

PLAGIOSAURID AND CAPITOSAURID AMPHIBIAN MATERIAL FROM THE LATE TRIASSIC OF MEDERNACH, GRAND-DUCHY OF LUXEMBOURG : PRELIMINARY NOTE

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ABSTRACT. A series of fragments of temnospondyl amphibians are described from a bone bed in the Steinmergelgruppe of Medernach, Luxembourg. Much of the material is attributable to one of the two most derived genera of the Plagiosauridae, subfamily Plagiosaurinae, either *Gerrothorax* or *Plagiosaurus*, but is not determinate at generic level. Other material is attributable to the Capitosauridae and probably belongs to the terminal genus *Cyclotosaurus* but is not strictly determinate. The presence of a derived plagiosaurine together with ? *Cyclotosaurus* supports an Upper Triassic age for this fauna but does not permit any finer resolution.

KEYWORDS: temnospondyl amphibians, Plagiosauridae, Capitosauridae, Triassic, Luxembourg.

RESUME. Sont décrits ici des fragments d'Amphibiens Temnospondyles, provenant d'un bone-bed du Steinmergelgruppe de Medernach, Luxembourg. La majorité du matériel est attribuée, sans pouvoir être plus précis au niveau générique, aux Plagiosauridae, soit *Gerrothorax*, soit *Plagiosaurus*, les deux genres les plus évolués de la sous-famille Plagiosaurinae. D'autres spécimens semblent attribuables aux Capitosauridae, probablement au genre terminal *Cyclotosaurus*. La présence conjointe d'un Plagiosaurinae évolué et de ? *Cyclotosaurus* conforte l'attribution de cette faune aux Trias Supérieur, sans permettre une résolution temporelle plus fine.

MOTS-CLES: amphibiens temnospondyles, Plagiosauridae, Capitosauridae, Trias, Luxembourg.

ZUSAMMENFASSUNG. Aus einem Bonebed der Steinmergelgruppe von Medernach, Luxemburg, werden Fragmente temnospondyler Amphibien beschrieben. Ein Teil des Materials gehört zu einer der zwei höchstspezialisierten Gattungen der Plagiosauridae, Unterfamilie Plagiosaurinae, *Gerrothorax* oder *Plagiosaurus*. Andere Stücke sind den Capitosauridae zu zuordnen; sie gehören wahrscheinlich zur jüngsten Gattung *Cyclotosaurus*, sind aber nicht sicher bestimmen. Das Vorkommen eines spezialisierten Plagiosauriers zusammen mit ? *Cyclotosaurus* spricht für Obertrias-Alter; eine genauere Datierung ist nicht möglich.

SCHLÜSSELWÖRTER: temnospondyle Amphibien, Plagiosauridae, Capitosauridae, Trias, Luxembourg.

1. INTRODUCTION

Geological background

The greater part of the Grand Duchy of Luxembourg is a dissected plateau of Lower Mesozoic beds (Müller 1964, 1966; Feuth 1966). The amphibian material described here was collected from the

Rinkebiert, a small hill on the western outskirts of Medernach in east-central Luxembourg (Text-fig. 1a-b). The original section was made during the construction of National Road 14. The succession (Text-fig. 2) comprises 1.1 m of Lower «Rhaetic» strata underlain by approximately 12 m of marls and dolomites assigned to the Steinmergelgruppe (Hary & Müller 1967; Duffin 1993) on lithological grounds. Approximately 6 m below the base of the «Rhaetic» is

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a bone bed, the fauna of which was originally described briefly by Hary and Müller (1967). They identified teeth of the hybodont selachian *Hybodus*, actinopterygian fish scales, chondrosteian teeth resembling those of *Saurichthys*, and teeth of *Sargodon tomicus* (as *Sphaerodus minimus*; Hary & Müller 1967 p. 339). Dermal armour fragments were cited as resembling those of the phytosaur *Belodon*, and some isolated amphicoelous centra were reported.

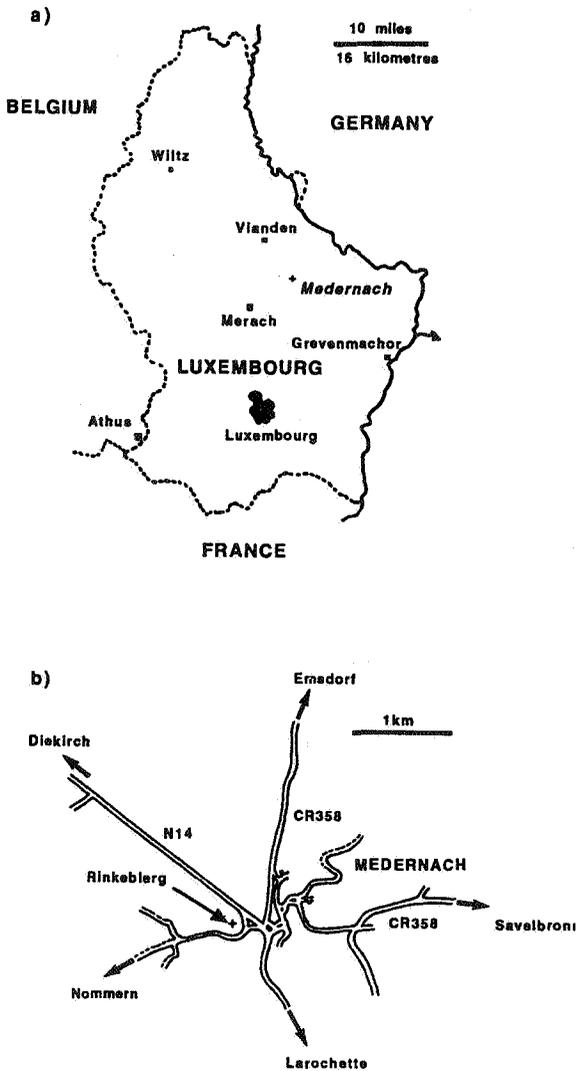


Figure 1.
a) Map of Luxembourg showing location of Medernach.
b) Map of vicinity of Medernach showing location of road cutting at Rinkebiert. After Duffin (1993).

Wouters, Lepage and Coupatez excavated the bone bed in 1983, obtaining a rich vertebrate fauna by acetic acid treatment of the matrix, followed by concentration using the bromoform flotation method. Possible therapsid teeth were described in a preliminary paper by Wouters, Lepage & Coupatez (1983) and later, in more detail, by Hahn, Lepage & Wouters (1984). Further excavations by Lepage, and to a less-

er extent by Duffin, yielded more material which formed the basis of a description of the selachian component of the fauna (Duffin, 1993). Cuny, Godefroit & Martin (1995) have recently described microvertebrate material from the fauna on the basis of collections made from excavations in 1991 by the Musée national d'Histoire naturelle de Luxembourg and the Institut royal des Sciences naturelles de Belgique. The work of these authors has failed to substantiate the identifications of the actinopterygian remains made by Hary & Müller (1967) but has substantially increased the known diversity of the assemblage (see faunal list below).

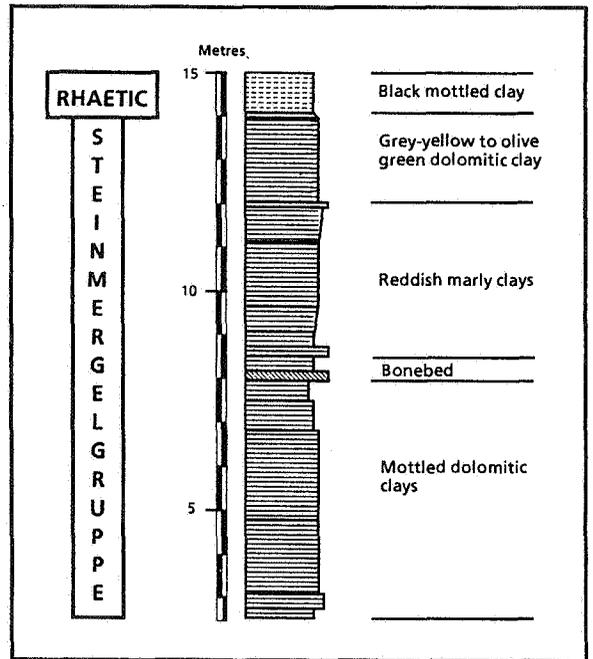


Figure 2. Stratigraphic section of the Upper Triassic beds exposed at Rinkebiert, near Medernach, based on information in Hary & Müller (1967 fig.2). After Duffin (1993).

The Lepage collection contains about a hundred fragments of temnospondyl amphibians. A few of the more determinate elements from this collection form the basis of the present work, which should be seen as a preliminary account of the temnospondyl amphibians of Medernach pending study of the material held by the IRSNB and in the Musée national d'Histoire naturelle de Luxembourg.

The vertebrate fauna of the Late Triassic bone bed of Medernach can be summarised as follows:

- SELACHII**
Hybodus minor Agassiz (1837)
Lissodus lepagei Duffin (1993)
4 types of dermal denticle

ACTINOPTERYGII

Colobodus sp.

cf. *Dipteronotus*

Perleidus cf. *stoschiensis*

Perleidus sp.

cf. *Semionotus*

undetermined carnivorous actinopterygians

undetermined pycnodontiforms

DIPNOI

undetermined ceratodontiforms

AMPHIBIA

Plagiosauridae

Plagiosaurinae *incertae sedis*

Capitosauridae

? *Cyclotossaurus*

SAUROPSIDA

Small archosaurian carnivores

Undetermined phytosaurs

PTEROSAURIA

Eudimorphodontidae

Eudimorphodon sp.

THEROPOSIDA

CYNODONTIA

Pseudotricodon wildi Hahn *et al.* 1984

Gaumia cf. *incisa*

Cynodontia incertae sedis

MAMMALIA

Undetermined morganucodontid

2. SYSTEMATIC PALAEOLOGY

Order Temnospondyli Zittel, 1888

Family Plagiosauridae Jaekel, 1914

Subfamily Plagiosaurinae (Jaekel) Shishkin, 1986

Incertae sedis

Material : Six specimens registered in the collections of the Department of Palaeontology, The Natural History Museum, London (BMNH) as follows :

BMNH R.12345, Large fragment of base of right clavicle (Text-fig. 3a-b, Plate 1 figs 1-2);

BMNH R.12346, Posterodorsal strut of left cleithrum (Text-fig.4a, Plate 1, fig.3);

BMNH R.12347, Posterodorsal strut of smaller right cleithrum (Text-fig.4b, Pl.1 fig.4);

BMNH R.12348, Fragment of right surangular (Text-fig.4c, Pl.1 figs 5-6);

BMNH R.12349, Dorsal scute (Pl.1 fig.7);

BMNH R.12350, Large trunk vertebral centrum (Pl.1 fig.8).

Description : Much of the temnospondyl material in this assemblage bears the pustulate dermal ornament characteristic of the Triassic temnospondyl family Plagiosauridae, subfamily Plagiosaurinae.

The family first appears in the Lower Triassic of Australia (*Plagiobatrachus* Warren, 1985), a record that cannot be readily placed in either of the named subfamilies. All later determinate material can be placed in one of the two subfamilies created by Shishkin (1986, 1987), namely the Plagiosterninae and the Plagiosaurinae. Plagiosternines have conventional temnospondyl dermal ornament, not pustular ornament and so are not the source of the plagiosaurid material described in this work. The subfamily Plagiosaurinae (Shishkin 1986 using Jaekel's family name) is characterized by pustulate ornament on the dermal bones of the skull, pectoral girdle and the dorsal scales, and even small scraps can be diagnosed to this subfamily quite readily. The earliest known plagiosaurines are from the Anisian of Orenburg Province and Kazakhstan, and later forms have been found in the Ladinian of Europe and Russia, the Carnian and Norian of Europe and the Norian of

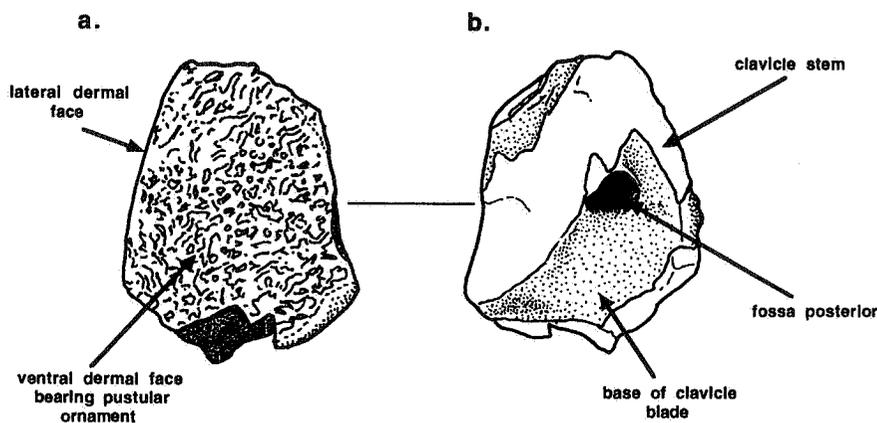


Figure 3. Plagiosaurine material from the Steinmergelgruppe of Medernach, Luxembourg :
a-b. BMNH R.12345 : large fragment of base of right clavicle.

Thailand. Within the Plagiosaurinae is a terminal clade formed by two Upper Triassic genera *Plagiosaurus* and *Gerrothorax*, characterized by highly derived, massive pectoral girdles which are very different from those of all other temnospondyls including the Ladinian plagiosaurines. The stem of the clavicle becomes abbreviated and the cleithrum has an abbreviated stem and an expanded head bearing dermal ornament. The two elements are in broad sutural contact and form massive box-like sides to the shallow pectoral region. Shishkin (1987 fig.30) depicted a morphological series of lateral profiles of the cleithro-clavicular region of the pectoral girdles of the stereospondyl *Benthosuchus* (unmodified), the primitive plagiosaurine *Plagioscutum* (slightly expanded) and the derived *Plagiosaurus* (greatly expanded; reproduced as Text-fig.5e). Even fragments of the cleithro-clavicular region of the *Gerrothorax-Plagiosaurus* type can be readily identified. The two genera *Gerrothorax* and *Plagiosaurus* can, at present, only be distinguished from relatively complete material of the skull table or interclavicle. On the skull table of *Gerrothorax*, the supratemporal retains the conventional contact with the parietal (Nilsson 1937), but uniquely in *Plagiosaurus*, the skull table is so modified that the postparietal sutures with the postfrontal excluding the supratemporal from contact with the parietal (Jaekel 1914). The interclavicles of *Gerrothorax* and *Plagiosaurus* are distinctly different in shape as shown by Shishkin (1987 fig. 27). The interclavicle of *Gerrothorax* has a relatively narrow anteromedial ramus and an acutely triangular anterior region of sculpture overlying it (Shishkin 1987 fig.27b,d). Also in *Gerrothorax*, the lateral wings of bone which underly the clavicles are only about twice as large as the posterolateral wings which extend behind the posterior edge of the clavicles (Shishkin 1987 figs 27b,d, 28b). In *Plagiosaurus*, the anteromedial ramus is broader and the anterior sculptured area forms an equilateral triangle (Shishkin 1987 fig. 27c); the lateral wings are slightly broader, but the posterolateral wings are much smaller and the former are five or six times the area of the latter (Shishkin 1987 fig.27c).

The material described here largely comprises fragments or elements up to about 30 mm in the longest dimension. There are many small pieces of dermal bone bearing the pustulate ornamentation characteristic of plagiosaurines and also numerous rolled plagiosaur centra, but only six of the more diagnostic specimens have been registered and are described here.

BMNH R.12345 is a fragment of the base of a right clavicle (Text-fig. 3a-b; Pl.1 figs 1-2), and has been interpreted in relation to the right clavicle of *Plagiosaurus* (Specimen MB Am.631 in the Museum

für Naturkunde, Humboldt Universität, Berlin) figured by Nilsson 1939 (Taf I figs 1-3; Taf.II figs 7-8) and examined by ARM. BMNH R.12345 comprises part of a thick plate of bone - the base of the clavicle blade - bearing pustular ornament on the flat ventral dermal face. It curves through 90 degrees, still bearing ornament on the lateral dermal face. The latter flange is the expanded and ornamented clavicle stem and has a natural edge representing the low sloping dorsolateral clavicle edge posterior to the claviculo-cleithral suture. The smooth interior face bears a deep pocket-like fossa at the base of the curvature, and a low ridge next to it. The fossa is that identified as the fossa posterior of the clavicle by Nilsson (1939 Taf.1, fig.2). The dermal ornament is not composed of discrete pustules but of groups of 2-3 pustules connected in short chains by low ridges. The pustular ornamentation of BMNH R.12345 identifies it as a plagiosaurine plagiosaurid and the expansion of the base of the clavicle stem into a broader ornamented flange identifies it as a plagiosaurine of the *Gerrothorax/Plagiosaurus* terminal clade.

BMNH R.12346 (Text-fig. 4a and Pl. 1 fig.3) and R.12347 (Text-fig.4b and Pl.1 fig.4) are the posterior regions of dorsal laminae of cleithra of an advanced plagiosaurine, again either *Gerrothorax* or *Plagiosaurus*. R.12346 belongs to a larger left cleithrum and R.12347 to a smaller right cleithrum. Each bears pustulate ornament on the dermal face which narrows to a wedge-like edge with a smoothly ridged surface angled slightly downwards on both sides. The medial smooth face corresponds to that identified by Nilsson 1945 fig.2 as a_2 - an area of attachment for dermal plates or scales. There is a broadly-based deep crest of bone on the ventral surface - the posterior extension of the medial lamina (Nilsson 1945 fig.2A, B, D and F). This is intact in R.12346 but only the basal region is present in R.12347. In both specimens, the posterior extension to the medial lamina is deep at the broken anterior end of the bone, becoming shallower at the wedge-like posterior end. This lamina is not perpendicular to the main body of the bone but angled at about forty degrees off the perpendicular. These specimens appear to belong to the highly derived type of cleithrum found only in *Plagiosaurus* and *Gerrothorax*. In these two genera, the cleithrum is not a rod-like bone with a dorsal expansion as in most temnospondyls. The dorsal expansion has become a massive block of dermal bone, the clavicle stem has shortened and the cleithrum stem has become a short blunt wedge of bone buttressed by the medial lamina. In a sutured cleithrum and clavicle of *Plagiosaurus* (MB Am.631) preserved in the round, the main vertical medial lamina can be seen clearly (Nilsson 1939 Taf.I fig.2) but its posterior extension can only be partly seen in Nilsson *op. cit.* Abb. 2B and Taf.II fig.7. In a separate cleithrum of *Gerrothorax pulcherrimus*,

Nilsson (1945 Figs 1 and 2) identified it as the posterior part of the medial lamina (Text-fig. 5c-d). As with the clavicular fragment, these cleithral specimens diagnose a derived plagiosaurine, either *Plagiosaurus* or *Gerrothorax* as only these genera have an expanded and flattened dorsal lamina on the cleithrum.

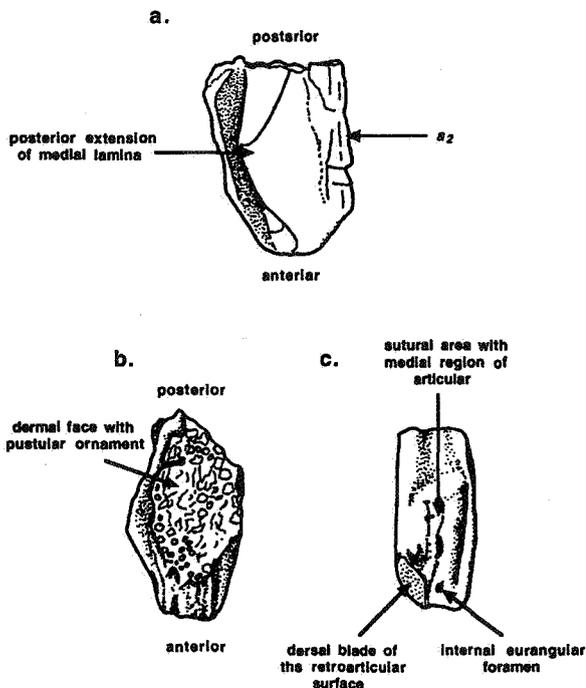


Figure 4. Plagiosaurine material from the Steinmergelgruppe of Medernach, Luxembourg :

- a. BMNH R.12346 Posterodorsal strut of large right cleithrum in ventral aspect.
- b. BMNH R.12347, Posterodorsal strut of smaller right cleithrum in dorsal aspect.
- c. BMNH R.12348, Fragment of right surangular in ventral aspect.

BMNH R.12348 (Text-fig. 4c, Pl.1 figs 5-6) is a broken central portion of a right surangular, bearing the sutural surface for the articular. It bears pustular ornament on its dermal face and a rugose oval patch on its medial face where the medial region of the articular sutures to it. The internal surangular foramen can be seen anteromedial to the rugose patch. At the posterior is the base of a broad ridge which forms the dorsal blade of the retroarticular surface. The specimen is a close match for that figured by Shishkin 1987 (Plate II figs 8,17 and text-figs 12a-c). The specimen is plagiosaurine but otherwise not diagnostic.

BMNH R.12349 (Pl.1 fig.7) is a dorsal dermal scute of a plagiosaurine. It is a small plate of bone with one uniformly pustulate ornamented face and one smooth face bearing a low medial ridge. Most of the border of the bone narrows to a fine edge and there is no evi-

dence of marginal sutural surfaces. It must therefore be a dermal scute from the dorsal surface of the animal. Plagiosaurids are covered in a dense armour of dorsal and ventral dermal scutes, and the dorsal scutes of the Plagiosaurinae bear pustulate ornament (e.g. *Gerrothorax* figured by Nilsson 1946).

The trunk centrum BMNH R.12350 (Pl.1 fig.8) is diagnostically plagiosaurid. It comprises a holospondylous centrum, clearly of endochondral bone and amphicoelous. Not only does it resemble those of the advanced plagiosaurines in shape - somewhat low with flattened dorsal surface - but it has the characteristic parapophyses at both anterior and posterior dorsolateral corners.

To summarize, specimens BMNH R.12345-R.12350 are all diagnostically attributable to the Plagiosauridae. The trunk centrum R.12350 can be identified only to family but the remaining specimens can all be placed in the subfamily Plagiosaurinae and the pectoral elements clearly belong to one of the derived plagiosaurines, either *Gerrothorax* or *Plagiosaurus*. In the absence of skull table or intact interclavicle specimens, the material cannot be identified to genus.

Family Capitosauridae Watson, 1919

? *Cyclotosaurus* Fraas, 1889

Material : Two specimens in the collections of the Department of Palaeontology, The Natural History Museum, London. BMNH R.12351 (Pl.1 figs 9-10), an eroded intercentrum of a large stereospondylous temnospondyl amphibian. BMNH R.12352 (Pl.1 figs 11-12), a fragment of the right ectopterygoid comprising the anterior margin of the subtemporal fossa. There are also numerous scraps of temnospondyl dermal bone with the honeycomb ornament characteristic of most large temnospondyls, but none is diagnostic, even to family.

Description : BMNH R.12351 (Pl.1 figs 9-10) is an eroded intercentrum of a large temnospondyl amphibian. It is a complete disc, narrow dorsally and broader ventrally, with a prominent notochordal pit on both faces the dorsal half of the disc. Eroded stumps of rib facets are present on the lateral faces of the centrum. This is clearly an anterior trunk intercentrum of one of the genera of large temnospondyl characterized by the stereospondylous condition. In such forms, only the anterior trunk vertebrae form a complete disc with a dorsally situated notochordal pit. Of the three known Triassic families including genera which possess stereospondylous trunk centra, metoposaurids possess thick centra with parallel anterior and posterior faces; mastodontosaurids (which barely extend into the Carnian) have intercentra which are only slightly wedge-shaped in lateral view; whereas the capi-

tosaurid genus *Cyclotosaurus* has anterior trunk intercentra which are pronouncedly wedge-shaped in lateral aspect (Romer 1947). R.12351 closely resembles intercentra attributed to *Cyclotosaurus* such as MB Am.577 from the Norian Knollenmergel of Halberstadt. This specimen is a large uneroded trunk intercentrum which was one of the syntypes of *Hercynosaurus carinidens* Jaekel, 1914. Jaekel's material is now associated with *Cyclotosaurus* specimens collected later from the same locality and the binomen *Cyclotosaurus carinidens* was assigned to the Halberstadt capitosaur by Welles & Cosgriff (1965). No other capitosaurs are known from the Upper Triassic of Europe and so the Medernach centrum can be tentatively assigned to the genus *Cyclotosaurus*.

BMNH R.12352 (Pl.1 figs 11-12) is a fragment of skull which is clearly not plagiosaur but matches the

right ectopterygoid region of a capitosaurid. It bears a smooth concave posterior edge, the anterior edge of the adductor fossa, which slopes anterodorsally alongside an anteroposterior ridge running the length of the fragment. The ventral face also curves smoothly away from the posterior edge but is horizontal and bears some anteroposterior ridging on its out edge is a separate thickened rounded ridge running along the length of the element. This is attached to some eroded bone on the lateral face of the element and appears to be a separate ossification. Comparison with the literature and with some older capitosaur skulls suggests that this is the posterior end of the right ectopterygoid, together with an attached fragment of the posterior end of the maxilla. It is not necessarily diagnostic for the Capitosauridae but it is consistent with attribution to that family.

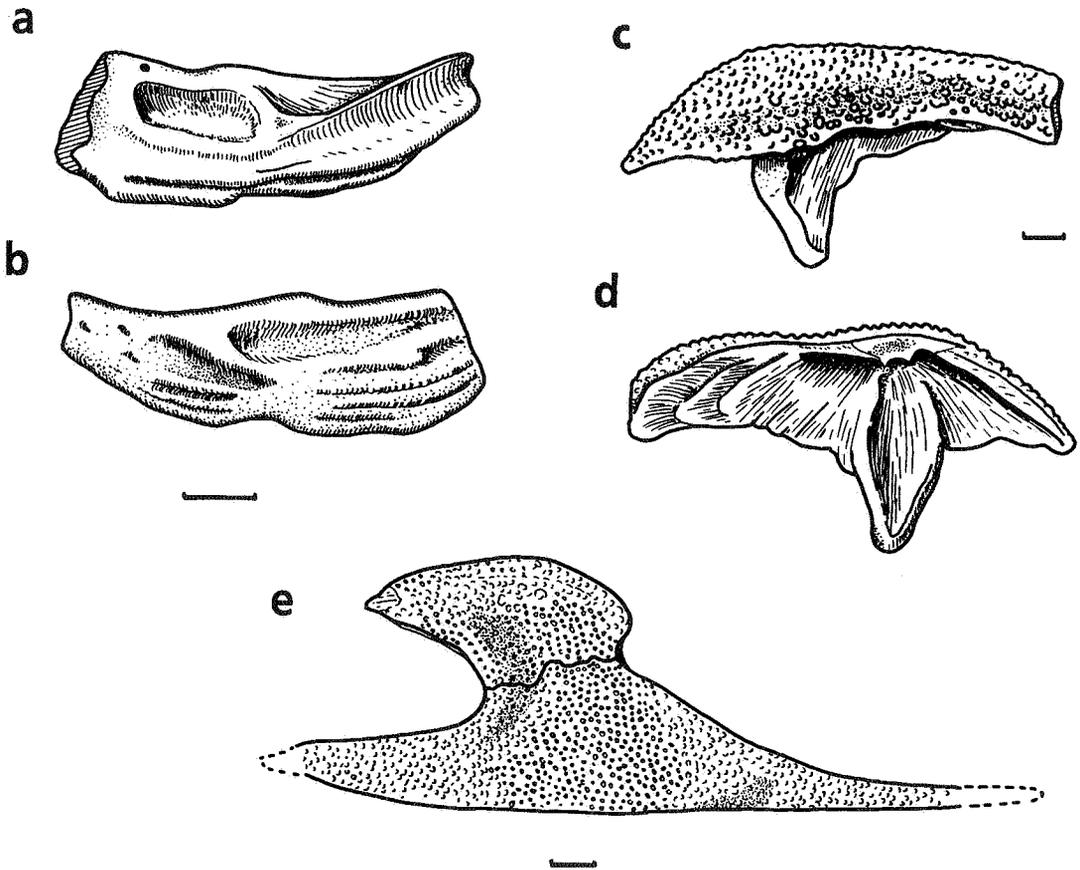


Figure 5. Comparative plagiosaurid material.

a-b. PIN 2340/31, fragment of left surangular of *Plagioscutum ochevi* Shishkin from the Anisian of Perovka, Orenburg Province, Russia (after Shishkin 1987) : a. in occlusal aspect, b. in lateral aspect; note articular surface. Compare with figure 4C and plate 1 figs 5-6.

c-d. SMNS 12038, left cleithrum of *Gerrothorax pulcherrimus* (Fraas) from the Norian Stubensandstein of Pfaffenhofen-im-Stromberg, Baden-Württemberg, Germany (after Nilsson 1945, fig.1), c. in lateral aspect (anterior to left), d. in medial aspect (anterior to right), e. reconstruction of the right cleithrum/clavicle complex of *Plagiosaurus depressus* Jaekel from the Norian Knollenmergel of Halberstadt, Germany, in lateral aspect (after Nilsson 1939, Abb.1). Scale = 10 mm. This exemplifies the condition found in advanced plagiosaurines in which the cleithral and clavicular stems are expanded to give a broad common suture.

4. DISCUSSION

4.1. UPPER TRIASSIC PLAGIOSAURINES AND CAPITOSAURIDS

4.1.1. Plagiosaurinae

The plagiosaur material described above clearly belongs to one of the highly derived Upper Triassic plagiosaurines characterized by a uniquely modified cleithro-clavicular complex, and a brief review of the previously described Upper Triassic plagiosaurines follows.

Plagiosaurus is only known certainly from the holotype and associated material from the Norian Knollenmergel of Halberstadt, Germany, described by Jaekel (1914) as *P. depressus*. Buffetaut & Wouters (1986) have referred material from the Upper Triassic of St. Nicolas-de-Port, Meurthe-et-Moselle, France to cf. *Plagiosaurus*, but it lacks the critically diagnostic characters reviewed at the beginning of the descriptive section. Cuny & Ramboer (1991) treat this and further material from St Nicolas-de-Port as indeterminate plagiosaurid, and this view is endorsed here with the supplementary observation that the material can be assigned to the subfamily Plagiosaurinae.

Gerrothorax is represented by four species, namely *G. franconicus* from the Carnian Blasensandstein of Ebrach, Franconia, Germany (Kuhn 1932); *G. pulcherrimus* from the Norian Stubensandstein of Pfaffenhofen, Baden-Württemberg, Germany (Fraas 1913); *G. striopustulatus* from the Norian Stubensandstein of Stuttgart-Sonnenberg, Baden-Württemberg, Germany; and *G. rhaeticus* from the Rhaetian Lower Coal Measures of Bjuv, Scania, Sweden (Nilsson 1934, 1946). Indeterminate plagiosaurid material from the Keuper of Luneville, Meurthe-et-Moselle, France has been attributed to various genera but is probably indeterminate. A plagiosaurine scute from the Norian Huai Hin Lat Formation of Thailand was described by Suteethorn *et al.* 1988.

4.1.2. Capitosauridae

Most of the determinate capitosaurid material from the Upper Triassic is attributed to the genus *Cyclotosaurus*, the principal species of which are as follows: *C. robustus* from the Carnian Schilfsandstein of Feuerbacher Heide, Stuttgart, Germany; *C. ebrachensis* from the Carnian Blasensandstein of Ebrach, Franconia, Germany (Kuhn 1932); *C. posthumus* and *C. mordax* from the Norian Stubensandstein of Pfaffenhofen, Baden-Württemberg, Germany (Fraas 1913); and *C. carinidens* from the Norian Knollenmergel of Halberstadt, Germany (Jaekel

1914). Buffetaut & Wouters (1986) reported a possible capitosaurid fragment from Saint-Nicolas-de-Port, Meurthe-et-Moselle, France. Outside Europe the only cyclotosaur material appears to be a specimen referred to *C. posthumus* from the Norian Huai Hin Lat Formation of Thailand (Ingavat & Janvier 1981); and undescribed material from the Carnian Argana Formation of Morocco (Dutuit 1976: 373).

4.2. STRATIGRAPHICAL CONCLUSIONS

The simplest and most conservative stratigraphical conclusion is that, because this temnospondyl assemblage comprises one of the two Upper Triassic plagiosaur genera *Gerrothorax* or *Plagiosaurus*, and possibly the Upper Triassic genus *Cyclotosaurus*, it supports an Upper Triassic age for the productive horizon.

Until recently the two plagiosaurine genera were both perceived as exclusively Norian and were considered to be of potential stratigraphical value. Buffetaut and Wouters (1986) suggested a Norian age for the St-Nicolas-de-Port material partly on the basis of the presence of *Plagiosaurus*, although in the absence of known Carnian plagiosaurs, this was using negative evidence as positive evidence. Plagiosaurine comparisons had to be made with either the Anisian/Ladinian primitive genera *Plagioscutum* and *Plagiosuchus* or the Norian derived genera *Plagiosaurus* and *Gerrothorax*. Consequently there has been a tendency for identification of scraps to polarise up to the Norian or down to the Ladinian (e.g. Buffetaut & Wouters 1986). Recent reassessment of the age of the Blasensandstein of Franconia (once thought of as Norian), equates it with the Schilfsandstein and places both in the Carnian (Hunt & Lucas 1991 and references cited therein). A consequence of this conclusion is that one species of *Gerrothorax* (*G. franconicus*) would also be Carnian, and hence that the genus *Gerrothorax* spanned both Carnian and Norian. Thus, advanced plagiosaurine material of the *Gerrothorax* - *Plagiosaurus* clade of organisation cannot yet be used to specify a stratigraphical age more precisely than the Upper Triassic. The known occurrences of the genus *Cyclotosaurus* show that it too spanned both Carnian and Norian and cannot be used to resolve the age of the assemblage with any greater resolution.

4.3. PALAEOECOLOGY

The Medernach assemblage provides further support for a distinct *Cyclotosaurus*-plagiosaurine association in the Upper Triassic, as the two taxa occur together in many of the assemblages where they are known, namely in the Blasensandstein at Ebrach, Germany; the Stubensandstein at Pfaffenhofen, Germany; the Knollenmergel at Halberstadt, Germany; the Huai Hin

Lat Formation in Thailand; possibly at Saint-Nicolas-de-Port, France; and now at Medernach in Luxembourg.

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PLATE 1

Temnospondyl amphibian material from the Steinmergelgruppe of Medernach, Luxembourg.
All specimens are x 1.

PLAGIOSAURINAE INCERTAE SEDIS.

1-2. BMNH R.12345 : large fragment of base of right clavicle in 1. ventral and 2. dorsal aspect.

3. BMNH R.12346 : posterodorsal strut of larger left cleithrum in ventral aspect.

4. BMNH R.12347 : posterodorsal strut of smaller right cleithrum in dorsal aspect.

5-6. BMNH R.12348 : fragment of right surangular in 5. dorsal and 6. ventral aspects.

7. BMNH R.12349 : dorsal scute.

8. BMNH R.12350 : large trunk vertebral centrum in left lateral aspect.

CAPITOSAURIDAE INCERTAE SEDIS

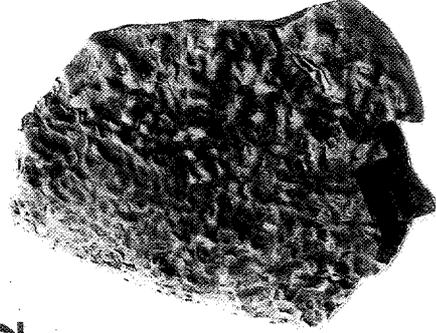
9-10. BMNH R.12351 : anterior trunk intercentrum in 9. anterior and 10. lateral aspects.

11-12. BMNH R.12352 : right ectopterygoid and fragment of maxilla in 11. dorsal and 12. ventral aspects.

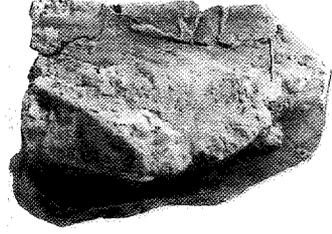
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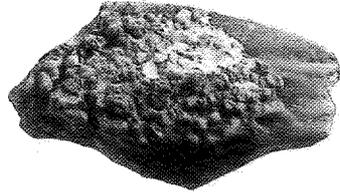
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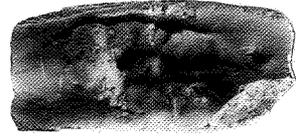
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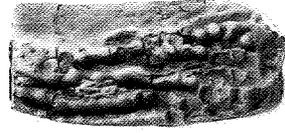
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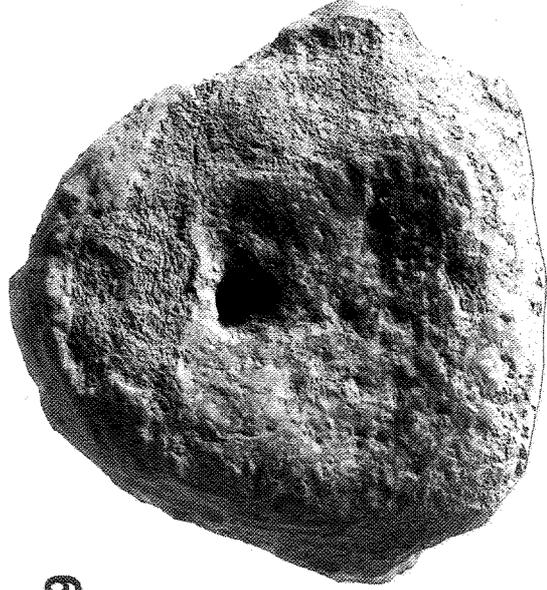
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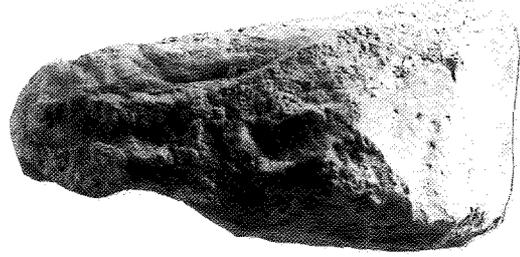
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