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CYMBOSPONDYLUS VERTEBRAE (ICHTHYOSAURIA, SHASTASAURIDAE) FROM THE UPPER ANISIAN PREZZO LIMESTONE (MIDDLE TRIASSIC, SOUTHERN ALPS) WITH AN OVERVIEW OF THE CHRONOSTRATIGRAPHIC DISTRIBUTION OF THE GROUP

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Abstract. Four vertebral centra from the well known fossil-bearing Prezzo Limestone (Upper Anisian, Middle Triassic) at the newly discovered locality Piazza Brembana (Bergamo) are described. The four bones were found exposed on the bed surface in an articulated position. Despite the incompleteness of three centra due to erosion, their otherwise fairly good preservation facilitated their study and attribution to a shastasaurid ichthyosaur. Even though the classification of isolated vertebral centra at the genus level is controversial, the presence of diapophyses truncated by the cranial margin of the centra is still considered to be diagnostic for *Cymbospondylus.* The new discovery comes from an ammonoid-bearing facies, which is not unusual for ichthyosaurs, and the bio-chronostratigraphic position of the Piazza Brembana bones is accurately defined by ammonoids from the lowest part of the Trinodosus Zone (Illyrian, Middle Triassic). Records of *Cymbospondylus* in the Southern Alps, Germanic Basin, western United States and Spitsbergen are summarized and all previous occurrences of the genus are bio-chronostratigraphically correlated by utilizing the abundant ammonoid literature. The single occurrence of *Phantomosaurus neubigii* is also considered, since this species is regarded in the literature as the sister - taxon of *Cymbospondylus.* Material referred to *Cymbospondylus* extends from a single occurrence in the Olenekian (late Early Triassic) to the Longobardian (Late Ladinian), and its stratigraphic distribution is strictly controlled by the development of the sedimentary basins. Within these basins the distribution of specimens appears to include relatively protected and shallow waters. Such a distribution is consistent with the mode of life of this group of ichthyosaurs as suggested by morphofunctional analysis. *Cymbospondylus*, like most Triassic Ichthyosaurs, probably was an undulatory swimmer, more maneuverable but slower than their Jurassic successors.

Riassunto. In questo lavoro vengono descritte quattro vertebre provenienti da una nuova località fossilifera dal Calcare di Prezzo (Anisico superiore), presso Piazza Brembana (Bergamo). Le vertebre erano articolate, ma sono in parte incomplete in quanto sono state rinvenute su una sezione di strato esposta all'erosione. Sono attribuite a *Cymbospondylus* Leidy, 1868 (Ichthyosauria, Shastasauridae) sulla base del contorno subpoligonale delle vertebre in vista frontale e per le diapofisi che entrano in contatto con il margine craniale del centro vertebrale.

Il ritrovamento è stato effettuato in una facies con ammonoidi, come spesso avviene per gli ittiosauri. Sulla base degli ammonoidi la posizione stratigrafica della vertebre è attribuibile alla parte inferiore della Zona a Trinodosus (Illirico, Triassico medio). La taratura biocronostratigrafica del nuovo ritrovamento fornisce lo spunto per riesaminare la posizione cronostratigrafica di tutti i precedenti rinvenimenti di *Cymbospondylus* nelle Alpi meridionali, nel Bacino germanico, in Nord America e alle Spitsbergen. Viene inoltre considerato l'unico rinvenimento di *Phantomosaurus neubigii* dal Muschelkalk, in quanto questa specie in letteratura è stata classificata come sister taxon di *Cymbospondylus* malgrado la morfologia delle vertebre dorsali posteriori sia sconosciuta. *Cymbospondylus* compare nell'Olenekiano (Triassico inferiore) e scompare nel Ladinico superiore. La distribuzione stratigrafica risulta strettamente controllata dallo sviluppo dei bacini sedimentari, ma all'interno dei bacini la distribuzione degli esemplari sembra comprendere, almeno in parte, aree abbastanza protette e non particolarmente profonde. Questa distribuzione è coerente con la modalità di vita dei questo gruppo di ittiosauri dedotta da analisi morfofunzionali, secondo le quali *Cymbospondylus* con il corpo allungato e assenza di pinna caudale a due lobi, sarebbe stato caratterizzato da nuoto ondulatorio, con buona manovrabilità ma relativamente bassa velocità, più adatto ad acque relativamente poco profonde, e caccia all'agguato al contrario degli ittiosauri del Giurassico, caratterizzati da un nuoto oscillatorio veloce e ben adattati all'inseguimento.

Introduction

The Prezzo Limestone (Rosenberg 1962; Assereto & Casati 1965) is one of the most fossiliferous Triassic

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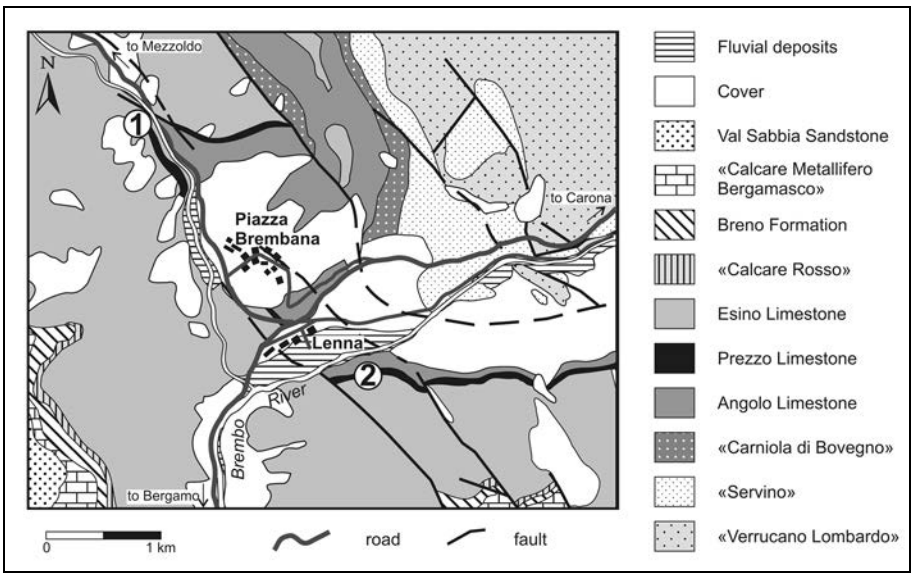


Fig. 1 - Geological sketch map showing the location of section Piazza Brembana (1) with respect to the well-known site Lenna (2). Redrawn from Carta Geologica della Provincia di Bergamo (2000).

lithostratigraphic units in the Southern Alps. The first report of fossils from this unit occurred in 1866, when Benecke described two new ammonoid species and one new bivalve species from Scalve Valley (Bergamo). Since then several authors have reported fossils from tens of localities scattered over all the formation's outcrop areas from Grigne in the West to the Giudicarie Valley in the East.

The most frequent and important fossil group recorded from the Prezzo Limestone is represented by the cephalopods, and in particular the ammonoids, which played a crucial role in both the development of Triassic ammonoid taxonomy and the evolution of the Triassic ammonoid bio-chronostratigraphic scale (see Balini et al. 2010 for historical summary).

Ammonoids from the Prezzo Limestone have provided the basis for the definition of several tens of new taxa (species and genera) and have been illustrated in several papers and monographs (Benecke 1866; Hauer 1866; Mojsisovics 1882; Arthaber 1896; Riedel 1949; Assereto 1963; Assereto & Casati 1966; Casati & Gnaccolini 1967; Venzo & Pelosio 1968; Gaetani 1969; Balini 1992a,b, 1998; Monnet et al. 2008). From a bio-chronostratigraphic point of view, ammonoid faunas from the Prezzo Limestone have contributed significantly to the definition of the Trinodosus Zone (Mojsisovics 1882) as well as to the definition of the Illyrian substage (Pia 1930) of the Anisian. More recently they have played a major role in several papers dealing with Upper Anisian bio-chronostratigraphy (Gaetani 1969, 1979 [in Jadoul et al.]; Balini 1992a; Brack & Rieber 1993; Mietto & Manfrin 1995a; Mietto et al. 2003; Monnet et al. 2008).

Although the Prezzo Limestone is known worldwide for its ammonoid faunas, the fossil record of this unit actually includes a much wider variety of groups such as bivalves (e.g., Benecke 1866; Casati & Gnaccolini 1967), brachiopods (e.g., Gaetani 1969), gastropods (e.g., Casati & Gnaccolini 1967; Tichy 1980) and conodonts (e.g., Kovacs et al. 1980). Field experience has shown the presence of trace fossils, which sometimes are rather common, and last but not least, the vertebrates. This paper focuses on the first description of four isolated vertebral centra belonging to a large shastasaurid ichthyosaur discovered in a new stratigraphic section of Prezzo Limestone in Brembana Valley (Bergamo), close to Lenna, a fossiliferous locality first reported by Mojsisovics (1882).

Stratigraphic section and material

The specimens described in this paper were collected from a new fossiliferous locality about 1.5 km NW of the village Piazza Brembana and 2.9 km NW of the well-known fossiliferous locality Lenna (Mojsisovics 1882; Venzo & Pelosio 1968; Fig. 1). At this new site, here named "Piazza Brembana", an approximately 17 meter thick section of the Prezzo Limestone is well exposed in the Brembo di Mezzoldo riverbed (Fig. 2).

The stratigraphic setting of the new site is very similar to that of Lenna. In both localities the Prezzo Limestone conformably overlies the Angolo Limestone and is conformably overlain by the shallow water Esino Limestone. The overall thickness of the formation is notably thinner at Piazza Brembana-Lenna than in the rest of Lombardy, where the unit usually reaches a thickness of several tens of meters (about 60-80 m in Camonica Valley and 40-70 m in northern Grigna: Gaetani 1970). In addition, the average thickness of both limestone beds and marl/shale interbeds (Fig. 2) is also thinner in the two Brembana Valley sections (about 10-15 cm) than in the sections from eastern Lombardy – Giudicarie (20-30 cm). This setting is rather consistent with deposition in a sector of the western Southern Alps characterized during Late Anisian times by low subsidence with respect to eastern Lombardy – Giudicarie, where the transgressive trend documented by the Prezzo Limestone continued in the Early Ladinian with deposition of basinal sediments of the Buchenstein Formation.

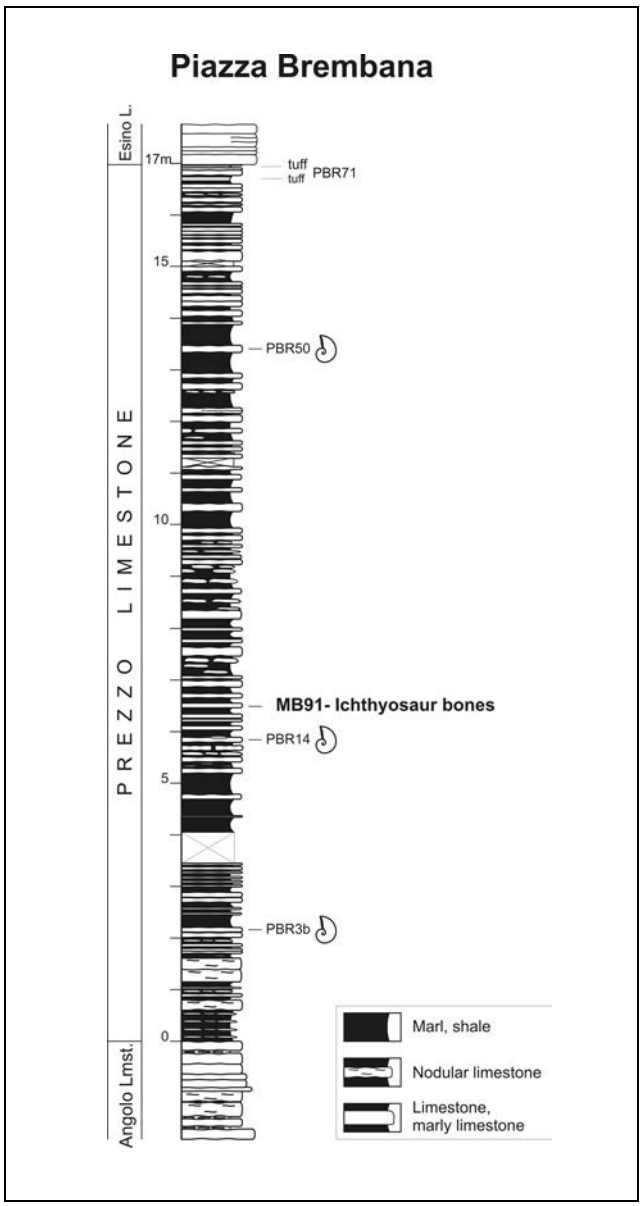


Fig. 2 - Stratigraphic section Piazza Brembana exposed in the Brembo di Mezzoldo riverbed showing the position of sample MB91.

Exposures of the entire formation in the riverbed combined with their continuous washing by the river make the Piazza Brembana section an ideal outcrop for the discovery of fossils on the surface of the limestone beds. However, it can be difficult to collect well preserved specimens because the un-weathered limestone beds are usually very hard and the fracture cleavage of the marl/shale interbeds occasionally extends into the limestone levels.

A preliminary survey of the section conducted by the first author in the 1990's lead to the discovery of four vertebral centra in a limestone bed about 6.5 m above the base of the Prezzo Limestone (MB91, Fig. 2). These centra were immediately extracted and brought to the Laboratory of Paleontology of Milano University, where they were removed from the matrix by chemical preparation with acetic acid. A detailed study of the Piazza Brembana locality initiated three years ago has provided a well defined biostratigraphic framework for this bone-bearing level.

Palaeontological description

Reptilia Linnaeus, 1758
Diapsida Osborn, 1903
Ichthyosauria Blainville, 1835
Shastasauridae Merriam, 1908
Cymbospondylus Leidy, 1868

Cymbospondylus sp.

Pl. 1, figs A-F; Pl. 2, figs A-F; Fig. 3

Repository: Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Italy (MCSNB).

Material: specimens MCSNB 11689 A, B, C, D (Pl. 1-2), consisting of one complete (MCSNB 11689A) and three partial (MCSNB 11689B-D) vertebral centra. The four centra were found in a closely positioned manner, which most likely reflects their original anatomical connection; thus, it can be assumed with confidence that they belonged to the same individual. Three of the four specimens are incomplete due to the effects of erosion because the centra were exposed on the rock surface at the time of their discovery. The lack of the associated neural arches and spine is rather usual in ichthyosaurs since they were weakly connected to the centra.

Locality and formation: Piazza Brembana section (Brembana Valley, Bergamo), Prezzo Limestone.

Description. The outer surfaces of the centra are heavily worn/eroded; therefore, several details are difficult to observe. They are also slightly deformed, but their general outline can be reconstructed with confidence. Specimen MCSNB 11689A is completely preserved and only slightly deformed (Pl. 1 A-F). Vertebral centrum MCSNB 11689B is eroded on its left side (Pl. 1 G-L) as is MCSNB 11689C (Pl. 2 A-F), from which nearly half of the centrum is missing. Specimen MCSNB 1169D is represented only by the dorsal portion of the centrum, with the pedicels for the neural arches (Pl. 2 G-H). The most complete centra exhibits a discoidal rather than cylindrical shape (Maisch & Matzke 2000) (height/length = 2.47 for MCSNB 11689A and 2.44 for MCSNB 1689C), which is deeply amphicoelous, with an hourglass cross section but not notochordal. They are polygonal in cranial or caudal view, being higher than wide. Their articular margins are thickened and form a distinct rim, while the lateral surfaces are medially concave. In all specimens the articular surfaces for the neural arches are preserved; they are two distinct ridges sulcated by longitudinal furrows. Small diapophysial processes project out of their lateral surfaces, reaching the cranial margin of the centrum.

Dimensions (in mm)

	height	length	width	h/l ratio
11689A	47	19	34	2.47
11689B	-	19	34	
11689C	44	18	-	2.44
11689D	-	18	-	

Discussion. The height to length ratio, together with their overall size allows us to consider MCSNB 11689A-D as belonging to a shastasaurid ichthyosaur (Sander 1989). The best known shastasaurids of the Middle Triassic are 1) *Cymbospondylus* Leidy, 1868 from Nevada (Merriam 1908), Germany (Huene 1916), Monte San Giorgio (Sander 1989), and the Buchensteiner Schichten of the Dolomites of Seceda (Kuhn-Schnyder 1980, Sander 2000); and 2) *Besanosaurus* Dal Sasso & Pinna, 1996 from Monte San Giorgio. In addition, *Mikadocephalus* (Maisch & Matzke, 1997) and *Wimanius* (Maisch & Matzke, 1998) are only represented by fragmentary material, but Sander (2000) suggested that they may be strictly related to, or even junior synonyms of *Besanosaurus*. *Phantomosaurus neubigii* (Sander, 1997) is another medium sized ichthyosaur, known by only one specimen from the lower Upper Muschelkalk. This species was originally attributed to the genus *Shastasaurus* by Sander (1997), but subsequently Maisch & Matzke (2000) in their comprehensive phylogenetic analysis of ichthyosaur relationships, assigned it to a new genus considered to be the sister-taxon of *Cymbospondylus*.

Overall, the morphology of the vertebral centra from Prezzo Limestone closely resembles that of the shastasaurid of Seceda (Kuhn-Schnyder 1980 fig. 6) but on a smaller scale. The Seceda specimen (housed in the "Museum de Gherdëina", Museo Ladino della Val Gardena, Ortisei, Bolzano/Bozen, Italy) was originally attributed to the genus *Shastasaurus* by Kuhn-Schnyder (1980), but Sander (2000) provided detailed evidence for its attribution to *Cymbospondylus*.

Cymbospondylus was a medium to very large sized (length possibly 10 m or longer) shastasaurid ichthyosaur that fed on fishes, cephalopods and small marine reptiles in open waters. Its skull was elongate but robust with a distinct sagittal crest, suggesting a powerful jaw musculature. The four centra here described do not reach the maximum size recorded for the genus, but it is feasible that they may have belonged to either a small or juvenile individual of a large species like *C. buchseri* Sander, 1989, well known from the Swiss localities of Monte San Giorgio, or to a fully grown individual of a smaller species such as *C. piscosus* Leidy, 1868 (Massare & Callaway 1994), whose centra are approximately the same size of those from the Prezzo Limestone. *Cymbospondylus parvus* (Huene, 1916) is another small sized species, known only by two dorsal vertebral centra (Sander 1989), which reach approximately half the height of our vertebrae (25 and 27mm); thus, a detailed comparison is difficult.

Since Sander (1989, 1992, 1997) considered the morphology of the centra to be sufficiently diagnostic for attribution to the generic level, then according to this author the subrectangular or subtriangular outline of the centra exhibited by specimens MCSNB 11689 A-C is typical of the anterior/mid caudal centra of *Cymbospondylus* (*Besanosaurus* centra are more rounded in shape). Furthermore, Sander (1989) considered the presence of a diapophysis truncated by the cranial margin of the centrum in MCSNB 11689A to be diagnostic for *Cymbospondylus*. However, controversy has arisen more recently about the validity of considering isolated centra as diagnostic to the generic level. Motani (1999), Maisch & Matzke (2000) and McGowan & Motani (2003) suggested that the morphology seen in *Cymbospondylus* is plesiomorphic in shastasaurid ichthyosaurs, and thus not diagnostic for the genus, but rather only indicative of an evolutionary grade. This may also be supported by the discovery of *Cymbospondylus*-type vertebrae in the Olenekian (Massare & Callaway 1994). However, Maisch & Matzke (2000) and Frobisch et al. (2006), retained the morphological feature "posterior diapophyses truncated by the cranial margin of the centra" as a valid diagnostic guide for the genus *Cymbospondylus*; thus, it seems reasonable to consider MCSNB 11689A-D (Pls. 1-2) as *Cymbospondylus* sp. (Fig. 3) as well as the Olenekian specimen of Massare & Callaway (1994).

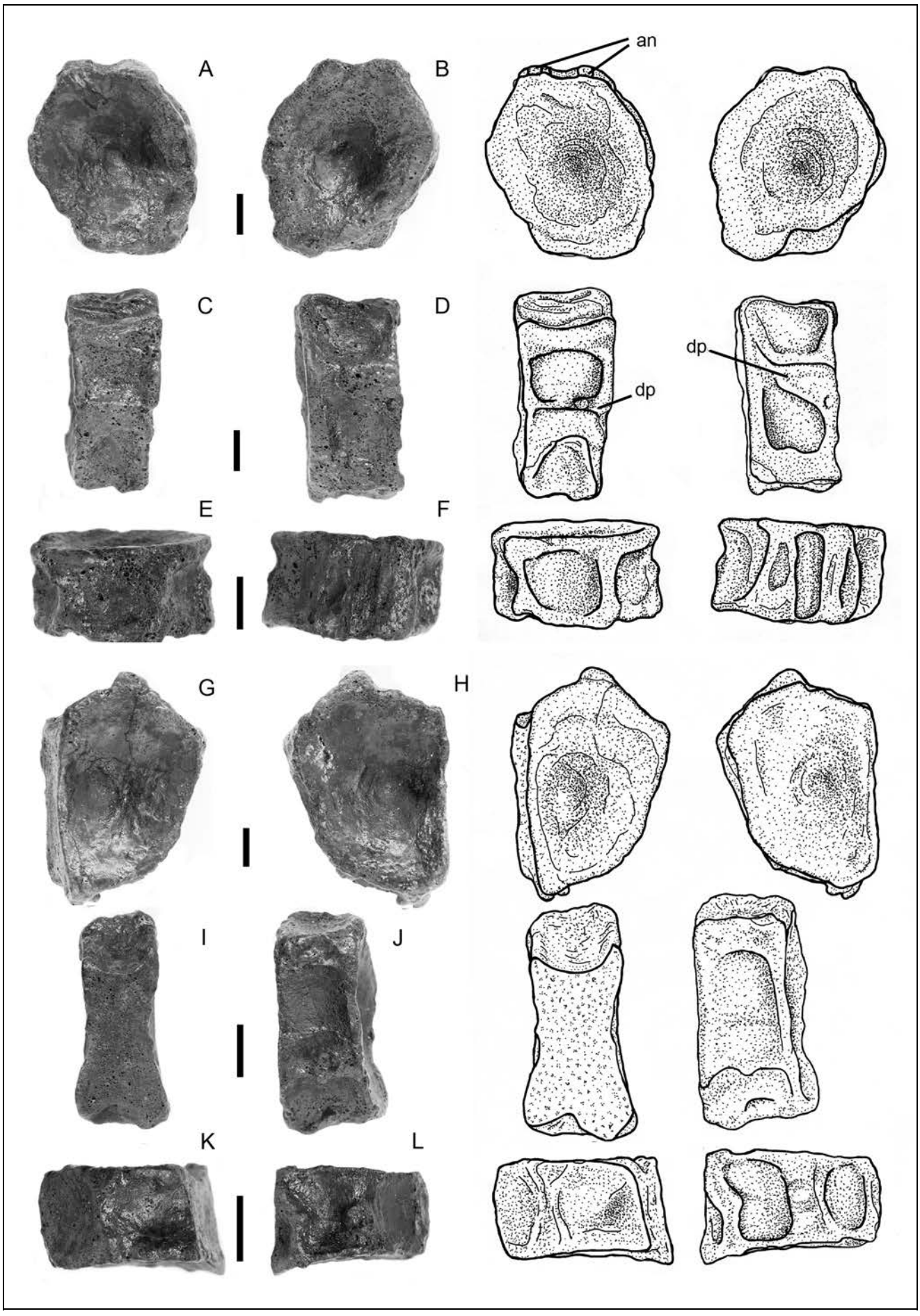
Age. Late Anisian, Trinodosus Zone (see discussion below).

Ammonoids as a tool for calibration of *Cymbospondylus*-type ichthyosaur distribution

Ichthyosaurs were typical of open marine environments and are frequently found in the same facies as ammonoids. According to Kuhn Schnyder (1964), Rieber (1970), Massare (1987) and Sander (1989), the relationship of the two groups was very close since the ammonoids, together with endocochleate cephalopods (e.g., belemnites), and fishes were likely the ichthyosaurs' main source of food. Notwithstanding the very common co-occurrence of the two groups, ichthyosaur and ammonoid studies are usually reported in separate and totally independent papers by vertebrate and inver-

PLATE 1

A-F - *Cymbospondylus* sp. Specimen MCSNB 11689A isolated vertebra, in different views with interpretative drawings shown at right. A) Cranial, B) caudal, C) left, D) right, E) ventral F) dorsal views. G-L - *Cymbospondylus* sp. Specimen MCSNB 11689B, isolated vertebra, in different views with interpretative drawings shown at right. G) Cranial, H) caudal I) left J) right K) ventral and L) dorsal views. Scale bars equal 1 cm. Abbreviations: an) articular area for neural arch; dp) diapophyses.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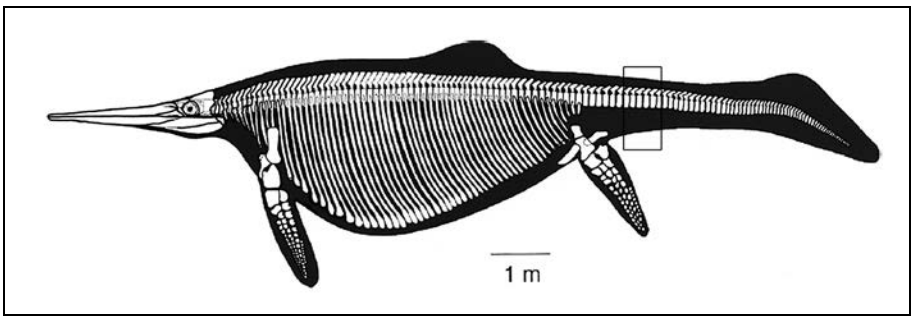


Fig. 3 - Reconstruction showing the presumed original position of the vertebral centra under study.

tebrate paleontologists, respectively. Despite the high resolution power provided by ammonoids, which normally is a chronozone or even higher (e.g., Balini et al. 2010), the chronostratigraphic range of several genera and species of ichthyosaurs is no more accurate than substage or stage (e.g., Sander 1989, 2000) or even series (e.g., Li & You 2002). Such low accuracy cannot always be explained by the occurrence of rare ichthyosaur specimens in float blocks, but it may also be related to a lack of communication between vertebrate and invertebrate paleontologists.

During the last 25 years an impressive amount of new data concerning ammonoid bio-chronostratigraphy and high resolution integrated correlation has been produced in the framework of multidisciplinary investigations for the definition of the GSSP (Global Stratotype Section and Point) of the Ladinian and the Carnian Stages. These new data can be used to refine the chronostratigraphic position of many ichthyosaur discoveries. In this chapter we provide the correlation for the new discovery at Piazza Brembana and we discuss the chronostratigraphic position of all occurrences of *Cymbospondylus*-type ichthyosaurs (*Cymbospondylus* Leidy, 1868 and *Phantomosaurus* Maisch & Matzke, 2000). According to recent literature, the attribution to *Cymbospondylus* of some of the isolated vertebral centra reported in the older literature, should be considered as uncertain, but in the following section we take into account all of these isolated discoveries in order to summarize the stratigraphic distribution of the *Cymbospondylus*-type remains. The taxonomic revision of the group is beyond the scope of the present work.

Cymbospondylus-type ichthyosaurs are known from the Southern Alps, the Germanic Basin, the western United States and Spitsbergen. However, the different paleobiogeographic affinities of the ammonoid faunas (Tozer 1981; Dagys 1988; Balini et al. 2010) lead to a less than precise correlation of the North American and Arctic successions with the World standard reference from the Southern Alps. The correlation of the Germanic Basin successions with the Southern Alps is somewhat better because of the occurrence of few Tethyan forms.

Chronostratigraphic position of the Piazza Brembana bone-bearing level

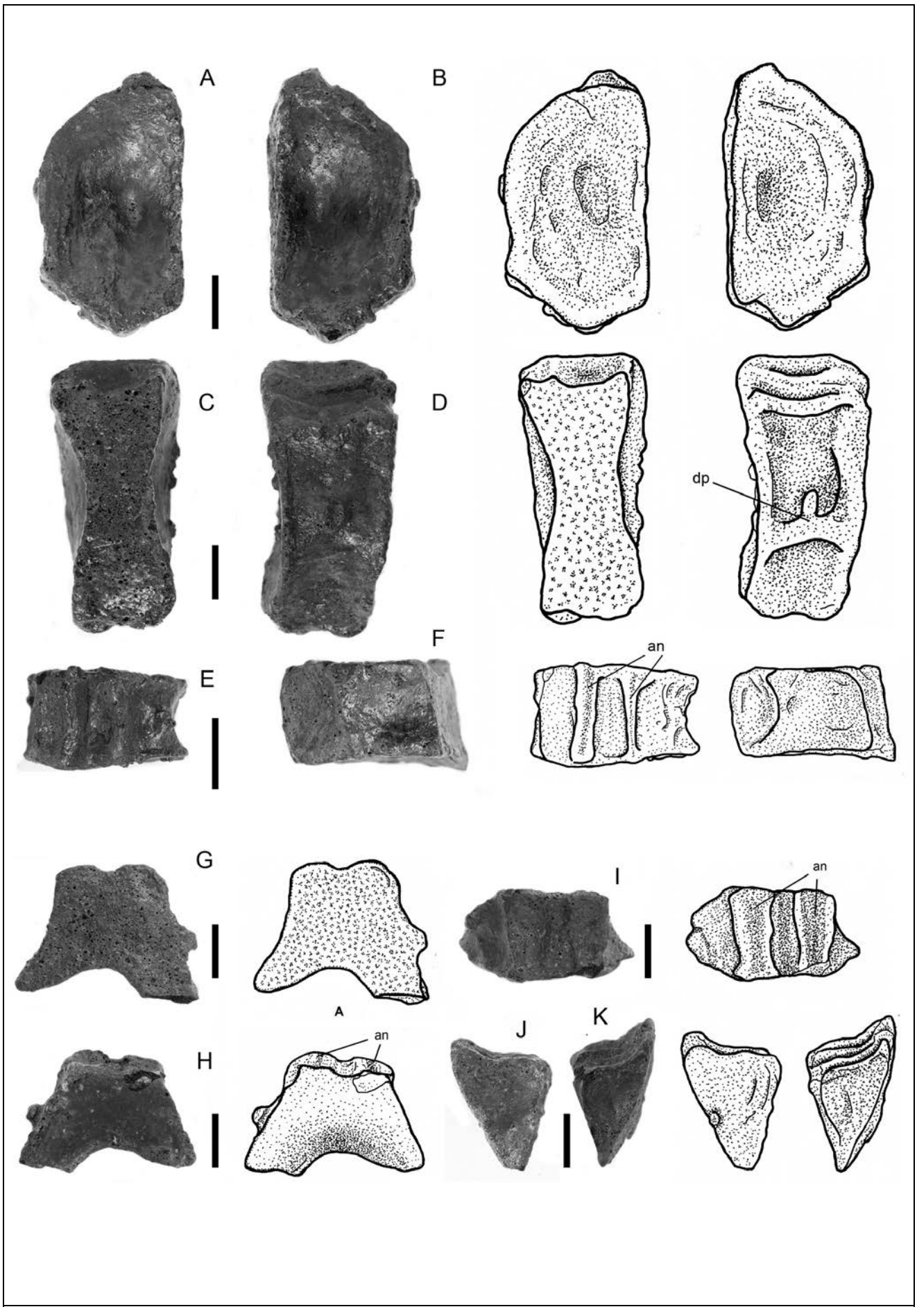
The most complete and best known ammonoid record from the Prezzo Limestone is the Stabol Fresco section in western Lombardy – Giudicarie (Gaetani 1969; Balini 1992a,b, 1998). Ammonoid faunas recorded in the Brembana Valley localities are slightly different with respect to those from the Giudicarie, but direct correlations are still possible.

The most frequent macrofossils recorded in the Piazza Brembana section are brachiopods and ammonoids, with daonellid bivalves being extremely rare. Brachiopods mainly consist of *Tetractinella*, which occurs in several levels from the upper part of the Angolo Limestone to the lower part of the Prezzo Limestone. Ammonoids also occur in the upper part of the Prezzo Limestone, but they are difficult to extract from the matrix. Thus far, only a few specimens from levels PBR3b, PBR14 and PBR50 can be classified (Fig. 4). Most of them belong to short ranging taxa, which permit very precise bio-chronostratigraphic correlations with the ammonoid record from the Prezzo Limestone in the Giudicarie, i.e., with the Stabol Fresco and Adanà sections (Balini 1992a, b, 1998; Fig. 4).

Levels PBR3b and PBR14 are located stratigraphically below the bone sample MB91 (Fig. 4), while PBR50 is located above it. Level PBR3b yields *Judicarites* cf. *meneghinii* together with ceratitids belonging to the group of "*Beyrichites*" *orobicus* Venzo & Pelosio (1968).

PLATE 2

A-F - *Cymbospondylus* sp. Specimen MCSNB 11689 C isolated vertebra, in different views with interpretative drawings shown at right. A) Cranial, B) caudal, C) left, D) right, E) ventral F) dorsal views.
G-K - *Cymbospondylus* sp. Specimen MCSNB 11689D, dorsal portion of an isolated vertebra. G) Mid section, H) ?caudal, I) dorsal, J-K) lateral views.
Scale bars equal 1 cm. Abbreviation: an) articular area for neural arch.; dp) diapophyses.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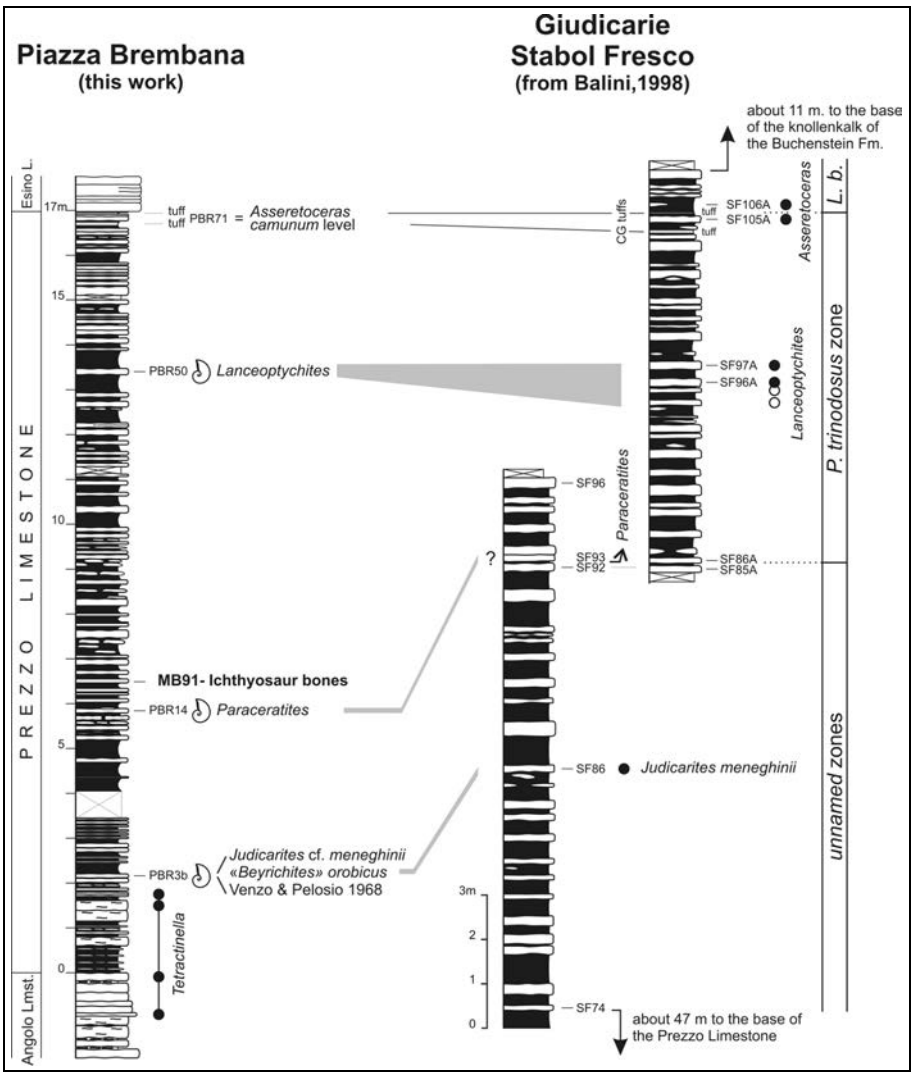


Fig. 4 - Ammonoid levels at the Piazza Brembana section and their correlation with the Stabol Fresco section in Giudicarie. The best ammonoid record for the Prezzo Limestone is from Stabol Fresco section (Balini 1992a, b, 1998) that is also the reference section for the formation (Gaetani 1970). Biostratigraphy is from Balini (1998): L.b.= *Lardaroceras* beds; CG tuffs= Contrada Gobbia tuffs. Black circle: occurrence in Stabol Fresco section; open circle: occurrence in the Adanà section, located about 400 m from Stabol Fresco section.

Judicarites meneghinii Mojsisovics, 1882 is relatively rare in the Giudicarie and occurs only in level SF86 of the Stabol Fresco section, about 4.5 meters below the first occurrence of *Paraceratites*, documented in level SF93. *Beyrichites orobicus* Venzo & Pelosio 1968, described from Lenna on the basis of specimens without stratigraphic position, is very similar to some of the specimens from Stabol Fresco level SF92, which are attributed in the literature to *Beyrichites* ? *abichi* (Mojsisovics, 1882) by Gaetani (1969, 1970).

The occurrence of *Paraceratites* in level PBR14 leads us to refer sample MB91 to the Trinodosus Zone. In meaning of Balini (1998: 151), based on the study of Prezzo Limestone ammonoid faunas, this zone is redefined on the basis of a taxon range zone with the genus *Paraceratites* as index.

Level PBR50, about 7 meters above MB91, yielded one specimen of *Lanceoptychites*, a genus documented from the Trinodosus Zone to the Avisianum subzone by a succession of a few short ranging chronospecies (Balini 1998; Manfrin et al. 2005). The occurrence of this genus in the Prezzo Limestone is restricted to the middle part of the Trinodosus Zone at the Stabol Fresco and Adanà sections (Balini 1998).

Up to the present time, fossils have not been documented from the upper part of the Trinodosus Zone at Piazza Brembana, but this part can be indirectly correlated by two-1 cm thick tuff layers bracketing level PBR71. These thin tuff layers can be correlated with the Contrada Gobbia tuffs (CGt) of Brack et al. (2005: fig. 6-8), which have proven to be a most useful tuff-marker for correlation purposes. The CG tuffs are also recognized at the Stabol Fresco section, where they bracket level SF105A, which is characterized by a rich ammonoid fauna dominated by *Asseretocetas camunum* (Assereto, 1963).

Chronostratigraphic record of *Cymbospondylus* and *Phantomosaurus*

Southern Alps

The Middle Triassic marine record of the Southern Alps has provided a huge amount of information for

the reconstruction of the ammonoid faunal succession (Brack & Rieber 1986, 1993; Mietto & Manfrin 1995a, b; Mietto et al. 2008) and for its integration with conodont and pelagic bivalve bio-chronostratigraphy, as well as with magnetostratigraphy and radioisotopic dating of tuff layers (see Brack et al. 2005 for summary of the Anisian/Ladinian boundary data and Mietto et al. 2007 for the Ladinian/Carnian). These integrated high resolution data provided crucial support for the formal definition of the GSSPs of the Ladinian stage at Bagolino (east Lombardy) and the Carnian stage at Prati di Stuores/Stuores Wiesen (Dolomites), and are nowadays of great interest for the high resolution correlation of *Cymbospondylus*-type ichthyosaur occurrences in the Southern Alps (Fig. 5).

An examination of the literature has resulted in the selection of several specimens that definitely can be traced back to their original stratigraphic level. These occurrences are listed in stratigraphic succession as follows (numbering as in Fig. 5):

1) Pian delle Streghe (Bivera Mountain, Forni di Sotto; Carnia). Rieppel & Dalla Vecchia (2001: 5) reported one vertebral centrum, a neural spine and three fragments of ribs, all from a block belonging to the Dont Formation. This block also yielded ammonoids of the Balatonicus Subzone sensu Mietto & Manfrin 1995 (P. Mietto, pers. comm 2011). The bones were originally attributed with doubt to *Cymbospondylus* sp. and indeed, the shape and position of the diapophyses may support their interpretation.

2) Piazza Brembana, this work. *Cymbospondylus* sp.

3) Tre Fontane (Monte S. Giorgio, Canton Ticino; Switzerland). Sander (1989) described the new species *Cymbospondylus buchseri* on the basis of a rather complete specimen collected from an underground mine at locality "Tre Fontane" in 1927. The mine is no longer accessible, but some information is available from Rieber, who worked extensively in the area in the 1960s. He reported three stratigraphic sections from the ravine above "Tre Fontane" (Rieber 1973, fig. 2), all well correlated with the main section sampled at site "902". The same succession, exposed at each of the three sites, is equivalent to the interval between beds 28 and 63 of the succession exposed at site "902". This interval (Brack & Rieber 1993; Brack et al. 2005, fig. 7) underlies the tuff layer Tc and is placed between the upper part of the Reitzi Zone and the very base of the Secedensis Zone.

4) Seceda (Gardena Valley, Dolomites). Kuhn-Schnyder (1980) described four groups of bones and three isolated vertebral centra from a very well defined level of the "Buchensteiner Schichten" at Seceda. This level was reported (Kuhn-Schnyder 1980: 232) to be 3 to 4 m above the upper boundary of the "Unteren Bänderkalke" (= Lower Plattenkalk *sensu* Brack & Rieber 1993: 426). Data resulting from the very accurate bed-by-bed investigation carried out at Seceda by Brack & Rieber for over ten years (Brack & Rieber 1993; Brack et al. 2005: fig. 7) allow us to safely refer the specimen to the middle part of the Secedensis Zone, just above the tuff layer Te. The specimen was originally described as *Shastasaurus* (?) sp., but we here confirm its attribution to *Cymbospondylus* as already suggested by Sander (1989).

5) Clap di Val (Forni di Sotto; Carnia). Rieppel & Dalla Vecchia (2001: 4-5) reported two vertebral centra, one from interval UA5 of Pisa (1966) "Formazione delle calcareniti rosse e grige" and one from an unknown level of the same section. The section is notably condensed (Mietto & Manfrin 1995a), but interval UA5 yields ammonoids of the Longobardicum-Neumayri Subzones of the Longobardian (P. Mietto, pers. comm. 2011), thus permitting precise dating of the first sample. Both specimens were questionably attributed to *Cymbospondylus* sp., but the morphology of the diapophyses supports this attribution.

Germanic Basin

Over the past 20 – 30 years, knowledge regarding the lithostratigraphic and bio-chronostratigraphic aspects of the Muschelkalk has improved significantly, resulting in a much improved understanding of the marine Middle Triassic evolution of the Germanic Basin. Detailed lithostratigraphy, sequence stratigraphy and cyclostratigraphy for both the Lower and Upper Muschelkalk are well documented (for summary and literature see Hagdorn et al. 1991; Bachmann & Kozur 2004). Bio-chronostratigraphy has been notably improved, but correlation with the Tethyan scale is still complex due to the development of endemic ammonoids and conodonts in the Muschelkalk basin. The bio-chronostratigraphy of the Lower Muschelkalk is especially complex because the few occurrences of Tethyan ammonoids and conodonts have been reported only from the eastern part of the basin (Poland: Kaim & Niedzwiedzki 1999; Narkiewicz & Szulc 2004). Ammonoid biostratigraphy is better defined for the Upper Muschelkalk, which is subdivided into 13 ammonoid zones (Urlichs & Mundlos 1980, 1987) that can be partially correlated with the Tethyan scale (Brack et al. 1999) due to the occurrences of few Tethyan taxa.

In the Germanic Basin *Cymbospondylus*-type ichthyosaurs, represented by both *Cymbospondylus* Leidy, 1868 and *Phantomosaurus* Maisch & Matzke, 2000, have been reported from the Lower and the Upper Muschelkalk. The Lower Muschelkalk has yielded *C. parvus* Huene, 1916, but no species identification is available for the *Cymbospondylus* from the Upper Muschelkalk. The single specimen known so

far of *Phantomosaurus neubigii* (Sander, 1997) is also from the Upper Muschelkalk. These discoveries are listed in stratigraphic order as follows (numbering as in Fig. 5):

6) Laufenburg am Rhein (Kt. Argau, Switzerland). *Cymbospondylus parvus* Huene, 1916: two vertebral centra (p. 27-28), including the type of the species, were collected from the "Wellendolomit". No information regarding the stratigraphic position of the two specimens was reported and recent literature for the area (NAGRA 2001; Marchant et al. 2005) provides only a very general description of the stratigraphic succession. The "Wellendolomit" is apparently a shallow water equivalent of the "Wellenkalk", but the precise chronostratigraphic position of this facies is actually not known and the occurrence of *C. parvus* cannot be more precisely dated than Pelsonian.

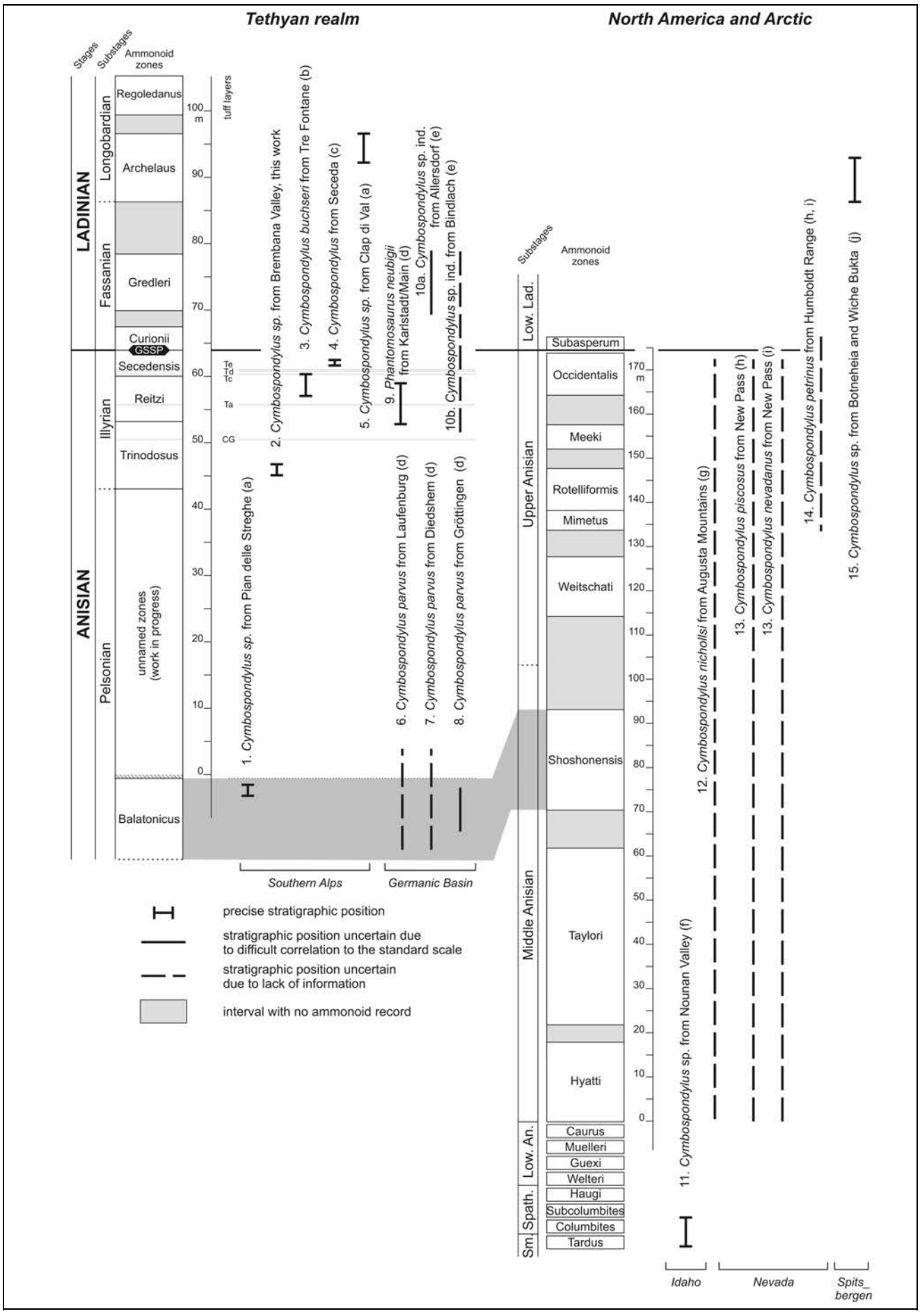
7) "Schreckberg bei Diedeshiem, Amt Mosbach im nordlichen Baden". One vertebral centrum from an unknown level of the "Wellenkalk" was included by Huene (1916: 28, fig. 46) in *C. parvus*. The "Wellenkalk" is a rather thick part of the Lower Muschelkalk, which is referred to the Pelsonian (e.g., Hagdorn et al. 1991). The occurrence of *Judicarites* in the uppermost part of the "Schaumkalk" (Kozur 1974; Brack et al. 1999), i.e., in the upper part of the "Wellenkalk", suggests a correlation of the "Wellenkalk" with the lower part of the Prezzo Limestone and possibly with the uppermost part of the Angolo Limestone.

8) Gröttingen, West of Karlsruhe. Another vertebral centrum recorded from this site (p. 28, fig. 47) was included by Huene (1916) in *C. parvus*. The lithostratigraphic position of this bone is much better defined than the others, as it was collected from the "Terebratelbank" of the "Wellenkalk". The two "Terebratelbank" (lower and upper) known so far from the Lower Muschelkalk are located in a rather thin interval in the middle of the Pelsonian, above the *Beneckeia buchi* interval and within the Kockeli zone of Kozur (1974).

9) Karlstadt/Main, Franconia. Sander (1997) described a new species *Shastasaurus neubigii* based on several elements (part of the skull, two sections of the vertebral column and some pelvic girdle and hind-limb elements) from the skeleton of a specimen discovered during railroad construction. The species was later reassigned to the new monotypic genus *Phantomosaurus* by Maisch & Matzke (2000). We include it here for the sake of completeness because it is considered to be the sister genus of *Cymbospondylus*. The structure of its posterior dorsal vertebrae is unknown, but it must be taken into consideration that Motani (1999) excluded this genus from his analysis of ichthyosaur phylogeny as did Thorne et al. (2010) because it is too poorly known to be included in their analyses. The skeleton was collected from limestones of the Pulcher/Robustus zones (Sander 1997) in the lower part of the Upper Muschelkalk. This interval is somewhat below "Tonhorizont ß1", which contains *Nevadites*, and is thus correlated with the Secedensis Zone of the Tethys (Brack et al. 1999). Therefore, the level from which *Phantomosaurus* was collected falls within the upper part of the Trinodosus Zone and the Reitzi Zone.

10) Allersdorf and Bindlach, near Bayreuth. Huene (1916: 36-37) reported one lower mandible (fig. 62: 10a in Fig. 5) and a vertebral centrum (fig. 63: 10b in Fig. 5) of *Cymbospondylus* from the Upper Muschelkalk. The mandible (10a) was collected from the "obersten glaukonitreichen", a distinct marker level attributed to the Semipartitus Zone (Urlichs & Mundlos 1987). This zone is definitely Ladinian, but its position with respect to the Fassanian/Longobardian boundary is not yet well defined, as this boundary is unknown in the Germanic Basin. The distribution of palynomorphs *Echinosporites iliacoides* and *Heliosaccus dimorphus*,

Fig. 5 - The Anisian-Ladinian record of *Cymbospondylus*-type ichthyosaurs, correlated with the standard chronostratigraphic scale. Occurrences from the Southern Alps and Germanic Basin are correlated with a reference based on the Bagolino GSSP section (from Brack et al. 2005, fig. 3; scale in meters, level 0 is the base of Prezzo Limestone), where all zones, except the Balatonicus Zone, are recognized (summary in Brack et al. 2005). Duration of the Balatonicus Zone is not to scale. The position of the Pelsonian/Illyrian boundary is as suggested by Brack et al. (2005) and Vörös et al. (2003). The Fassanian/Longobardian boundary is drawn at the base of the Archelaus Zone. Both boundaries are shown with dashed lines to emphasize that their position is still a matter of debate. Intervals without ammonoids are shown in gray. The long-debated *cimeganus*-level (Gaetani 1969; Monnet et al. 2008), emphasized with oblique gray bars, is here separated from the Balatonicus Zone. Ammonoid zones from Trinodosus to Regoledanus, are as interpreted by Brack et al. (2005). Tuff layers (gray lines) are labeled following Brack & Rieber (1993) and Brack et al. (2005). The reference standard for North America is based on the studies of Bucher and co-authors in Nevada (Bucher 1988, 1989, 1992a, 1992b and Monnet & Bucher 2005). The relative thickness of the zones, when available, is taken from Silberling & Nichols 1982; Bucher op. cit; Monnet & Bucher op cit. Since no thickness information is available for the Tardus to Caurus Zones, and for Subasperum Zone, their thickness is not to scale. A discussion of correlation between the two scales would be too complex and is beyond the scope of this paper. In order to help the reader, two main correlations are emphasized: Balatonicus-Shoshonensis and Curioni-Subasperum.
Cymbospondylus occurrences are grouped according to area and chronologic succession. Numbering is the same as in the text. References for specimens: (a) Rieppel & Dalla Vecchia (2001); (b) Sander (1989); (c) Kuhn-Schnyder (1980); (d) Sander (1997); (e) Huene (1916); (f) Massare & Callaway (1994); (g) Fröbisch et al. (2006); (h) Leidy (1868); (i) Merriam (1908); (j) Sander (1992).


Tethyan realm
North America and Arctic
Stages
Substages
Ammonoid zones
LADINIAN
ANISIAN
Longobardian
Fassanian
Illyrian
Pelsonian
Regoledanus
Archelaus
Gredleri
Curionii
GSSP
Secedensis
Reitzi
Trinodosus
unnamed zones (work in progress)
Balatonicus
tuff layers
Te
Td
Ta
CG
100 m
90
80
70
60
50
40
30
20
10
0
1. Cymbospondylus sp. from Pian delle Streghe (a)
2. Cymbospondylus sp. from Brembana Valley, this work
3. Cymbospondylus buchseri from Tre Fontane (b)
4. Cymbospondylus from Seceda (c)
5. Cymbospondylus sp. from Clap di Val (a)
6. Cymbospondylus parvus from Laufenburg (d)
7. Cymbospondylus parvus from Diedshem (d)
8. Cymbospondylus parvus from Gröttingen (d)
9. Phantomosaurus neubigii from Karlstadt/Main (d)
10a. Cymbospondylus sp. ind. from Allersdorf (e)
10b. Cymbospondylus sp. ind. from Bindlach (e)
Southern Alps
Germanic Basin
Substages
Ammonoid zones
Low. Lad.
Upper Anisian
Middle Anisian
Low. An.
Sm. Spath.
Subasperum
Occidentalis
Meeki
Rotelliformis
Mimetus
Weitschati
Shoshonensis
Taylori
Hyatti
Caurus
Muelleri
Guexi
Welteri
Haugi
Subcolumbites
Columbites
Tardus
170 m
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
11. Cymbospondylus sp. from Nounan Valley (f)
12. Cymbospondylus nicholsi from Augusta Mountains (g)
13. Cymbospondylus piscosus from New Pass (h)
13. Cymbospondylus nevadanus from New Pass (i)
14. Cymbospondylus petrinus from Humboldt Range (h, i)
15. Cymbospondylus sp. from Botneheia and Wiche Bukta (j)
Idaho
Nevada
Spits_ bergen
precise stratigraphic position
stratigraphic position uncertain due to difficult correlation to the standard scale
stratigraphic position uncertain due to lack of information
interval with no ammonoid record

documented in both the Southern Alps and Germanic Basin (see Brack et al. 1999 for discussion) would suggest a possible correlation with the Gredleri Zone. Another approach for a very tentative (and weak) correlation would be to consider the position of the Semipartitus Zone with respect to the Anisian/Ladinian boundary. This boundary is not older than the Spinosus Zone, and since *Nevadites* is recorded in the Thonhorizon ß1 (Brack et al. 1999), the Semipartitus Zone would then be the 6th zone of the Ladinian in the Germanic Basin. Such a position would more likely belong to the Longobardian (= Upper Ladinian) than to the Fassanian.

Since no detailed information is available for the stratigraphic position of the isolated vertebral centrum (10a in Fig. 5), this occurrence then can only be referred to the interval between the upper Trinodosus and the Gredleri zones, as shown by Brack et al. (1999).

Western United States

The Middle Triassic successions of Nevada, and in particular the Prida and Favret formations, are well known for their rich fossil record of invertebrates (ammonoids and pelagic bivalves) as well as vertebrates, consisting of different marine reptiles. *Cymbospondylus* from Nevada are among the best known specimens in the world, and indeed, it was this material that was studied by Leidy, who subsequently proposed the name of the genus in 1868. Unfortunately, the material Leidy utilized to describe the species *C. piscosus*, *C. petrinus* and *Chonespondylus grandis*, two of which were later synonymized with *C. petrinus* (see Merriam 1908), actually consisted only of vertebral centra. Much of the knowledge concerning *Cymbospondylus* should be credited to J.C. Merriam, who carried out extensive field work in Nevada and collected several relatively articulated, large-sized specimens that he subsequently described in an outstanding monograph (Merriam 1908). During the last two decades a few additional discoveries of *Cymbospondylus* have been reported from Idaho (Massare and Callaway 1994) and Nevada (Fröbisch et al. 2006).

Despite the availability of high resolution ammonoid biochronology and bio-chronostratigraphy especially for Anisian successions (Silberling & Nichols 1982; Bucher 1988, 1989, 1992a, 1992b; Monnet & Bucher 2005), but also for the Olenekian (Guex et al. 2010), the dating of *Cymbospondylus* occurrences in the literature often is not very accurate because of limited information regarding collection sites and invertebrate fossils accompanying the vertebrate remains. An additional hindrance is the lack of lithologic marker levels within the rather thick and relatively homogeneous Prida and Favret formations. Discoveries from the Western U.S. are listed as follows (numbering as in Fig. 5):

11) Nounan Valley, west of the Bear River and Stauffer Creek crossing, west of Georgetown, Idaho. Massare & Callaway (1994) reported five vertebrae and one unidentifiable bone, which they attributed to *Cymbospondylus*. These specimens were collected as surface float from the Thaynes Formation, most likely from below the Platy siltstone Member (Massare & Callaway 1994). Their exact chronostratigraphic position is uncertain, but it is most likely located between the Gracilitatis Zone and the *Columbites* beds, based on the scheme of Silberling & Tozer (1968) or Tardus and Columbites Zones, based on that of Guex et al. (2010). In each case, the chronostratigraphic position cannot be more accurately defined than simply upper Smithian to lower Spathian, or Olenekian.

12) Augusta Mountains, Pershing County, Nevada. Fröbisch et al. (2006) recently described the species *Cymbospondylus nichollsi* based on the anterior half of an articulated skeleton (including the skull) from the Fossil Hill Member of the Favret Formation. In the Augusta Mountains the Fossil Hill Member is exposed in several canyons and is almost always rich in ammonoids. Monnet & Bucher (2005) documented the biochronostratigraphy of several different stratigraphic sections, but since precise locality information for *C. nichollsi* is not documented, we simply refer this species to the relatively long interval spanning the Hyatti to Occidentalis Zones, (Middle to Upper Anisian), which amounts to the entire age of the Fossil Hill Member (Nichols & Silberling 1978; Bucher 1992a; Monnet & Bucher 2005).

13) New Pass, New Pass Range (central Nevada). This site provided Leidy (1868) with the best vertebral centra material (one complete dorsal vertebral centra and parts of four others, cf. Merriam 1908: 123), with which he utilized to describe *Cymbospondylus piscosus*, the type species of the genus. Additional material included worn or distorted vertebral centra from Star Canyon (Humboldt Range) and the Toyabe Range (NE of Austin, Leidy 1868: 178). Merriam (1908) conducted further research at New Pass with the intention of finding additional specimens to improve the description of *C. piscosus*, but this work lead him to a different conclusion. He found on a same bed surface a few anterior caudal vertebral centra, fragments of ribs and elements of the posterior limbs that exhibited features sufficiently different from *C. piscosus* such that they justified, according to him, the description of the new species *C. nevadanus*. In actuality, Merriam's new species was based on specimens that were not that much more complete than the type series of *C. piscosus*, and consequently, the significance of both taxa is under re-examination (see McGowan & Motani 2003 for discussion). As regards the stratigraphic position of the specimens from the New Pass area, the description of the lithology

provided by Merriam (1908: 19) allows us to refer them to the Fossil Hill Member of the Favret Formation. At New Pass, this unit is exposed in a few relatively small outcrops, but its ammonoid content has never been investigated in detail. Bucher (1988, 1992b) reported the occurrence of the Hyatti to Shoshonensis Zones, and Nichols & Silberling (1978) reported the occurrence of ammonoid and bivalve faunas representative of the entire Upper Anisian.

14) Eastern side of the Humboldt Range (west-central Nevada). A few vertebral centra from an unknown site in the range and from Star Canyon provided supplemental material for Leidy's (1868) description of *Cymbospondylus petrinus* and *Chonespondylus grandis* (later synonymized with *C. petrinus*). Extensive field work by Merriam (1908) in several localities (Cottonwood, Buena Vista, Straight, Indian, American and Fisher Canyons) resulted in the collection of excellent material consisting of a few well-articulated and rather large sized specimens from the unit presently known as the Fossil Hill Member of the Prida Formation. A number of beautiful specimens were attributed to *C. petrinus* Leidy, 1868 and they allowed Merriam to redescribe in great detail this species, such that it now is likely the best known species of *Cymbospondylus*. The best specimens were collected from two very close sites, Fossil Hill and Saurian Hill, in the American Canyon area, both of which have been known for their invertebrate faunas since the beginning of the 20th century (Smith 1914). In their now classic monograph, Silberling & Nichols (1982) provided for these sites very accurate and detailed ammonoid bio-chronostratigraphy, which was later enhanced and further refined by Monnet & Bucher (2005). It is possible to provide chronostratigraphic correlation for *C. petrinus* through the use of direct and indirect evidence. Leidy (1868: 177) identified the ammonoid *Ammonites blakei* and bivalve *Posidonomia stella* in the same rock slab from which the type of *C. petrinus* was collected. Although Leidy's identification of these taxa may not be totally accurate, *A. blakei* Gabb, 1864, type of *Gymnotoceras* Hyatt, 1877, is restricted to the Rotelliformis Zone. *Gymnotoceras* occurs from the Weitschati through the Mimetus and Rotelliformis Zones, but the Weitschati Zone has not been documented at Fossil Hill (Monnet & Bucher 2005). Even though the well preserved *Cymbospondylus* specimens described by Merriam cannot be directly dated, they can be referred to the Upper Anisian Mimetus to Lower Ladinian Subasperum zones by the rich ammonoid faunas described from Fossil and Saurian Hills (Silberling & Nichols 1982; Monnet & Bucher 2005), the two main sites from which they were collected.

Other occurrences

Cymbospondylus has been also reported from Spitsbergen and China. Sander (1992) described a semi-articulated string of vertebrae, vertebral centra and ribs from Botneheia as well as other vertebral centra from Wiche Bukta. These specimens (number 15 in Fig. 5) cannot be classified at the species level, and their stratigraphic position is given only as from the Upper Ladinian Upper Saurian Niveau (Weitschat pers. comm. to Sander: Sander 1992).

The species *Cymbospondylus asiaticus* described by Li & You (2002) from the Upper Triassic of Guizhou (China) may be the youngest occurrence of the genus, but Sander at al. (2011) has recently suggested that this species should be synonymized with *Guizhouichthyosaurus tangae*.

Final remarks

The stratigraphic positions of specimens belonging to the *Cymbospondylus*-type group (Fig. 5) are much better defined in the Southern Alps and Germanic basin than in the western United States. This lack of knowledge is simply due to the limited availability of information regarding the original stratigraphic position from which specimens were collected. A consequence of these uncertain stratigraphic positions is that it is impossible to attribute the specimens to a specific facies. Silberling & Nichols (1982) and Bucher (1992a) outlined different facies within the Prida and Favret formations, but the lack of precise positioning of the ichthyosaur specimens within these units hampers their attribution to the original facies. On the other hand, it is worth mentioning that a detailed description of facies for the ichthyosaur-bearing successions of Nevada and Idaho is not available, whereas the facies of the Middle Triassic successions from the Southern Alps and Germanic Basin have been described and interpreted in several papers published during the last two decades. This is also true for paleogeography at the scale of the sedimentary basin.

In this section we discuss several issues related to *Cymbospondylus*-type ichthyosaurs, taking into account chronostratigraphic correlation, facies and paleogeography. For the aforementioned problems we focus only on the southern alpine and germanic occurrences. The relatively low number of available specimens (five or six ichthyosaurs from the Southern Alps and six from the Germanic Basin) does not provide solid ground for complex analyses and interpretation, especially since most of the original specimens are known only from very few or just a single vertebral centra.

Controls on the distribution of *Cymbospondylus*

The stratigraphic distribution of *Cymbospondylus* in the Southern Alps and Germanic Basin is directly controlled by the development of sedimentary basins, which are influenced by relative sea level changes and tectonics.

The oldest record in the Southern Alps is from the eastern part (Cadore), where a basinal depositional setting (Dont Formation) was already established in the Pelsonian, while more shallow, and protected environments prevailed in the western Southern Alps (e.g., Angolo Limestone). Middle to late Illyrian discoveries at Piazza Brembana and Tre Fontane (western Southern Alps) are consistent with the Illyrian transgression documented by the westward migration of the basinal facies. Such a transgression, most likely driven by a sea level rise (e.g., Gianolla & Jacquin 1998), also affected the western Dolomites (e.g., Seceda area), where Late Anisian to Early Ladinian basinal sediments of the Buchenstein Formation conformably overlie the Late Anisian carbonate platform of the Contrin Formation.

The stratigraphic distribution of *Cymbospondylus* in the Germanic Basin is slightly different with respect to the Southern Alps, as there is no record of this genus in the early to middle Illyrian. Such a record is perfectly consistent with the well-known sedimentary evolution of the Germanic Basin, which is different with respect to the Southern Alps. Marine transgressions in the Germanic epicontinental Basin were controlled not only by the relative sea level rise, but also by the tectonic evolution of the depressions (gates) connecting the Germanic Basin to the western Tethys (Ziegler 1990; Szulc 2000). During the early to middle Illyrian these connections (Silesian-Moravian and East-Carpathian gates) were temporarily closed and marine sedimentation of the Lower Muschelkalk was replaced by the dolomitic-evaporitic conditions of the Middle Muschelkalk. In the late Illyrian the Burgundy gate opening to the West led to the reestablishment of marine sedimentation in the basin with the transgression of the Upper Muschelkalk.

The occurrence of *Cymbospondylus* in North America was apparently influenced in a similar manner. Relatively deep marine environments were already developed during the Olenekian, as documented by the ammonoid bearing facies, and this may explain the *Cymbospondylus*-like record of ichthyosaurs in Idaho.

Taxonomy, evolutionary trends and paleobiogeography

Cymbospondylus parvus Huene, 1916 is recognized from the Pelsonian of the Germanic Basin and *C. buchseri* Sander, 1989 from the late Illyrian of the Southern Alps. *Phantomosaurus neubigii* (Sander, 1997) is of middle late Illyrian age, i.e., slightly older or coeval with *C. buchseri*. So far, the three species from the Southern Alps and Germanic Basin have a well defined and rather short stratigraphic range, but taken together, they occupy a relatively long interval, i.e., from late Middle Anisian to earliest Ladinian. However, given the present state of knowledge, the incomplete preservation of these specimens does not allow the identification of possible evolutionary trend(s) within this relatively long distribution. Vertebral centra are much more common than relatively articulated specimens, but they cannot be classified at the species level and they do not provide sufficient information for the identification of trends in the evolution of this group of ichthyosaurs.

As for the Nevada species, based on the available stratigraphic data, the relative chronologic position of *C. nevadanus*, *C. piscosus* and *C. nichollsi* is unknown. *C. petrinus,* of Late Anisian to earliest Ladinian age, could be coeval or slightly younger than the previous three species.

Comparison of Ichthyosaur faunas from the Southern Alps and Germanic Basin would be of great interest since it is a well known fact that the Germanic Basin was characterized by the development of endemic forms, which were dominant over Tethyan immigrants during the Middle Triassic. Stimulating papers on this topic have been recently published on brachiopods, crinoids (Hagdorn 1985), ammonoids (Urlichs & Mundlos 1985; Brack et al. 1999; Klug et al. 2005) and conodonts (Narkiewicz & Szulc 2004). However, since ichthyosaur discoveries are rather scarce, such a comparison would be more speculation than a true analysis. At the genus level, *Phantomosaurus* is known only from the Germanic Basin, while *Cymbospondylus* is common to both areas. *Phantomosaurus* data, however, is not abundant as this genus is known only from a single specimen.

Paleoecology

The morphology of *Cymbospondylus*-like ichthyosaurs suggests a mode of life similar to other Triassic ichthyosaurs, which most likely were coastal surface predators according to Massare & Callaway (1990). These authors suggest that the evolutionary trend, which gradually shifted ichthyosaurs from the elongate, crocodile-like Triassic forms to the deep-bodied, dolphin/tuna-like Jurassic forms, corresponded to an ecological shift from slower swimming, ambush predators in shallow waters to fast swimmers and pursuit predators in more open waters. Fröbisch et al. (2006), in an effort to explain the scarcity of specimens in shallow water deposits, agreed that *Cymbospondylus* may have been an ambush predator, but hypothesized that it lived mainly in open water and rarely ventured close to the coast. However, anatomical evidence such as its rather elongate neck (Motani 2005) and long tail with a low caudal fluke, which was not forked with a high dorsal

lobe as in the Jurassic species (Massare 1988), suggests that Triassic ichthyosaurs were mostly undulatory swimmers and more manueverable but slower than their Jurassic descendants with their forked tails and short caudal peduncle, both of which support fast oscillatory swimming. Ambush predation and especially undulatory swimming, are more consistent with life in shallow water. Thus, it seems more feasible that Triassic ichthyosaurs lived in the parts of the basin close to the coast, whereas Jurassic ichthyosaurs may have thrived in more open and deeper waters. As already noted by Massare & Callaway (1990) the evolution of ichthyosaur morphology may superficially parallel that of toothed whales, where the more primitive forms, e.g., basilosaurs, were elongate-bodied coastal dwellers, while later forms were compact-bodied and faster swimmers living in the pelagic areas.

The paleoenvironmental distribution of the few *Cymbospondylus* from Europe is rather consistent with such a mode of life. Notwithstanding the strong limitation due to the scarce number of specimens and the effect of possible post-mortem drifting on their distribution, a few considerations can be presented:

– specimens from Europe are all from marine facies with nectonic/nectobenthonic faunas, namely ammonoids and cephalopods in general, but often with benthic organisms. Specimens from Nevada exhibit the same type of facies relations.

– So far *Cymbospondylus* is known from different marine facies ranging from rather restricted environments (e.g., Besano Formation, Tre Fontane) to low oxyc/disoxyc facies (e.g., Prezzo Limestone, Piazza Brembana) to more open environments (e.g., Dont Formation). Only one occurrence (Clap di Val) is from "Ammonitico Rosso"-like pelagic facies.

– It is worth noting that most of the occurrences are not from the deepest part of the basins or from parts closer to open marine/oceanic connections. This is especially true for occurrences from the Lower Muschelkalk and the Prezzo Limestone. Discoveries from the Lower Muschelkalk are all from southwest Germany-northern Switzerland (Hessian depression-Eifel South, s.l.), very far from the Silesian-Moravian and East-Carpathian gates. This part of the Lower Muschelkalk basin, according to the most accepted reconstructions, was a type of "dead end". The Prezzo Limestone occurrence at Piazza Brembana is also similar, since this section was located in a relatively shallower part of the basin with respect to the depocenter located in Camonica Valley-Giudicarie. Such occurrences may even be related to post-mortem drifting of carcasses, but nevertheless, they are consistent with the mode of life as suggested by their functional anatomy.

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