

Rupert WILD *

**AËTOSAURUS (REPTILIA: THECODONTIA) FROM THE UPPER TRIASSIC
(NORIAN) OF CENE NEAR BERGAMO, ITALY,
WITH A REVISION OF THE GENUS**

Dedicated to Prof. Dr. E. KUHN-SCHNYDER on his 85th birthday

RIASSUNTO: Si descrive un frammento cervicale di corazza dorsale di *Aëtosaurus ferratus* O. Fraas dalla formazione del Calcare di Zorzino di Cene presso Bergamo, Italia. Il confronto con gli altri aetosauri richiede una revisione del genere *Aëtosaurus*. *Aëtosaurus ferratus* e *Aëtosaurus crassicauda* E. Fraas sono specie distinte. Non esistono strette affinità tra *Aëtosaurus* e *Stagonolepis* e questo ultimo differisce anche stratigraficamente. L'età Norico media dell'*Aëtosaurus ferratus*, sostenuta con considerazioni biocronologiche, dimostra la stessa età anche nel caso dello Stubensandstein inferiore della Germania sudoccidentale. Questo fatto definisce le correlazioni stratigrafiche delle unità triassiche continentali a tetrapodi su basi più esatte.

SUMMARY: A fragment of the cervical armour of *Aëtosaurus ferratus* O. Fraas is described from the Calcare di Zorzino Formation of Cene near Bergamo, Italy. Comparison with other aetosaurs requires a revision of the genus *Aëtosaurus*. *Aëtosaurus ferratus* and *Aëtosaurus crassicauda* E. Fraas are distinct species. There are no relationships between *Aëtosaurus* and *Stagonolepis*, which also differ stratigraphically. The biochronologically supported Middle Norian age of *Aëtosaurus ferratus* indicates to the same age for the Lower Stubensandstein in Southwest Germany. This places stratigraphical correlations of tetrapod bearing terrestrial Upper Triassic units on a more exact basis.

ZUSAMMENFASSUNG: Aus der Calcare di Zorzino-Formation von Cene bei Bergamo, Italien, wird ein Dorsalpanzer-Fragment aus dem Halsbereich von *Aëtosaurus ferratus* O. Fraas beschrieben. Um einen Vergleich mit anderen Aetosauriern durchführen zu können, war es erforderlich, die Gattung *Aëtosaurus* zu revidieren. Hierbei zeigte es sich, dass *Aëtosaurus ferratus* und *Aëtosaurus crassicauda* E. Fraas eigenständige Arten sind. Zwischen *Aëtosaurus* und

* Curator of Vertebrate Paleontology of Staatliches Museum für Naturkunde in Stuttgart.

Stagonolepis, die sich auch stratigraphisch unterscheiden, bestehen keine sehr engen Verwandtschaftsbeziehungen. Das biochronologisch abgesicherte mittelnorische Alter von *Aëtosaurus ferratus* lässt sich auf den Unteren Stubensandstein Südwestdeutschlands übertragen. Dadurch können Tetrapoden-führende terrestrische Obertrias-Einheiten miteinander stratigraphisch genauer korreliert werden.

PAROLE CHIAVE: Triassico Superiore; Norico medio; Aëtosauria; Correlazione stratigrafica; Bergamo, Italia.

KEY WORDS: Upper Triassic; Middle Norian; Aëtosauria; Stratigraphical correlation; Bergamo, Italy.

SCHLUSSELWORTER: Obertrias; Mittelnor; Aëtosauria; stratigraphische Korrelation; Bergamo, Italien.

INTRODUCTION

The rich Upper Triassic vertebrate fauna of Cene near Bergamo and adjacent localities is composed of fishes and reptiles (Tintori, Muscio & Nardon 1985; Pinna 1987). Skeletons and skeletal parts of reptiles are of special interest since they represent partly marine faunal elements, which are autochthonous, and partly allochthonous terrestrial forms. In addition to a single specimen of the marine eosuchian *Endennasaurus* (Renesto 1984), marine placodonts (Pinna 1979, 1987), the probable marine *Macrocnemus*, and pterosaurs with a partly marine way of life (Wild 1978) several terrestrial reptiles are found at the Bergamo localities. These include the ?burrowing ?lepidosaur *Drepanosaurus* (Pinna 1980, 1984, 1986), a phytosaur skull cf. *Mystriosuchus planirostris* Meyer (Pinna 1987), *Vallesaurus* an arboreal eolacertilian (Wild, in preparation), and some indefinable fragments of other reptiles. An additional find of a terrestrial reptile, a fragment of the dermal armour of *Aëtosaurus* is described herewith. It was collected by the preparator of the Museo Civico di Scienze Naturali Bergamo (MCSNB), Mr. M. Pandolfi, in 1974 at the mountain slope of Cene. It is housed under N° 4864 in the museum of Bergamo.

DESCRIPTION OF *AËTOSAURUS FERRATUS* O. FRAAS, MCSNB 4864

A small slab of black laminated limestone with a maximum length of about 6,5 cm contains fragmentary dorsal armour of *Aëtosaurus*. There are two complete and two fragmentary elements from the left paramedian row of plates. The right paramedian row is represented by the medial fragments of the corresponding four elements. Both rows are in almost natural connection with three

partly fragmentary lateral plates from the left side (Figs. 1-2). The plates are crushed. The only completely preserved plates are the wide rectangular paramedian ones. They have a slightly concave

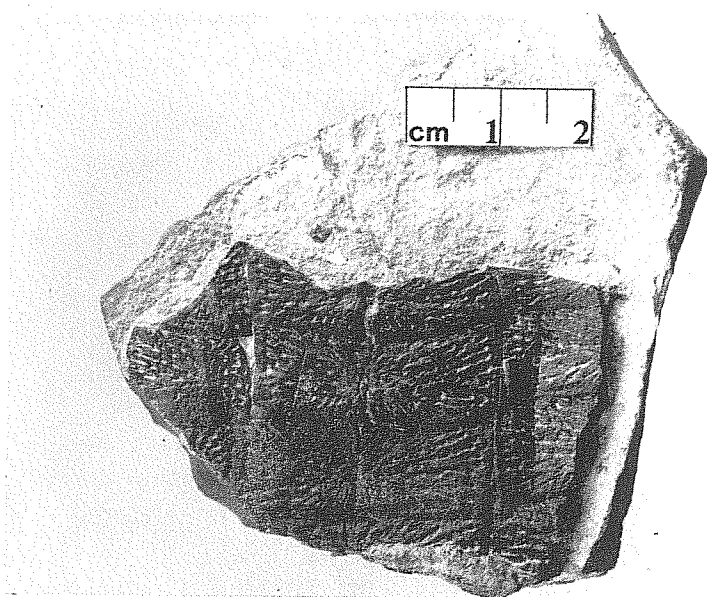


Fig. 1 - *Aëtosaurus ferratus* O. Fraas; fragment of the cervical dorsal armour; Middle Norian, Cene near Bergamo, Italy; MCSNB 4864.

anterior margin and a slightly convex posterior one. The posterior end of each paramedian plate overlaps the anterior margin of the posterior plate. Each plate bears a narrow gliding fold anteriorly, which is overlapped by the posterior plate (so-called "Gleitfalz" of Huene 1920). The lateral and medial margins of each paramedian plate lie at right angles to the anterior and posterior margins. The paramedian plates are sculptured dorsally by elongated grooves radiating from a faintly pitted area, the center of ossification. The plates bear neither a longitudinal crest nor knob-like enlargement as can be seen in *Aëtosaurus crassicauda* E. Fraas (Fig. 4b).

From the left lateral row of armour plates only one element is almost completely preserved. It also possesses the radial pattern of elongated grooves. They extend from a slightly raised crest,

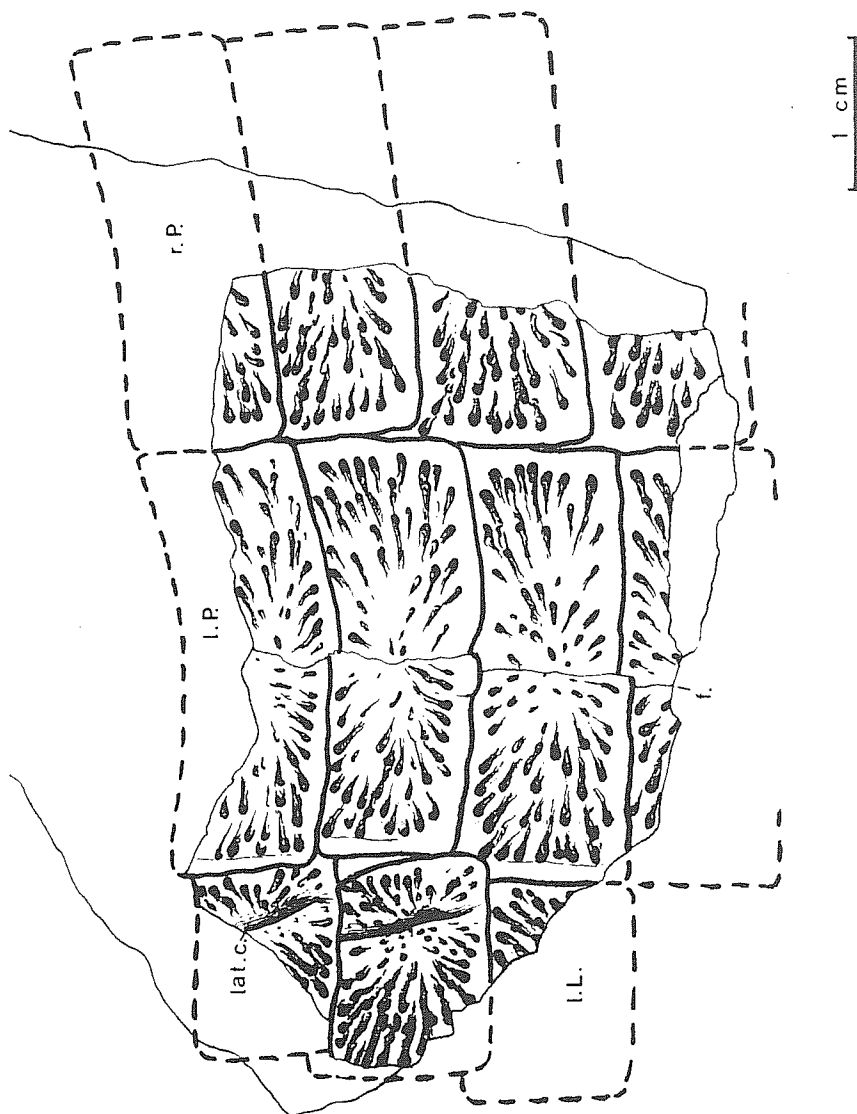


Fig. 2 - *Aëtosaurus ferratus* O. Fraas; drawing of the fragment of the cervical dorsal armour; Middle Norian, Cene near Bergamo, Italy; MCSNB 4864.

Abbreviations: f. = fracture; l. L. = Left lateral plate; l. P. = left paramedian plate; lat. c. = lateral crest; r. p. = right paramedian plate; dashed line: reconstructed outline.

which is shifted from the middle of the plate more closely to the paramedian plates. This crest runs from anterolateral to posteromedial. The width of the lateral plates is almost 1,4 times their length. The crest of the fragmentary anterior plate is more prominent than that of the posterior one. It reaches its greatest height in the posterior half of the plate.

Compared with *A. ferratus* SMNS 5770, the fragment of the dermal armour can be attributed to the body region just behind the shoulder girdle. It corresponds to about the 6th to 7th row of plates. In this region the paramedian plates increase in width posteriorly as can also be seen in SMNS 18554 (Fig. 3) and in N° XVI SMNS 5770 (O. Fraas 1877) of the *A. ferratus* group. Both these specimens are similar in size to MCSNB 4864. The crest of the lateral plates in the latter specimen diminishes posteriorly from plate row to plate row. The width/length ratio of the completely preserved anterior paramedian plate is 2,6, and that of the next anterior plate is 2,8. The corresponding ratio of the only preserved left lateral plate is 1,4. The size of the armour plates and their ratios allow an assignment to the 6th or 7th row of plates of *A. ferratus* of the above mentioned specimens in SMNS. From these plates a total body length of about 80-90 cm can be estimated for MCSNB 4864. It therefore represents an adult specimen of *A. ferratus* (p.7).

SYSTEMATIC PALEONTOLOGY

Class Reptilia Laurenti, 1768

Subclass Archosauria Cope, 1869

Order Thecodontia Owen, 1859

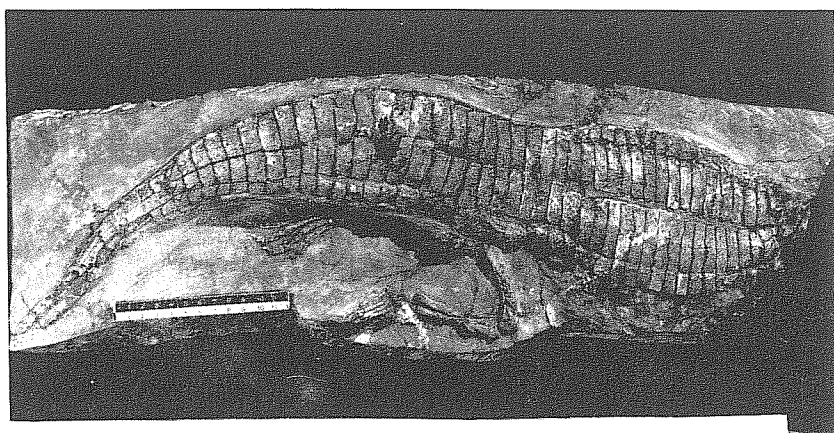
Suborder Aetosauria Lull, 1915 *

Family Aetosauridae

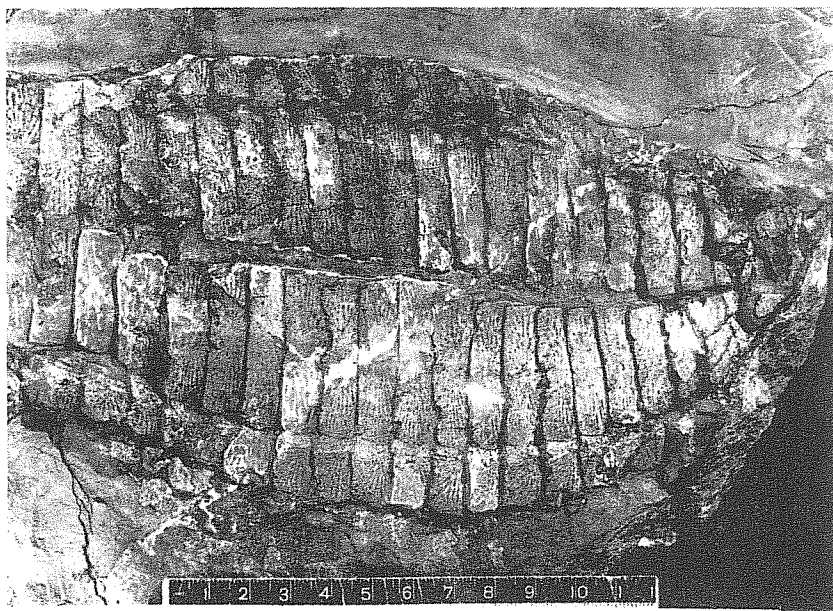
Family Aetosauridae Baur, 1887 (see Walker 1961: 182)

Synonym: Stagonolepidae Huene. - Huene, 1908: 395.
 non Proterosuchidae. - Schmidt, 1928: 419.
 Stagonolepidiidae. - Bonaparte, 1971: 88.
 Stagonolepidiidae. - Bonaparte, 1978: 302.
 Stagonolepidae. - Gregory, 1953: 8.
 non Stagonolepididae Lydekker, 1877. - Small, 1989: 302.

* The term Aetosauria was first erected by Huene (1908), however, without designing the range of this taxon. Therefore the authorship for naming the suborder Aetosauria is due to Lull (1915).



a



b

Fig. 3 - *Aëtosaurus ferratus* O. Fraas; incomplete skeleton; Lower Stubensandstein from near the ruins of castle Blankenhorn, Stromberg Mountains, Württemberg, West Germany; SMNS 18554: (a) as preserved, (b) detail for comparison to MCSNB 4864.

Genus *Aëtosaurus* O. Fraas, 1877

Type species: *Aëtosaurus ferratus* O. Fraas, 1877

Diagnosis: See Huene 1921 and Walker 1961. Armour: Body completely surrounded by bony dermal plates fitting to movable rings; each ring of plates correspond to a vertebra; plates ornamented by grooves and sometimes faint ridges radiating from a medial center of ossification, from a keel or crest, the latter sometimes knobbed; dorsal armour consisting of a pair of rectangular paramedian plates and on both sides by a row of more or less quadrangular lateral plates; up to 12 longitudinal rows of ventral plates; tip of the tail with sheath consisting of fused plates; limbs covered by small rounded plates.

Discussion: It has been suggested (Walker 1961; Krebs 1976) that *A. crassicauda* does not represent a distinct species, although it differs from *A. ferratus* in having broader anterior caudal and dorsal plates, in the angulation of the lateral dorsal plates and in the greater size of the complete skeleton (E. Fraas 1907). Walker (1961) accepted only body size as a valid criterion to distinguish the two species, however, with reservation. The following features shall emphasize the distinctness of the two species.

The maximal total length of *A. ferratus* in SMNS 5770, the famous group of 22 specimens in SMNS (Walker 1961), is about 80-90 cm in Nos. VII, X, XIII, XIX and XXIII (numbering of O. Fraas 1877). This length can be calculated by the skull length in Nos. II, V, VIII and XVI or by the skeletons without skulls Nos. VI, XII, XV and XXII. All these specimens are doubtless adult (Walker 1961). The specimens Nos. I, III, IV, XIV and XVII may represent subadults with a total body length of about 60-70 cm. Finally the specimens Nos. IX, XX, XXI and XXIV are considered to be juveniles with an estimated total length of about 40-50 cm. Adults and subadults include about 82% of all specimens, while the juveniles represent about 18%. No specimen of SMNS 5770 exceeds a total body length of about 90 cm. This includes also SMNS 5771, an isolated fragment of a skeleton, consisting of the sacrum to middle caudal region. This specimen was found near SMNS 5770. SMNS 18554, an incomplete skeleton of *A. ferratus* without shoulder girdle and skull from near the ruins of castle Blankenhorn in the Stromberg Mountains, Württemberg, Southwest Germany (Fig. 3-4a), is 68 cm in length from the tip of the tail to the posterior margin of the shoulder girdle as preserved. This specimen points to a total length of about 85 cm, corresponding to N. XVI of SMNS 5770. All this material of *A. ferratus* points to a maximum size of the adults of about 90 cm. In contrast to *A. ferratus* all specimens of *A. crassicauda* are much larger. SMNS 11837, the holotype of E. Fraas (1907) (Fig. 4b), is estimated to have a total length of about 150 cm. The skeletal remains of SMNS 12670 described by Huene (see also Walker 1961) reveal the same body length. A third specimen of *A. crassicauda*, SMNS 14882, consists of a skeleton

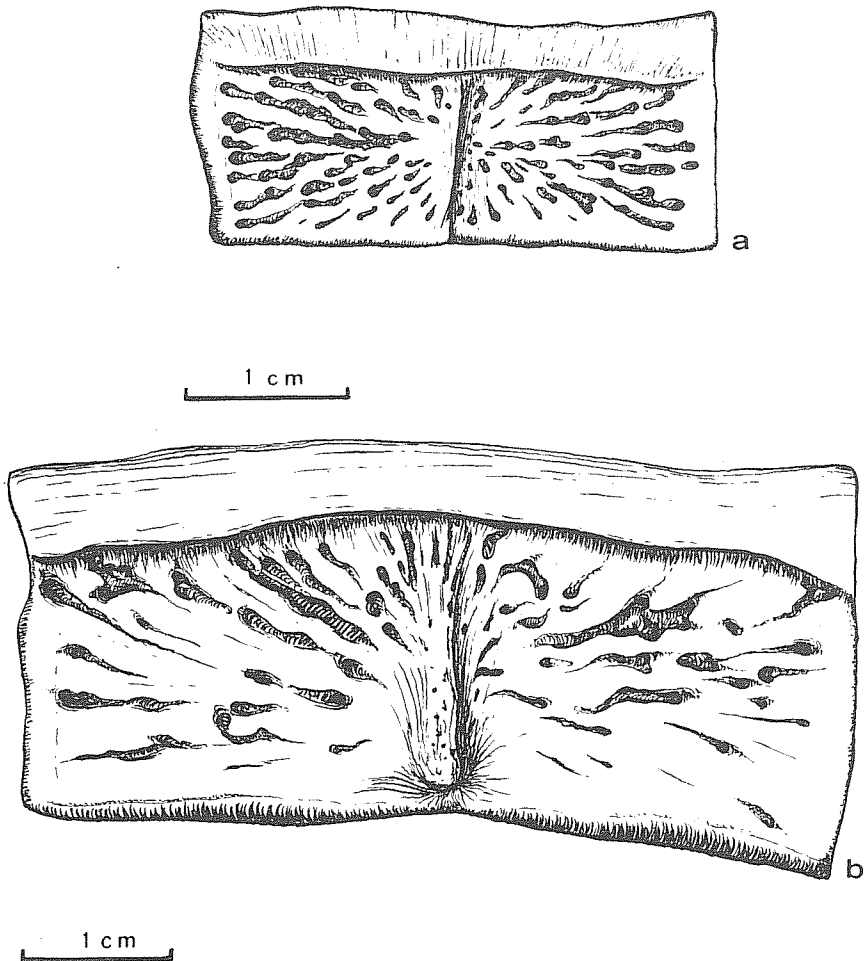


Fig. 4 - *Aëtosaurus ferratus* O. Fraas, SMNS 18554 (a) and *Aëtosaurus crassicauda* E. Fraas, SMNS 11837 (b) from the Middle Stubensandstein of the community's quarry of Pfaffenhofen, Stromberg Mountains; ca. 23rd left paramedian plate with reconstructed articulating surface, according to corresponding plates exposed anteriorly.

from posterior to the sacrum through the middle caudal region of an individual of approximately the same size. All these specimens are considered to be adults by the grade of ossification. All come from the community's quarry of Pfaffenhofen in the Stromberg

Mountains. Its stratigraphical age is Middle Stubensandstein, nor Upper Stubensandstein as E. Fraas (1907) stated. All specimens of *A. ferratus* are from the Lower Stubensandstein, none from the stratigraphical unit of *A. crassicauda* as asserted by E. Fraas. There is not only the size difference, which separates the two species but also a stratigraphical distinction.

Both species differ also in the width/length ratio of the paramedian plates of the anterior caudal region. Regarding the ca. 27th to 29th plate row in *A. crassicauda* (SMNS 11837) this ratio is 3,2 to 3,3. In the largest specimens of *A. ferratus* (SMNS 5770 Nos. XVI and VI) this ratio is 2,6 to 2,8, respectively. In *A. ferratus* (SMNS 18554) and in the juvenile specimen n. XXIV it is only 1,6. It could be argued that this ratio increases from juvenile specimens to adult specimens of *A. ferratus* and finally to the large species *A. crassicauda*, which therefore is not a distinct species but a very old specimen of *A. ferratus*. However, the ornamentation of the dermal plates, that is customarily used to distinguish aetosaur taxa (Gregory 1953, 1962; Long & Ballew 1985; Long & Padian 1986) differs strikingly between the two *Aëtosaurus* species.

In *A. ferratus* the paramedian plates of the anterior caudal region are ornamented by oblong grooves, which are incised in the smooth surface of the bony plate. They radiate from a median center of ossification and are lying close together. In the adult specimens (SMNS 5770 N. XVI and in SMNS 18554) these plates possess an additional longitudinal medial keel (Fig. 4a). *A. crassicauda* has strongly arched paramedian plates in the anterior causal region. There are only a few slightly incised pits radiating from a medial crest (Fig. 4b). The latter is enlarged posteriorly to a knob. These differences alone justify the specific separation of the two species. The modification of the ornamentation from *A. ferratus* to a *A. crassicauda* in the development of crests and knobs reflects the trend within aetosaur phylogeny of developing the knobbed or spiny armour (*Aetosauroides* - *Aëtosaurus* - *Stagonolepis* *Neoaëtosauroides* - *Paratypothorax* - *Typothorax* - *Calyptosuchus* - *Desmotosuchus*; Bonaparte 1971, 1978, 1982; Walker 1961; Long & Ballew 1985).

Aëtosaurus ferratus O. Fraas, 1877

Figs. 1-4

- 1877 *Aetosaurus ferratus* O. Fraas. - O. Fraas, p. 1-22, Tab. 1-3, 2 Figs.
- 1896 *Aëtosaurus ferratus* Fraas. - E. Fraas, p. 17, Tab. 4.
- 1908 *Aëtosaurus ferratus* Fr. - Huene, p. 392-393, p. 399, Figs. 346-350.
- 1914 *Aëtosaurus ferratus* O. Fraas. - Huene, p. 18-19, Figs. 43, 44.
- 1915 *Aëtosaurus ferratus* Fraas. - Lull, p. 101, Fig. 9.
- 1920 *Aëtosaurus ferratus* O. Fraas. - Huene, p. 161, Fig. 1

- 1920 *Aëtosaurus ferratus* O. Fraas. - Huene, p. 465-491, Figs. 150.
 1928 *Aëtosaurus ferratus* O. Fraas. - Schmidt, p. 419, Figs. 1175 a-f.
 1938 *Aëtosaurus ferratus* Fraas. - Berckhemer, p. 191, Fig. 48.
 1955 *Aëtosaurus ferratus* O. Fraas. - Hoffstetter, p. 672-679, Fig. 5.
 1956 *Aëtosaurus ferratus* O. Fraas. - Huene, p. 450, Fig. 484 a,b.
 1956 *Aetosaurus*. - Romer p. 131, Fig. 69E.
 1961 *Aëtosaurus ferratus* O. Fraas. - Walker, p. 164-172, Tab. 12, Figs. 40, 41; Tab. 13, Figs. 42-45.

Holotype: Completely preserved adult specimen N° XVI SMNS 5770 of O. Fraas 1877, Tab. 1, to which refers Huene (1908, 1920) and Walker (1961) [designazione hoc loco].

Stratum typicum: 3 m above the Stubensandstein in a sandy clay concretion according to O. Fraas (1877: 2; Fig.), which corresponds to the "Lower Hangendletten" or "1. Hangendletten" above the First Stubensandstein (Brenner 1973: 153; Brenner & Villinger 1981: Fig. 6); Lower Stubensandstein.

Locus typicus: Former sandstone quarry in the field-part "Billert" in Stuttgart-Kaltental, where the Elsenbach flows into the Nesenbach; today overbuilt (Topographic map 1: 25.000 Stuttgart-Südwest, R 3509800, H 5400825).

Diagnosis: As for the genus, with the following additions: Up to about 90 cm long; paramedian armour plates with radiating oblong grooves, closely placed together and ending in rounded hollows; paramedian plates in anterior caudal region of adults with median keel; lateral plates with grooves and faint ridges lying closely together and a knoblike medially situated keel, which runs posteromedially; propodials covered by small rounded plates; these of the epipodials and of the manus and pes are more rhombic.

Distribution: Lower Stubensandstein Stuttgart-Kaltental, Lower Stubensandstein from near the ruins of castle Blankenhorn in the Stromberg Mountains, Württemberg, West Germany, and Calcare di Zorzino Formation of Cene near Bergamo, Italy.

Material: SMNS 5770; SMNS 5771, a fragment of a skeleton consisting mainly of an anterior caudal part found together with SMNS 5770 and probably belonging to this group; SMNS 18554 incomplete skeleton without shoulder girdle and skull; MCSNB 4864, fragment of dorsal armour.

Description: p. 2 ff.

Aëtosaurus crassicauda E. Fraas, 1907
Fig. 4b

- 1907 *Aetosaurus crassicauda* E. Fraas. - E. Fraas, p. 101-109, Tab. 1,2.

- 1921 *Aëtosaurus crassicauda* E. Fraas. - Huene, p. 329-335, Fig. 1-7; Tab. 1, Fig. 1-8.
 1928 *Aëtosaurus crassicauda* E. Fraas. - Schmidt, p. 420, Fig. 1176.
 1938 *Aëtosaurus crassicauda* Fraas. - Berckhemer, p. 192, Tab. 52, Fig. 34, 35.
 1955 *Aëtosaurus crassicauda* Fraas. - Hoffstetter, p. 677, Fig. 7E.
 1956 *Aë. crassicaudatus*. - Huene, p. 450, Fig. 484 b [ex errore pro *Aëtosaurus crassicauda* E. Fraas].
 1961 *Aëtosaurus crassicauda* E. Fraas. - Walker, p. 172-175.

Holotype: Fragment of a skeleton consisting of the pelvis to anterior caudal region, with dorsal armour, SMNS 11837; type to E. Fraas 1907.

Stratum typicum: The specimen comes from the community's quarry of Pfaffenhofen, whose age is Middle Stubensandstein. It was found in a 1-2 m thick marl intercalated between massive layers of Stubensandstein (E. Fraas 1907: 101). According to E. Fraas the stratigraphical niveau of the marl should correspond..." approximately exact"... to that of the *A. ferratus* group, SMNS 5770 from Stuttgart Kaltental. In the legend of plate 1 of the type of *A. crassicauda* E. Fraas writes... "Upper Stubensandstein of Pfaffenhofen"... These statements of E. Fraas are incorrect. The Pfaffenhofen quarry worked the Middle Stubensandstein (Linck 1938; Brenner 1973, 1978), while *A. ferratus*, SMNS 5770 is from the Lower Stubensandstein (p.10). Based on Brenner (1973) the marl in which SMNS 11837 was found corresponds either to the "Lower Zwischenletten" or to the "Upper Zwischenschichten" of the Middle Stubensandstein. Compared with Brenner's stratigraphical section of the quarry (1978: 115 f., N° 6) it is highly probable that *A. crassicauda*, SMNS 11837 comes from the "Lower Zwischenletten". Both types, *A. ferratus* and *A. crassicauda* differ in stratigraphical occurrence and therefore also in geological age (p.7).

Locus typicus: So-called "Weisser Steinbruch" on the top of the Stromberg Mountains, ca. 2,5 km SSW of the village Pfaffenhofen (known also as the community's quarry Pfaffenhofen or quarry Burrer Pfaffenhofen). Diagnosis (modified after E. Fraas 1907 and Walker 1961): Armour plates in the sacral and anterior caudal region with tendency to enlarge and to develop median crests on paramedian plates or knobs on lateral plates, and reduction of the ornamentation by diminishing the number of grooves, their depth and ray-like orientation (Fig. 4b), compared with *A. ferratus*; width/length ratio of antero-caudal paramedian plates ca. 3,2-3,3, in *A. ferratus* 2,62,8 in adult specimens.

Description: See E. Fraas (1907), Walker (1961) and chapter discussion (p. 7 ff.).

Distribution: Only at the locus typicus.

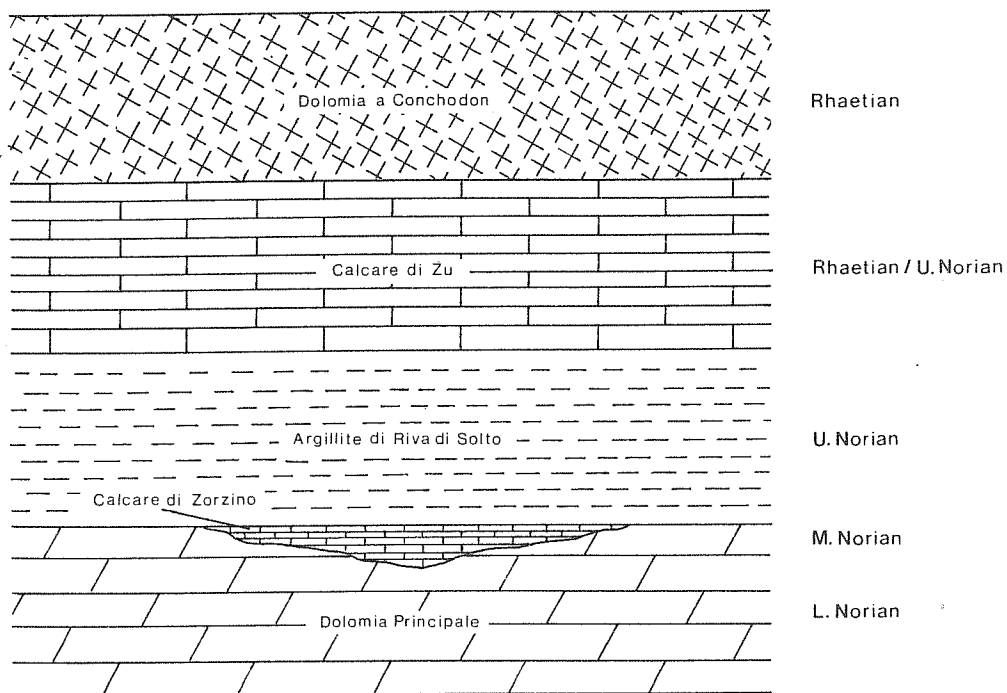


Fig. 5 - Stratigraphic scheme of the Upper Triassic of Cene near Bergamo in the Lombardian Alps, Province of Bergamo; modified from Zambelli 1986.
Abbreviations: L. = Lower, M. = Middle, U. = Upper.

Material: Holotype SMNS 11837; SMNS 12670 described by Huene (1921), see also Walker (1961); SMNS 14882, an anterior caudal fragment of a skeleton with 14 caudal vertebrae and partly disarticulated paramedian plates; specimen does not justify a detailed description, since it adds no further knowledge to *A. crassicauda*.

AGE OF MCSNB 4864

The fragment of the dermal armour of *A. ferratus*, MCSNB 4864 comes from the Calcare di Zorzino Formation, which is a heteropic calcareous-bituminous facies of the Norian Dolomia

Principale or Hauptdolomit. The Calcare di Zorzino was deposited in local shallow basins under anoxic conditions. These basins developed within or to the end of the sedimentation of the Dolomia Principale as a consequence of tectonic events in the Tethys region between the Eurasian and African plates (Tintori 1980; Jadoul 1986; Pinna 1987). Terrigenous material of the Zorzino sediments and the predominant allochthonous reptile fauna (p. 2) show that the land was not far from these basins. Since the discovery of the Bergamo fossil localities there is no doubt that the age of the Zorzino Formation near the top of the Dolomia Principale is Norian. Zambelli (1975) concluded an Upper or uppermost Norian age for the Cene locality, what was confirmed for the age of the Zorzino Formation by Casati & Gaetani (1979), Tintori (1980, 1981) and Tintori, Muscio & Nardon (1985). More recently, the age of the Zorzino Formation has been more precisely established. At Cene this formation is overlaid by the Argillite di Riva di Solto, which is again overlaid by the Calcare di Zu (Fig. 5). The latter limestones yielded *Choristoceras ammonitifforme* (Gümbel) (MCSNB 4617), *Choristoceras* sp. (MCSNB 4615) and ? *Cladiscites* sp. (MCSNB 4616) (see also Zambelli 1978) found at different localities close, northwest and east of Cene. These ammonoids point to an uppermost Norian and perhaps also lowermost Rhaetian age (Tozer 1967)* of the Calcare di Zu. From near the type locality of the Calcare di Zorzino at Solto Collina, ca. 15 km east of Cene, comes an ammonoid, however unstratified, designated as *Dionites* sp. (MCSNB 4819). It refers to an Upper Norian age (Krystyn 1973: 132). The top of the Triassic is represented by the Dolomia a Conchodon (Fig. 5), which is generally accepted to be Rhaetian. Consequently the Calcare di Zorzino has to be older than Upper Norian which is represented by the Calcare di Zu and the Argillite di Riva di Solto. The Calcare di Zorzino are now considered as Middle Norian (Zambelli 1978, 1980, 1986; Tintori & Sassi 1987), what is confirmed by ammonoid find mentioned above. The fossiliferous localities in the Dolomia di Forni Formation, comparable with that of the Calcare di Zorzino, reveals a similar but little older fauna than that of Cene or Endenna (Dalla Vecchia, Muscio Wild 1989; Zambelli in press).

* This stratigraphical age is altered to uppermost Norian if the Rhaetian stage is included into the Norian, as proposed by Tozer (1974, 1979; however, see Wiedmann 1974, Wiedmann & al. 1979, Krystyn & Wiedmann 1986). The Rhaetian is retained in the South Alps since it is a well-defined and -mapped stratigraphical unit (Tintori, Muscio, Nardon 1985; Jadoul 1986).

COMPARISON AND STRATIGRAPHICAL IMPLICATIONS

As Walker (1961) has pointed out, *Aëtosaurus* could be closely related to *Stagonolepis* from the Upper Triassic Lossiemouth Sandstone of Scotland. However, there are important differences between the two genera, which clearly separate *Stagonolepis* from both species of *Aëtosaurus*. Apart from the morphological differences of the skull, teeth, dental formula, girdles and limbs (Walker 1961: 176 f.), *Stagonolepis* shows a distinct ornamentation of the dermal armour plates. The radiating sculpture of the plates in *Aëtosaurus* consists mainly of elongated grooves, not grooves and ridges (with the exception of the lateral dorsals) as in *Stagonolepis*. Keels are developed in the paramedian plates only in adult specimens of *A. ferratus* and in *A. crassicauda*. In *Stagonolepis* these keels are modified to crests, which bear posteriorly projected hornlike bosses. This latter feature connects *Stagonolepis* more closely to the North American aetosaur genera *Typothorax*, *Paratypothorax* (the latter genus is also known from the German Lower Stubensandstein; p. 16) and *Calyptosuchus* than to *Aëtosaurus*. Finally *Stagonolepis* exceeds adult specimens of *A. ferratus* more than three times by body length, and *A. crassicauda* by almost twice. In the size category, *Stagonolepis* corresponds to the large group of mainly North American aetosaurs. The close relationships of *Stagonolepis* to *Aëtosaurus* suggested by Walker is apparently deluded by the general pattern of aetosaur morphology.

Few affinities can be recognized between *A. ferratus* and *Aetosauroides* from the Carnian (Bonaparte 1982) or Norian (Benton 1986) Ischigualasto Formation of Argentina (Bonaparte 1971, 1978). *Aetosauroides* is much larger than *Aëtosaurus*. The armour plates of *Aetosauroides* are ornamented by central knobs and radiating deep grooves and strong ridges, so that *Aetosauroides* seems to be closer related to *Stagonolepis* than to *Aëtosaurus*. *Neo-aetosauroides* from the uppermost Triassic Los Colorados Formation of Argentina belongs to the group of large-sized North American aetosaurs of *Typothorax*-type. Relationships can be stated, however, of *Aëtosaurus* to the aetosaur remains described by Fraser (1988) from the Norian fissure fillings of the Bristol Channel region, England. The dorsal armour plate (Fraser 1988: 133, Fig. 4) can be designated as *Aëtosaurus* sp. Finally it is annotated that also in the North American Upper Triassic Chinle Formation of the Petrified Forest National Park a diminutive aetosaur was discovered (Murry & Long 1989), informally named "*Acaenasuchus geoffreyi*". Its total body length is estimated to about 60 cm, so reaching the size of subadult specimens of *A. ferratus* (p. 7).

In 1936 Kuhn described skeletal and armour remains of an aetosaur from the Blasensandstein of Franconia, northern Bavaria as *Ebrachosaurus singularis*. The Blasensandstein is more or less time-equivalent to the Kieselsandstein in Württemberg and is

therefore definitively older than the Stubensandstein (Gwinner 1980). There is a general correspondence in morphology of the dermal armour of *Ebrachosaurus* to *Aëtosaurus*, which applies, however, also to *Stagonolepis* or to the North American aetosaurs, e.g. *Typothorax* (Case 1932, Gregory 1953). Remarkable similarities can be seen in *Ebrachosaurus* and *Stagonolepis robertsoni* Agassiz, regarding the cervical paramedian plates (Kuhn 1936: Tab. 11, Fig. 1) or the dorsal laterals (Tab. 11, Fig. 2; Walker 1961: 155 f., Fig. 20 d-g). Both species correspond also in size. Despite the fragmentary preservation of *Ebrachosaurus* it is obvious it has close affinities with *Stagonolepis*, so close that I suppose they are congeneric. Admittedly this assumption is based also on the age of the Lossiemouth Sandstone: Early Norian (Benton 1980; 1983 a, b; Benton & Walker 1985: 229) or Carnian-Norian (Benton & Walker 1985: 216) or Middle to Late Carnian (Benton 1986: 306) or Upper Carnian (Benton 1986: 310). These datings for the Lossiemouth Sandstone differ considerably. However, they confirm an older age of *Stagonolepis* than supposed by Walker (1961: 196).

Stagonolepis is accompanied by the rhynchosaur *Hyperodapedon gordonii* Huxley. This species is contemporary with *Hyperodapedon huxleyi* Lydekker from the Indian Maleri Formation and presumably also with *Scaphonyx* from the Santa Maria Formation of Brasil and the Ischigualasto Formation of Argentina (Benton 1984). The Maleri Formation has yielded the phytosaur *Parasuchus hislopi* Lydekker (Chatterjee 1978), which is very similar to *Parasuchus broilii* (Kuhn) (Chatterjee 1986) from the Franconian Blasensandstein, from which *Ebrachosaurus* comes, too. It can be concluded that the Lossiemouth Sandstone with *Stagonolepis* is more or less time equivalent to the Blasensandstein of Franconia and the Kieselsandstein of Württemberg. These units must therefore be Upper Carnian (Kozur 1975; Gall, Durand & Muller 1977; Olsen & Galton 1977; Olsen, McCune & Thomson 1982; Schröder 1982; Olsen & Sues 1986; contra Benton 1986). Most likely the Carnian/Norian boundary of the Upper Triassic lies in Southwest Germany at the top of the Kieselsandstein and so the Upper Bunte Mergel are Lower Norian.

The Middle Norian age of *A. ferratus* from Cene- is assigned to the Lower Stubensandstein of Württemberg from where the type of *A. ferratus* comes. Unfortunately there is no evidence for the first appearance of *A. ferratus* below the Lower Stubensandstein. In the Middle Stubensandstein *A. ferratus* is replaced by *A. crassicauda*. The age of the Middle Stubensandstein is also Middle Norian. This conclusion is based on an isolated skull of cf. *Mystriosuchus planirostris* Meyer from the Zorzino Formation of Endenna, Province of Bergamo (Pinna 1987). This site is more or less at the same stratigraphical level as Cene (Zambelli 1986: 14, fig. 4). *M. planirostris* is hitherto known only from the Middle

Stubensandstein (Stoll 1929)*, while *Nicrosaurus* is restricted to the Lower Stubensandstein, respectively Middle Norian (see also Chatterjee 1986; Parrish 1989). The phylogenetic position within the evolutionary sequence of the phytosaurs sensu Gregory (1969), however, does not agree with the stratigraphical distribution of the two genera *Mystriosuchus* and *Nicrosaurus* within the Stubensandstein. Nevertheless *Mystriosuchus* from Endenna does not contradict the Middle Norian age of the Lower and Middle Stubensandstein.

In the Middle Norian Lower Stubensandstein of Stuttgart-Heslach were found the armour plates of the large aetosaur *Paratypothorax andressi* Long & Ballew (1985), which is hereby contemporaneous to *A. ferratus*. *Paratypothorax* is also known from the upper parts of the Chinle and Dockum Formations. It seems to be restricted to these units (Hunt & Lucas 1989; Murry & Long 1989; Parrish 1989; Small 1989; contra Murry 1986 and Olsen, McCune & Thomson 1982). Hence it can be concluded that the upper units of the Chinle and Dockum are partly Middle Norian (Parrish 1989; contra Murry 1986, 1987, 1989), which confirms the results of stratigraphic work in the Upper Triassic of the southwestern USA agreed upon by most colleagues (Lucas, Hunt & Morales 1985; Benton 1986; Kirby 1989; Murry & Long 1989; contra Tucker & Benton 1982, Ballew 1989, Long & Ballew 1985).

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ABBREVIATIONS: MCSNB = Museo Civico di Scienze Naturali
Bergamo
SMNS = Staatliches Museum für Naturkunde
in Stuttgart.

* A lower jaw of a phytosaur designated as *Mystriosuchus* aff. *plieningeri* Meyer by Kuhn (1932) does not belong to *Mystriosuchus*, but either to *Parasuchus* (= *Paleorhinus* = *Francosuchus*, based on Dutuit 1977b; Chatterjee 1986) or *Angistorhinus* (Dutuit 1977a, b). *Mystriosuchus* has a very elongated snout and slender conical teeth (Gregory 1962; Hunt & Lucas 1989), features which separate this genus from *Parasuchus* and *Angistorhinus*. For the same reason the phytosaur remains designated as aff. *Mystriosuchus* by Guth (1963) from the Triassic of Madagascar do not belong to this genus (Dutuit 1978).

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INDIRIZZO DELL'AUTORE: Rupert WILD
Paläont. Abtig.
Staatl. Museum f. Naturkunde
Rosenstein 1
D 7000 STUTTGART 1 - GERMANIA