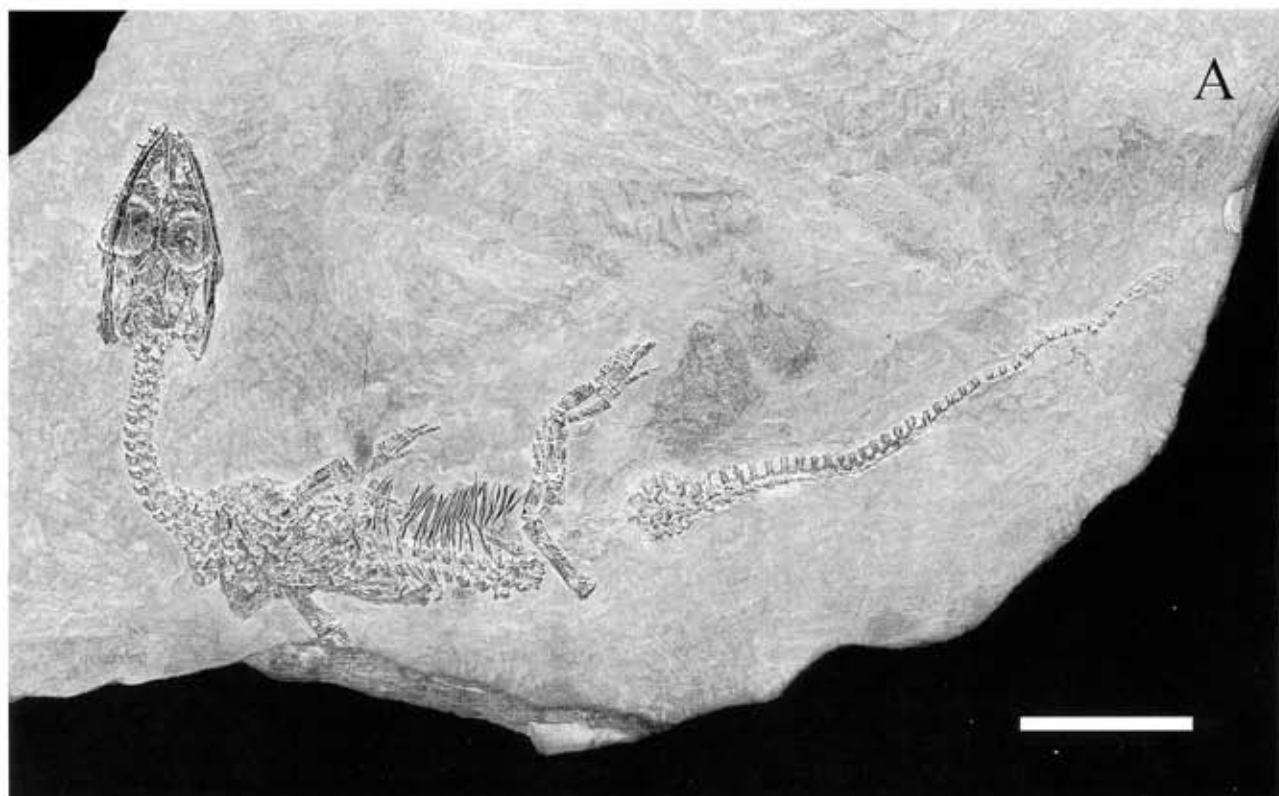
large eyeballs in the skull, Sanders 1989) was able to swing more freely over the bottom, so that the head was oriented parallel to the direction of the current. Also the drifting of the right rear limb and of the tail along with the asymmetrical (R) pose of the rear limbs may also be due to the action a current (Sander 1989). However, the clustering of the dorsal centra in the pectoral region does not fit into this scheme, because they seem to have moved against the current. In neustico-saurs, the dorsal centra are loosely attached to the neural arches (Sander 1989), and more so in juvenile specimens; thus the displacement of the centra per se is not surprising, what is odd, however, is the pattern, that suggests the vertebral bodies accumulated within the pectoral region, so that they separated the pectoral girdle elements. On the contrary, both the neural arches and the gastralia are still in place and both cervical and caudal vertebral bodies, along with nearly all other skeletal elements (even the tiny phalanges), are still in anatomical connection, ruling out disarticulation of the elements of the vertebral column due to the action of the bottom currents after decay of soft parts. This implies that displacement of the dorsal centra took place relatively shortly after death, probably in the floating car-

cass. The belly region may have arched the body (Fig. 5) and gravitational collapse of the vertebral centra occurred, so that they were clustered in the pectoral region that acted as a basket, while the cervical and caudal centra were kept in connection and in their original position until the carcass reached the bottom, because they were completely surrounded by neck and tail muscles. The same may apply to the neural arches kept in place by the epaxial musculature. It can be hypothesized that the long tail consisting of bone and muscles, was heavier and stiffer than the trunk and perhaps it become already semi-detached before reaching the bottom; subsequently it drifted slightly due to the action of the current.

Acknowledgements. I wish to thank Dr. Giorgio Teruzzi of the Museo Civico di Storia Naturale di Milano for the permission to study the specimen. Leslie Noè (Cambridge) and Michael Maisch (Tuebingen) revised the manuscripts, their comments and remarks were helpful and are greatly acknowledged. Thanks are due also to prof. A. Tintori (Milano) and Dr. C. Lombardo (Milano) for stimulating discussion about taphonomy of Monte San Giorgio vertebrates. Research supported by COFIN PRIN grant 2004-2006.

PLATE 1

Specimen BES 273 A) the whole skeleton, mainly in ventral view; B) the skull, ventral view; C) the trunk region showing undisturbed neural arches and, at a lesser degree, gastralia. D) the tail. Scale bars equal 5 mm.



REFERENCES

- Allison P. A. (1990) - Decay processes. In: Briggs E. G. & Crowther P.R. (eds.) - *Palaeobiology, a synthesis*: 213-216, Blackwell Sciences and Palaeontological Association, London.
- Andrews R. M. (1982) - Pattern of growth in reptiles. In: Gans C & Pough F.H. - *Biology of the Reptilia* vol. 13: 273-320, Academic Press, London.
- Carroll R. L. & Gaskill P. (1985) - The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Phil. Trans. R. Soc. London*, B, 309: 343-393, London.
- Cheng Y., Wu X. & Ji Q. (2004) - Triassic marine reptiles gave birth to live young. *Nature*, 432: 386, London
- Curioni G. (1847) - Cenni sopra un nuovo saurio fossile dei monti di Perledo sul Lario e sul terreno che lo racchiude. *Giorn. R. Ist. Lomb. Sci. Lett.*, 16: 159-170, Milano.
- Currie P. J. & Carroll R. L. (1984) - Ontogenetic changes in the cosuchian reptile *Thadeosaurus*. *J. Vert. Paleont.*, 4: 68-84, Lawrence.
- Deeming D. C. & Ferguson M. W. J. (1990) - Morphometric analysis of embryonic development in *Alligator mississippiensis*, *Crocodylus johnstoni* and *Crocodylus porosus*. *J. Zool.*, 221: 419-439, London.
- Fraas E. (1881) - *Simosaurus pusillus* aus der Lettenkhöle von Hoeneck. *Jahrb. Ver. Vaterl. Natur. Wurt.*, 37, 319-324, Stuttgart.
- Furrer H. (1995) - The Kalkschieferzone (Upper Meride Limestone; Ladinian) near Meride (Canton Ticino, Southern Switzerland) and the evolution of a Middle Triassic intraplatform basin. *Ecl. geol. Helv.*, 88: 827-852, Basel.
- Huene F. v. (1956) - *Paleontologie und Phylogenie der Niederen Tetrapoden* v. of 716 pp., Gustav Fischer, Jena.
- Moffat L. A. (1985) - Embryonic development and aspects of reproductive biology in the Tuatara, *Sphenodon punctatus*. In: Gans C. & Pough F.H. - *Biology of the Reptilia*, vol. 14: 494-521, Academic Press, London.
- Nopcsa F. (1928) - Palaeontological notes on reptiles. *Geol. Hungarica*, 1: 3-84, Budapest.
- Owen R. (1860) - *Palaeontology or a systematic summary of extinct animals and their geological relations*, vol. of xv + 420 pp., Adam & Charles Black, Edinburgh.
- O'Keefe R., Rieppel O. & Sander M. P. (1999) - Shape disassociation and inferred heterochrony in a clade of pachypleurosaurids (Reptilia, Sauropterygia). *Palaeobiology*, 25: 504-517.
- Renesto S., Lombardo C., Tintori A. & G. Danini (2003) - Nothosaurid embryos from the Middle Triassic of Northern Italy, an insight on the viviparity of nothosaurus. *J. Vert. Paleont.*, 23: 957-960, Lawrence.
- Rieppel O. (1987) - The Pachypleurosauridae, an annotated bibliography, *Ecl. geol. Helv.*, 80: 1105-1118, Basel.
- Rieppel O. (1989) - A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Phil. Trans. R. Soc. London*, B 323: 1-73, London.
- Rieppel O. (1993) - Middle Triassic reptiles from Monte San Giorgio: recent results and future potential of analysis. *Paleontologia Lombarda* N. S., 2: 131-144, Milano.
- Rieppel O. (1994) - Osteology of *Simosaurus* and the interrelationships of stem-group Sauropterygia. *Fieldiana (Geology)*, 28:1-85, Chicago.
- Rieppel O. (2000) - Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. In: Wellnhofer P. (ed.) - *Encyclopedia of Paleoherpétology*, 12: 1-134, Pfeil, Munich.
- Rieppel O. & Lin K. (1995) - Pachypleurosaurids (Reptilia: sauropterygia) from the Lower Muschelkalk and a review of the Pachypleurosauridae. *Fieldiana (Geology)*, 32: 1-44, Chicago.
- Sander M. P. (1988) - A fossil reptile embryo from the Middle Triassic of the Alps. *Science*, 239: 780-783, Washington.
- Sander M.P. (1989) - The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio, (Switzerland), with the description of a new species. *Phil. Trans. R. Soc. London* B, 325: 561-670, London.
- Seeley H. G. (1882) - On *Neusticosaurus pusillus* (Fraas) an amphibious reptile having affinities with terrestrial Nothosauria and marine Plesiosauria. *Q. J. Geol. Soc. London*, 38: 350-366, London.
- Zangerl R. (1935) - Die Triasfauna der Tessine Kalkalpen 9, *Pachypleurosaurus edwardsii*, Cornalia sp. Osteologie-Variationsbreite-Biologie. *Abb Schweiz Palaeont. Ges.*, 56: 1-80, Basel.