

SHORT NOTE – NOTA BREVE

REMAINS OF A JUVENILE PHYTOSAUR FROM THE LATE TRIASSIC OF NORTHERN ITALY

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Received: September 21, 2007; accepted: January 15, 2008

Key words: Caudal Vertebrae, Archosauria (Reptilia), Norian (Late Triassic), Ontogeny.

Abstract. A series of nine articulated caudal vertebrae collected from the Late Norian Argillite di Riva di Solto Shale (Bergamo, Northern Italy) are described. The caudal vertebrae belong to an archosaur, most probably an immature specimen of the phytosaur *Mystriosuchus*, as suggested by detailed comparison with the corresponding caudal vertebrae of the adult and complete *Mystriosuchus* specimen collected in the same area. The new specimen is of particular interest because material unequivocally belonging to juvenile phytosaurs is very rare and it gives support to the hypothesis that the closure of the neurocentral suture in phytosaurs possibly followed the same caudal to cranial path that occurs in crocodylians.

Riassunto. Viene descritta una serie di nove vertebre caudali articolate, provenienti da un affioramento delle Argilliti di Riva di Solto di età Norica (Triassico Superiore), presso Ponte Giurino (Bergamo). Lo studio ha consentito di considerare la serie caudale come appartenente ad un arcosauro, molto probabilmente ad un esemplare immaturo di fitosauro, come suggerito da una comparazione con l'esemplare adulto di *Mystriosuchus* rinvenuto nel Calcere di Zorzino (Norico) presso il giacimento di Endenna (Bergamo). Il nuovo esemplare è particolarmente interessante in quanto resti attribuibili a fitosauri immaturi sono rarissimi e inoltre dimostra come la chiusura della sutura neurocentrale segua una progressione craniocaudale come negli attuali coccodrilli.

Introduction

The main fossiliferous unit for Norian vertebrates in Northern Italy are the Calcere di Zorzino (Zorzino Limestone) and, to a lesser extent, the slightly younger Argillite di Riva di Solto (Riva di Solto Shale) (Renesto 1995; Paganoni & Renesto 1995; Tintori 1995). This latter unit consists of dark grey laminated shales, alter-

nating with marls and marly or micritic limestones from cyclic sedimentation in basinal conditions related to euxinic depressions with a North-South trend (Jadoul et al. 1992). The Argillite di Riva di Solto yields fishes, crustaceans, rare reptiles and insects only in the lower beds, which consist of black shales, marls and subordinate mudstones with parallel lamination (Jadoul et al. 1994). The upper, carbonate richer part of this unit, preserves rare and fragmentary remains of vertebrates in a storm layer very rich in bivalve shells (Tintori 1995) were recovered, among which a specimen of the pterosaur *Eudimorphodon* (Wild 1994; Dalla Vecchia 2003) and a drepanosaurid (Renesto & Paganoni 1995). In 1996 a small fossil was found in the debris of excavations lead by the staff of the Museo Civico di Scienze Naturali di Bergamo, in an outcrop of the Argillite di Riva di Solto, close to the village of Ponte Giurino (Bergamo, Lombardy, northern Italy; Tintori et al. 1985), but it was left unprepared until financial support by a grant of the Dean of Università dell'Insubria to the author, allowed the preparation of the specimen and the subsequent detailed study.

Systematic paleontology**Reptilia** Laurenti, 1768**Archosauria** Gauthier, 1984

Phytosauridae Jaeger, 1828

Cf. *Mystriosuchus* Fraas, 1896

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Fig. 1 - MCSNB 11341, lateral (right) view; scale bar equals 1 cm.

Material: MCSNB 11341 of the Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Lombardy, Italy, consisting of a series of nine caudal vertebrae in near articulation, exposed in lateral (right) view (Fig. 1).

Horizon and Locality: Argillite di Riva di Solto, Upper Norian (Upper Triassic), Ponte Giurino (Bergamo, Lombardy, Northern Italy).

Description. The overall structure of the vertebrae and the presence of haemal spines articulated with the centra, allow to identify the preserved elements as caudal vertebrae. The centra are non notochordal, weakly amphicoelous and constricted in their mid section and, in lateral view, their ventral margin is concave. The length of the centra varies from 10.5 to 12 mm. The first and the ninth vertebrae were already exposed when

the specimen was found, so they are poorly preserved from weathering; vertebrae 2 to 8 were instead covered by matrix and after preparation they revealed to be very well preserved allowing a detailed description. In the better preserved vertebrae (Fig. 2) compact bone is present only on the ventral and lateral portions of the centra; cancellous bone is exposed on the cranial, caudal articular surfaces and on the dorsal regions. The lateral surface of each centrum is marked by thin grooves and pierced by small foramina in all vertebrae. In addition, in all preserved vertebrae, close to the craniodorsal edge of the lateral surface of the second preserved centrum, a much larger, oval fossa is visible. No articular areas for the attachment of ribs are present, although short and

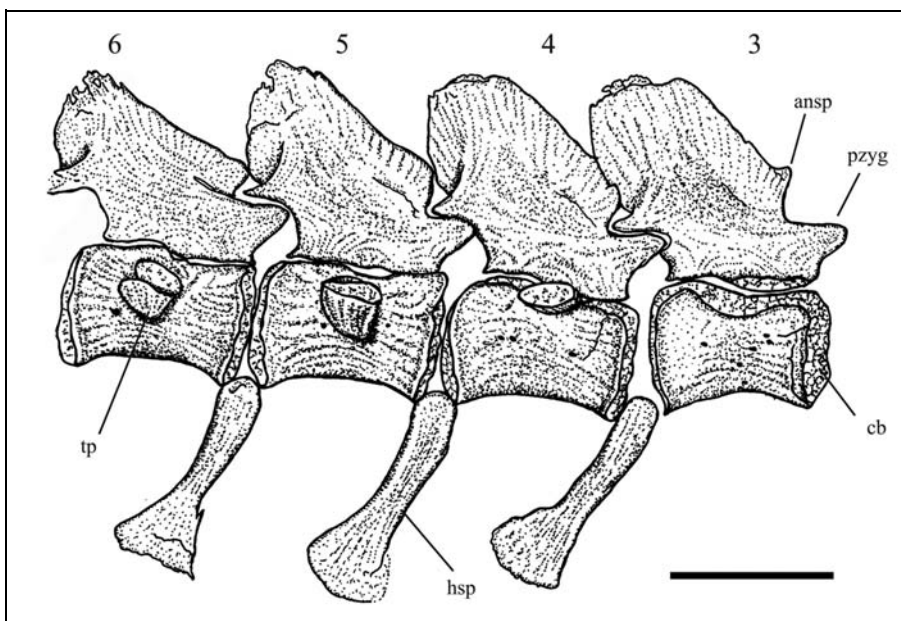


Fig. 2 - MCSNB 11341, drawing of the third to sixth preserved vertebra. Abbreviations: ansp) accessory spine; cb) cancellous bone; hsp) haemal spines; nsp) neural spines; pzyg) praezygapophysis; tp) transverse processes. Scale bar equals 1 cm.

stubby transverse processes can be observed on the dorsal border of the lateral surface of the centra, close to the neurocentral suture. This latter structure is broad, showing a wavy outline in lateral view, running almost flat in its caudal half, then forming a pronounced dorsal concavity in its cranial half. Following Brochu's (1996) and Irmis' (2007) definitions, in the present paper a vertebra is considered open when "the neurocentral suture is completely visible from all aspects" and the centrum and neural arch can be easily separated, while it is defined as closed when "the neurocentral suture is no longer visible", and partially closed when the suture has started to close, but it is still visible in some areas. In MCSNB 11341, all preserved vertebrae show a fully open neurocentral suture. In the six caudalmost preserved vertebrae there is only a slight rim between the neural arches and the vertebral body and the compact bone covers the suture, but in the first 3 vertebrae the compact bone does not even reach the area of the suture so that cancellous bone is clearly exposed, suggesting the presence of a broad area of cartilage.

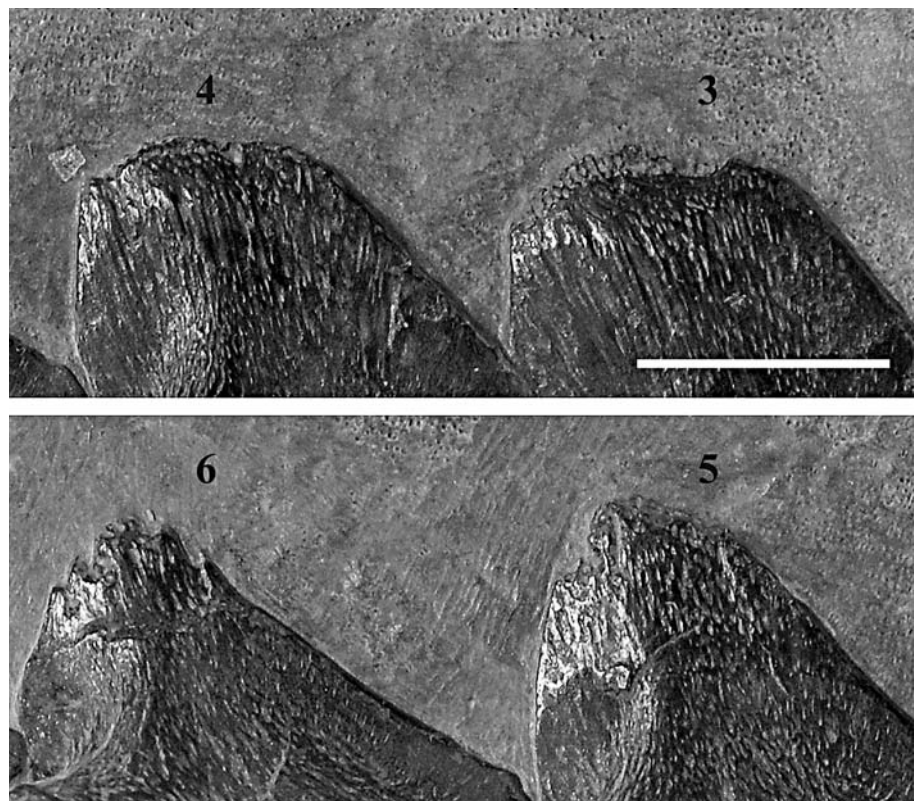
The neural arches are longer than high, they bear rather wide prezygapophyses and narrower postzygapophyses that articulate with each other with subhorizontal articular facets, suggesting lateral mobility for the tail.

The neural spines are slightly longer than tall; the taller ones reach 8 mm in height, and a very small accessory spine is clearly visible in vertebrae at the base of

their anterior margin, above the neural canal, similar to many basal archosaur taxa (Krebs 1965; Benton & Clark 1998). The morphology of the neural spine varies cranio-caudally along the series, those borne by vertebrae 3-4 are broader and sub trapezoidal in lateral view; the following spines gradually become more and more triangular, narrow, and their height increases slightly. Also, their major axis begin to slant caudally in the last two vertebrae. At their base the neural spines are rather robust and the surface of the bone is smooth, while toward their tip (Fig. 3) an abrupt reduction of the thickness occurs, so that the spine blade suddenly becomes very thin, and its surface is covered by a series of grooves and pits and the dorsal margin of shows an irregular outline. This morphology is not a result of erosion or damage, because the surface of the bone is smooth and unabraded, but it is probable that the thin section, the grooves and pits (which represent traces of vascularization of the inner layer of the periosteum), testify that the neural spine was not yet fully ossified and a cap of cartilage was still present.

Haemal spines are Y shaped, intercentral in position, approximately 1.75 times higher than the neural spines, reaching 14 to 14.5 mm in height. They are deep and robust, but narrower than the neural spines, almost cylindrical for most of their axis but ending ventrally with a spatulate expansion. Their main axis is gently curved caudally and the cranio-caudal expansion at the distal end of each spine shows some fluting at its ventral

Fig. 3 - Detail of the dorsal portion of the neural spines of the third to sixth preserved vertebra. Scale bar equals 0.5 cm.



margin, which shows a somewhat rugose “unfinished” appearance, suggesting that an outer rim of cartilage may have been present, but much less developed than in the neural spines. The haemal spines are not connected to the bony base, and their articular surfaces are inclined at approximately 45° with respect to the axis of the vertebra so that the pedicel shows a triangular, dorsally pointed, lateral outline.

Discussion. From the above description, it can be inferred that MCSNB 11341 represents a series of caudal vertebrae, which, being non-notochordal and showing small accessory spines at the base of the cranial margin of the neural spines can belong to some archosaur. The overall features exclude their belonging to dinosaurs since the centra are less constricted, not spool shaped and the zygapophyses do not project extensively beyond the margin of the centra.

Detailed comparison with the large and nearly complete *Myriosuchus* specimen MCSNB 10.087 collected in an outcrop of the Calcare di Zorzino which yielded also an isolated skull ascribed to the same taxon (Renesto & Paganoni 1998; Renesto & Lombardo 1999; Gozzi & Renesto 2003) revealed that, apart for size, the caudal vertebrae here described correspond in many details to the vertebrae of the mid section of the tail of that specimen. Both specimens show amphicoelous centra, slightly compressed laterally and with a concave ventral margin. Short, blunt transverse processes of similar size are present on the centra in both specimens and the morphology of the zygapophyses is also very similar. Finally in both specimens the morphology of haemal spines is identical and in both specimens these latter are loosely connected to the centra.

The main differences between the proximal caudal vertebrae of MCSNB 11341 and of MCSNB 10.087 (Fig. 4) are the much smaller size, the lower degree of ossification of the vertebral bodies of MCSNB 11341,

the lack of closure of the neurocentral suture, and the morphology of the dorsal portion of neural spines. Small size suggests that MCSNB 11341 may be a juvenile, but size, taken alone, cannot represent a reliable indicator of immaturity even among similar taxa, because it does not provide any mean to differentiate adult individuals of small species from young individual of large species, and also many variables may interfere with growth rates and attainment of terminal size (Johnson 1977; Deeming & Ferguson 1990; Brochu 1996). However, all other existing differences between MCSNB 11341 and MCSNB 10.087, can also be explained as due to early ontogenetic stage of MCSNB 11341, especially the lack of closure of the neurocentral suture. Brochu (1996) found that in extant crocodiles most centra caudal to the atlas axis complex may remain separate from each other for most of the ontogeny of the individual in several crocodylian taxa and Irmis (2007), found the same pattern in North American phytosaurs. The closure of the neurocentral sutures in the tail of extant crocodylians proceeds following a caudal to cranial sequence, so that even in hatchlings, presacral and sacral neurocentral sutures are open while majority of the caudal sutures are closed. Only the anteriormost caudal centra show open neurocentral sutures. If the parallel with crocodylian and North American phytosaurs is correct, the caudal vertebrae of MCSNB 11341 could belong to a immature individual. Also, the proportional difference in height between the neural spines of MCSNB 10.087 and MCSNB 11341 can also be explained by the early growth stage of MCSNB 11341, since the neural spine were not yet fully ossified, their dorsal portion being still cartilaginous as in very young specimens of many reptilian taxa (Rieppel 1992; Maisano 2002), as a consequence, the shape of the preserved ossified portion of the neural spines does not reflect that of the adult specimen. The grooves and small pits over the dorsal region of the neural spines, along

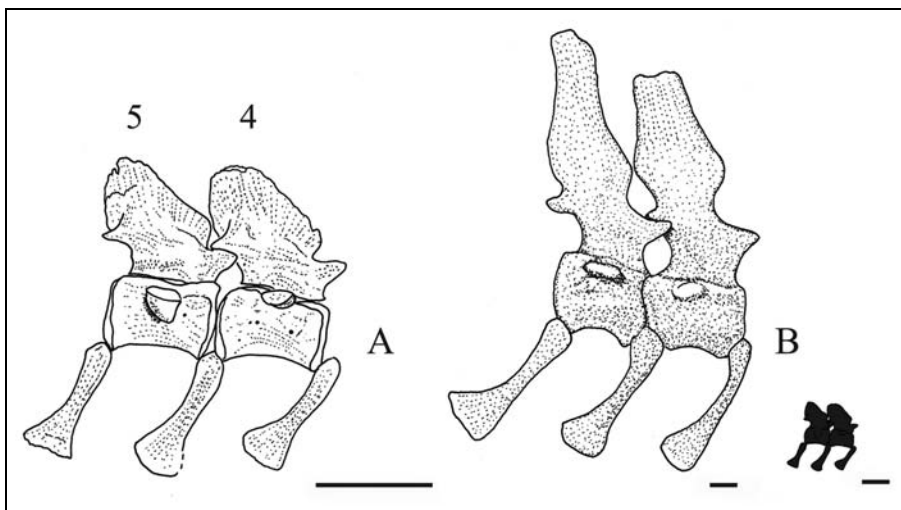


Fig. 4 - Comparison between the fourth and fifth caudal vertebrae of MCSNB 11341 (A) and the caudal vertebrae of the mid section of the tail of MCSNB 10.087 (B, stippled); in full black the fourth and fifth caudal vertebrae of MCSNB 11341 reduced to the same scale of (B) to enhance size difference with MCSNB 10.087. Scale bars equal 1 cm.

with the irregular outline of its dorsal edge may represent traces of vascularization of the inner layer of the cartilaginous cap, responsible for bone deposition as it occurs in extant crocodiles (Haines 1942; Johnson 1977).

In conclusion, all above mentioned characters support the hypothesis that specimen MCSNB 11341 may represent a series of caudal vertebrae roughly corresponding to caudal vertebrae 10-20 of a juvenile phytosaur, probably, as for MCSNB 10.087, referable to the genus *Mystriosuchus*. If this interpretation is correct, MCSNB 11341 is of particular interest, since remains of juvenile phytosaurs are very rare (Fara & Hüngrerbühler 2000), its study allow a better understanding of the ontogenetic changes occurring in phytosaurs. In addition, because preservation of MCSNB 10.087 does not permit observation of the pattern of closure of the neurocentral suture as pointed out by Irmis (2007: 355), MCSNB 11341 gives evidence that the closure of neurocentral suture in *Mystriosuchus* may have followed the same pattern that occurs in crocodylians and in North American phytosaurs (Brochu 1996; Irmis 2007).

Owing to the scarcity of preserved elements it is not possible to give a precise estimate of the total length of MCSNB 11341. The mean length of the preserved caudal centra reaches about 33% of that of the corresponding caudal centra of MCSNB 10.087 (approx. 35-40 mm) which has a total length of 3.720 mm and a snout-vent length of 1420 mm. Without taking into account any kind of allometric variation due to ontogeny (Hurlburt et al. 2003), specimen MCSNB 11341 could possibly have reached a total length of about 1200-1300 mm and a snout vent length of 520 mm, but very probably its actual length was less if, as it occurs in crocodiles (Hall & Portier 1994; Iordanski 1973), also in phytosaurs there was a significant positive allometry for the skull during growth.

Acknowledgements. A. Heckert (Boone NC, USA) and an anonymous reviewer commented an earlier version of the manuscript: their comments and remarks were very helpful. My sincere thanks to M. Malzanni and M. Confortini (Bergamo) for finding and careful preparation of the specimen and to A. Paganoni, Bergamo, for permission to study the specimen. Thanks are due to M. Delfino (Firenze) for stimulating discussion and help with literature on extant crocodylians. The study was financially supported by a CARIPLO special grant from the Dean of the Università dell'Insubria Varese.

REFERENCES

- Benton M. J. & Clark J. M. (1988) - Archosaur phylogeny and the relationships of the Crocodylia. In: Benton, M. J. (Ed.) - The phylogeny and classification of the tetrapods. Volume 1: Amphibians, reptiles, birds. The Systematics Association, Special Volume 35A: 295-338, Clarendon Press, Oxford.
- Brochu C. A. (1996) - Closure of neurocentral suture during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *J. Vert. Paleont.*, 16(1): 49-62, Lawrence.
- Dalla Vecchia F. M. (2003) - New morphological observations on Triassic pterosaurs. In: Buffetaut E. & Mazin M. (Eds) - Evolution and palaeobiology of pterosaurs: 23-43, *Geol. Soc. London Spec. Publ.*, 217, London.
- 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.
- Fara E. & Hüngrerbühler A. (2000) - *Paleorhynchus magnoculus* from the Upper Triassic of Morocco: a juvenile phytosaur (Archosauria). *C. R. Roy. Acad. Sci. Paris Sciences de la Terre et planets*, 331: 831-836, Paris.
- Fraas E. (1896) - Die Schwabischen Trias-Saurier. *Mitt. Konig. Nat.-Cab. Stuttgart*, 5: 1-18, Stuttgart.
- Gauthier J. A. (1984) - A cladistic analysis of the higher systematic categories of the Diapsida. (PhD dissertation). University Microfilms International, Ann Arbor, #85-12825, vii + 564 pp., Ann Arbor.
- Gozzi E. & Renesto S. (2003) - A complete specimen of *Mystriosuchus* (Reptilia, Phytosauria) from the Norian (Late Triassic) of Lombardy (northern Italy). *Riv. It. Paleont. Strat.*, 109: 475-498, Milano.
- Haines R. W. (1942) - The evolution of epiphyses and endochondral bone. *Biol. Rev. Cambridge Phil. Soc.*: 267-292, Cambridge.
- Hall P. M. & Portier K. M. (1994) - Cranial morphometry of New Guinea crocodiles (*Crocodylus novaeguineae*): ontogenetic variation in relative growth of the skull and an assessment of its utility as a predictor of the sex and size of individuals. *Herp. Mon.*, 8: 203-225, Tampa.
- Hurlburt G. R., Heckert A. B. & Farlow, J. O. (2003) - Body mass estimates of phytosaurs (Archosauria: Parasuchidae) from the Petrified Forest Formation (Chinle Group: Revueltian) based on skull and limb bone measurements. *New Mexico Mus. Nat. Hist. Sci. Bull.*, 24: 105-113, Albuquerque.
- Krebs B. (1965) - Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox* nov. gen. nov. sp. *Schweiz. Palaont. Abhandl.*, 81: 1-140, Zuerich.
- Iordansky N. N. (1973) - The skull of the Crocodylian. In: C. Gans & T. S. Parsons (Eds) - *Biology of the Repti-*

- lia. Vol. 4, *Morphology*: 201-262, Academic Press, London.
- Irmis R. B. (2007) - Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *J. Vert. Paleont.*, 27: 350-361, Lawrence.
- Jadoul F., Berra F. & Frisia S. (1992) - Stratigraphic and paleogeographic evolution of a carbonate platform in an extensional tectonic regime: the example of the Dolomia Principale in Lombardy (Italy). *Riv. It. Paleont. Strat.*, 98: 29-44, Milano.
- Jadoul F., Masetti D., Cirilli S., Berra F., Claps M. & Frisia S. (1994) - Norian-Rhaetian stratigraphy and palaeogeographical evolution of the Lombardy basin (Bergamasco Alps). In: Carannante G. and Tonielli R. (Eds) - Excursion B, 15h IAS regional meeting, Ischia, Italy, 1994: 5-38, International Association of Sedimentologists, Freda Press, Ischia.
- Jaeger G. F. (1828) - Uber die fossilen Reptilien welche in Wurttemberg aufgefunden worden Sind. 48 pp., J. B. Metzler, Stuttgart.
- Johnson R. (1977) - Size independent criteria for estimating relative age and the relationship among growth parameters in a group of fossil reptiles (Reptilia, Ichthyosauria). *Can. J. Earth Sci.*, 14: 1916-1924, Edmonton.
- Laurenti J. N. (1768) - Specimen Medicum, Exhibens Synopsis Reptilium Emendatam cum Experimentis circa Venena. 214 pp., Trattner, Wien.
- Maisano J. A. (2002) - Postnatal skeletal ontogeny in five xantusiid (Squamata Scleroglossa). *J. Morph.*, 254: 1-38, New York.
- Meyer H. v. (1863) - Der Schaus dem Stubendsandstein des oberen Keupers. *Palaeontographica*, 10: 236-265, Stuttgart.
- Paganoni A. & Renesto S. (1995) - Taphonomy of Norian (Late Triassic) Argillite di Riva di Solto Formation, Bergamo (Northern Italy). In: M. N. Mendelez (Ed.) - The II International Symposium on Lithographic Limestone: 113-114, Ediciones de la Universidad Autonoma de Madrid, Lleida-Cuenca, Spain.
- Renesto S. (1995) - Ecology and Taphonomy of the Reptiles from the Calcare di Zorzino (Norian, Late Triassic, N. Italy). In: M. N. Mendelez (Ed.) - The II International Symposium on Lithographic Limestone: 123-130, Ediciones de la Universidad Autonoma de Madrid, Lleida-Cuenca, Spain.
- Renesto S. (1999) - Adaptation toward aquatic life in a Norian (Late Triassic) phytosaur (Reptilia Archosauria). International Symposium on secondary adaptation to life in water, extended abstract: 54-57, University of Copenhagen, Copenhagen.
- Renesto S. & Lombardo C. (1999) - Structure of the tail of a phytosaur (Reptilia, Archosauria) from the Norian (Late Triassic) of Lombardy (northern Italy). *Riv. It. Paleont. Strat.*, 105: 135-144, Milano.
- Renesto S. & Paganoni A. (1995) - A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of Northern Italy. *N. Jahrb. Geol. Palaeont. Abh.*, 197: 87-99, Stuttgart.
- Renesto S. & Paganoni A. (1998) - A phytosaur skull from the Norian (Late Triassic) of Lombardy (Northern Italy). *Riv. It. Paleont. Strat.*, 104: 115-122, Milano.
- Rieppel O. (1992) - Studies on skeleton formation in reptiles I. The postembryonic development of the skeleton in *Cyrtodactylus pubisulcus* (Reptilia, Gekkonida). *J. Zool. London*, 227: 87-100, London.
- Tintori A. (1995) - The Norian (Late Triassic) Calcare di Zorzino fauna from Lombardy (Northern Italy): the state of the art. In: M. N. Mendelez (Ed.) - The II International Symposium on Lithographic Limestone: 139-142, Ediciones de la Universidad Autonoma de Madrid, Lleida-Cuenca, Spain.
- Tintori A., Muscio G. & Nardon S. (1985) - The Triassic fossil fishes localities in Italy. *Riv. It. Paleont. Strat.*, 91: 197-210, Milano
- Wild R. (1994) - A juvenile specimen of *Eudimorphodon ranzii* Zambelli (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Bergamo. *Riv. Mus. Civ. Sci. Nat. Bergamo*, 16(1993): 91-115, Bergamo.