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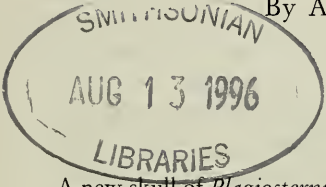
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### *Plagiosternum granulosum* E. FRAAS: a plagiosaurid temnospondyl from the Middle Triassic of Crailsheim, Germany

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With 5 figures

#### Summary

A new skull of *Plagiosternum granulosum* has been recovered from the same horizon as the Holotype, the Upper Muschelkalk Grenzbonebed, but is from a different locality. The skull is described and confirmed as a member of the Subfamily Plagiosterninae (SHISHKIN 1987) of the Family Plagiosauridae, Order Temnospondyli. A list of characters considered to be derived for the Subfamily Plagiosterninae and the species *Plagiosternum granulosum* is provided.

#### Zusammenfassung

Der neu aufgefundene und hier beschriebene Schädel von *Plagiosternum granulosum* stammt aus dem gleichen stratigraphischen Niveau wie der des Holotypus. Er erweist sich als der eines Vertreters aus der Unterfamilie der Plagiosterninae (SHISHKIN 1987) der Familie Plagiosauridae, Ordnung Temnospondyli. Die für die Unterfamilie Plagiosterninae und die Art *Plagiosternum granulosum* charakteristischen Merkmale werden aufgelistet.

#### 1. Introduction

A collection of cranial and postcranial material from the Upper Muschelkalk Grenzbonebed at Crailsheim, Germany, originally described as *Mastodonsaurus granulosus* (E. FRAAS 1889) was later transferred by E. FRAAS (1896) to *Plagiosternum granulosum*, apparently on the basis of interclavicular shape. It is interesting that this, the first described member of the family Plagiosauridae, is characterised by reticulate ornament rather than the pustular variety more characteristic of that family. This fact also accounts for E. FRAAS associating the material with *Mastodonsaurus* which was the commonest temnospondyl at Crailsheim, had reticulate ornament and was of a similar size. Another collection of postcranial material from Crailsheim has pustular ornament and was described as *Plagiosuchus pustuloglomeratus* (HUENE 1922).

In 1913 E. FRAAS referred cranial material to *Plagiosternum granulosum*, presumably because of its reticulate ornament, and reconstructed the skull on the basis of a right nasal, a partial left maxilla, and a portion of the left postorbital region, including both parietals (SMNS 13168). This restoration was somewhat more conservative than that provided by ABEL (1919) who filled in the missing cranial areas. A restoration by HUENE (1922) reinterpreted the sutures on the original specimen and described some further skull fragments, a right mandibular ramus, fragments of a left ramus, and a collection of vertebral centra. One jaw fragment referred to *P. granulosum* by E. FRAAS (1913) belongs to *Mastodonsaurus* (NILSSON 1937, footnote p. 47).

A second species of *Plagiosternum*, *P. nanum* SCHMIDT was erected for two fragments of interclavicle, from the Lettenkohle of Hochstedt (SCHMIDT 1931) but should be considered a nomen nudum.

SHISHKIN (1986) described a partial skull from the Ladinian Bukobay Formation of the Cis-Urals as *Plagiosternum danilovi*, referred a mandibular ramus described as *Plagiorophus paraboliciceps* (KONZHUKOVA 1955) to *Plagiosternum*, and erected the Subfamily Plagiosterninae for all described species of that genus plus *Melanopelta antiqua*. In his review of the Plagiosauroida (SHISHKIN 1987) he extended these descriptions adding postcranial material to the hypodigm. A third Russian plagiosternine, the early Middle Triassic *Arenetsia improvisa*, was described by NOVIKOV & SHISHKIN (1992).

An as yet undescribed specimen referred to *Plagiosternum* (PANCHEN 1959) was found in Carnian deposits on Bear Island in the Norwegian Arctic in 1948, but left in situ. It was subsequently rediscovered (DORÉ & WANDAS 1984) and is now being prepared by the Paleontologisk Museum, University of Oslo. Its referral to *Plagiosternum*, as with all the above material, was made largely on the basis of its undoubted plagiosaurid shape together with a reticulate pattern of ornament.

In his review of plagiosaurs and plagiosaur relatives, PANCHEN (1959) expressed some doubts as to the plagiosaurid affinities of the genus *Plagiosternum*, because of the reticulate nature of its ornament, its lack of dermal armour, and the unusual shape of the interclavicle. In this he echoed JAEKEL (1914) who separated *Plagiosternum* from the other plagiosaurs which he placed in a separate order of temnospondyls. It is now known that the Bear Island *Plagiosternum* had dermal armour and it is suggested below that the unusual shape of the interclavicle of *P. granulosum* may not be correct.

In this paper I describe a new, more complete skull of *Plagiosternum granulosum* which was recovered in 1980 by H. BERNER, a veterinary surgeon of Grossbottwar, from the SCHNEIDER quarry in Ummenhofen near the town of Schwäbisch Hall approximately thirty kilometres west of Crailsheim, the locality of the Holotype. It comes from the Upper Muschelkalk Grenzbened.

Unfortunately, the skull was crushed by quarrying but was recovered by BERNER in thirty four numbered pieces. Subsequently delicate mechanical preparation and restoration by D. HAGMANN of the Staatliches Museum für Naturkunde in Stuttgart has resulted in a magnificent specimen. As the condition of the bone was poor it was necessary to impregnate it with preservative in order to prevent further deterioration, while missing skull bones were restored in a polyester resin. Those areas restored are indicated by cross hatching in Figures 3–5. As the bone is now impermeable it is impossible to determine the position of many of the suture lines. Those

indicated on the specimen by solid lines are either plainly visible or have been determined from isolated plagiosaur bones of similar size, bearing reticulate ornament, and from the same bone bed.

In addition to the skull, a number of other cranial and postcranial fragments referable to *P. granulosum* are now in the collections of the Staatliches Museum für Naturkunde in Stuttgart.

## 2. Description of *Plagiosternum granulosum*, SMNS 56614

Skull Roof (Figures 1, 3). – The reticulate ornament which characterises this specimen is unusual in that the size of the ornament varies, with small (2–3 mm) pits near the centres of ossification of the postparietals, tabulars, squamosals and parietals, and larger (5–8 mm) pits elsewhere. This may be due, in part, to surface weathering, but several large, unweathered pits are present on the nasals and peripheral parts of the squamosals. It is of interest that no regions of intensive skull growth are indicated by ridged ornament. A small ornamented area of the quadratojugals extends onto the palate, and the pterygoids also appear to have carried some ornament.

In overall shape the skull is undoubtedly plagiosaurid, but it is much more laterally attenuated than in previous restorations of the genus. Of these, the dorsal skull roof drawn by E. FRAAS (1913) is the most accurate. Only E. FRAAS recognised that most of the skull roofing bones usually found between the orbits are missing, so that the median borders of the orbits are formed by the nasals, frontals and parietals. In my opinion the postfrontals restored by E. FRAAS are also absent so that the posterior border of the orbit is formed by the parietal and postorbital bones. This is true of isolated partial orbits in the collection; that is, the parietal is expanded laterally beneath the orbit so that it occupies the area usually taken up by the postfrontal. An isolated parietal referred to *Plagioscutum ochevi* (SHISHKIN 1987, fig. 9) bears part of the posterolateral border of the orbit, although the skull (fig. 8) is restored with a postfrontal in this position. My restoration also lacks a supratemporal. In this I follow E. FRAAS (1913) as there is no evidence for a supratemporal in the new specimen.

The structure of the antorbital area is less certain, especially as the left antorbital fragment described by E. FRAAS (1913) is now considered to be from a mandible (HELLRUNG, pers. com. 1994). There is no doubt that the nasal forms the anteromedial border of the orbit as it does in several plagiosaurs, but whether the bone present at the more anterolateral border of the orbit is formed by prefrontal or lacrimal or a lateral extension of the palatine is difficult to determine. It is in the position usually occupied by a lacrimal and extends anteriorly to take part in the posterior border of the nostril as does the lacrimal in other species. *Arenetsia improvisa* is described as having a lacrimal (NOVIKOV & SHISHKIN 1992); these authors follow HUENE (1922, fig. 13) in categorising as a lacrimal a bone described by E. FRAAS (1889, pl. 6, fig. 7) as a maxilla of *Plagiosternum*. As yet undescribed plagiosaurs from Greenland (JENKINS, pers. com. 1993) appear to have the nasal bordering the orbit and a single additional antorbital bone which is most likely a lacrimal. SHISHKIN (1987) illustrates a lacrimal in *Plagioscutum ochevi*.

In general, therefore, in plagiosaurs in which the area is preserved, the nasal bone is included in the orbital margin and there is a single additional laterally placed antor-

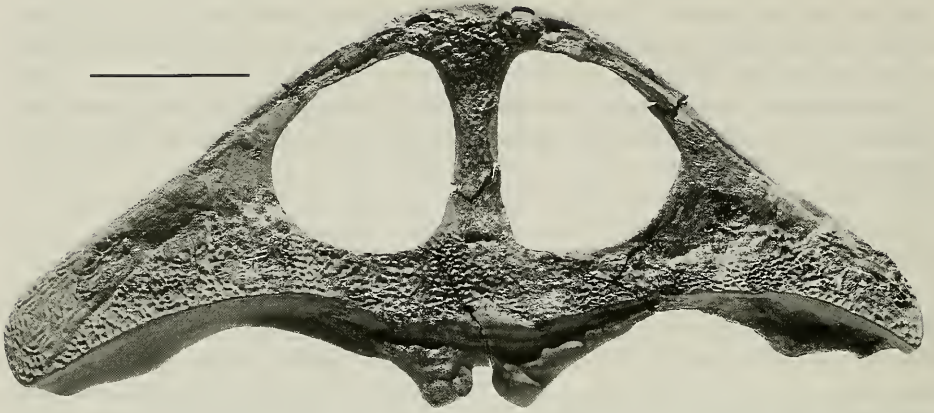


Fig. 1. *Plagiosternum granulosum* SMNS 56614: skull roof. In this and all subsequent figures the scale bar is equal to 100 mm.

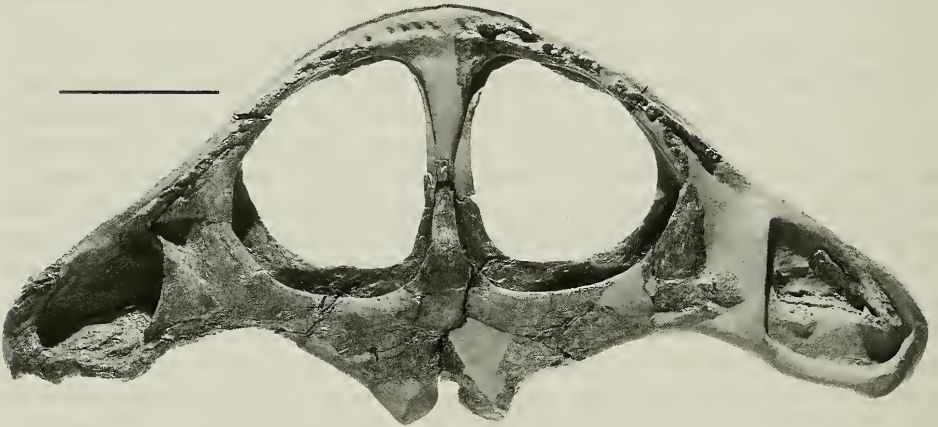


Fig. 2. *Plagiosternum granulosum* SMNS 56614: palate.

bital bone which appears to be the lacrimal. An exception appears to be present in *Gerrothorax pulcherrimus* as restored by HUENE (1922) in which the nasal bone is excluded from the margin of the orbit by a prefrontal situated medial to the lacrimal. It is possible that HUENE was mistaken and the prefrontal is absent in all plagiosaurs.

Palate (Figures 2, 4). – Features of taxonomic interest on the palate are the exclusion of the ectopterygoid from the margin of the interpterygoid vacuity and a palatal exposure of the suture between the exoccipital and the pterygoid.

A row of large teeth are present on the vomers, palatines and ectopterygoids, with a few smaller teeth present posteriorly on the ectopterygoids. Tusks are absent. Three tooth loci external to the left choana indicate that the maxillary teeth were smaller than those of the inner tooth row. Teeth seen in cross section in isolated bones from the collection show simple infolding characteristic of members of the family Plagiosauridae (WARREN & DAVEY 1992).

Occiput (Figure 5). – While the skull roof and palate are drawn as restored, the occiput is reconstructed using the more complete right side of the skull as a mirror

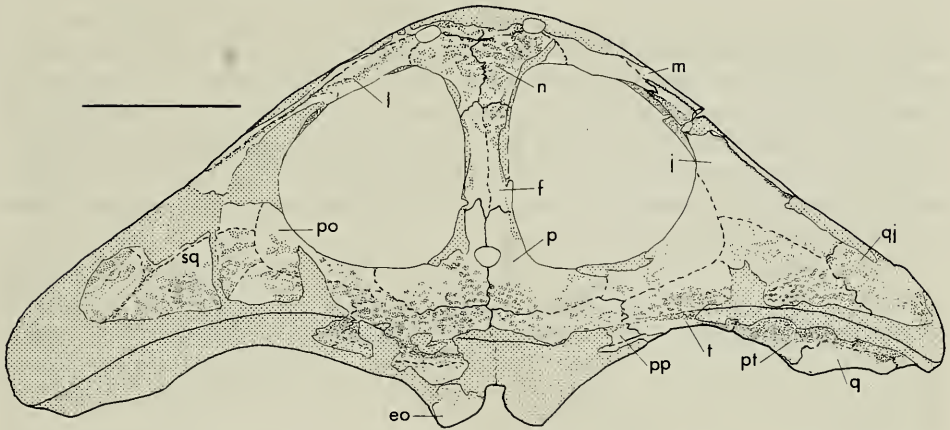


Fig. 3. *Plagiosternum granulosum* SMNS 56614: drawing of the skull roof. In figures 3–4 stippling represents areas which have been restored. Abbreviations used in figures 3–5: ar, articular; c, choana; eo, exoccipital; e, ectopterygoid; f, frontal; l, lacrimal; n, nasal; m, maxilla; j, jugal; p, pterygoid; pl, palatine; po, postorbital; pp, postparietal; pt, pterygoid; q, quadrate; qj, quadratojugal; SMNS, Staatliches Museum für Naturkunde in Stuttgart; sp, parasphenoid; sq, squamosal; t, tabular; v, vomer.

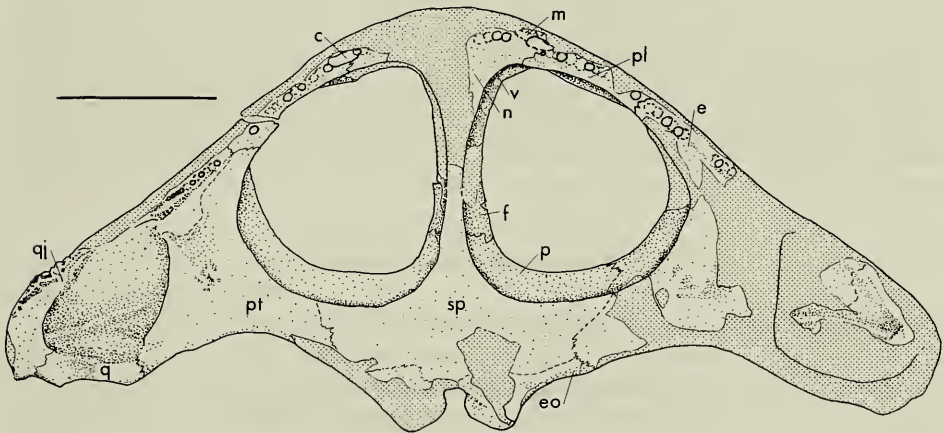


Fig. 4. *Plagiosternum granulosum* SMNS 56614: drawing of the palate. Abbreviations below figure 3.

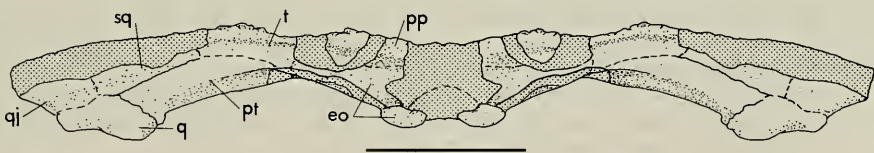


Fig. 5. *Plagiosternum granulosum* SMNS 56614: restoration of the occiput. Areas of the occiput not present on either side are stippled. Abbreviations below figure 3.

for the left, together with the left occipital condyle. Although the skull is undoubtedly a little dorsoventrally flattened it is not possible to extend the posterolateral parts of the quadratojugals ventrally more than shown in Figure 5, so the skull is much shallower than that of *Plagiosternum danilovi* (SHISHKIN 1987). Nevertheless, the free, unornamented, external portion of the quadratojugal shown by SHISHKIN (1987) to be characteristic of the Plagiosterninae is present but is directed more posteriorly than in *P. danilovi*. One result of this shallow occiput is that the cheek fenestrae found in *P. danilovi* are absent.

As the occipital area is not complete there is no evidence for posttemporal fenestrae in this specimen. It is likely that they were present as the dorsal border of a small fenestra was preserved on the occipital border of the postparietal in the partial skull roof described by E. FRAAS (1913). The area of the cranioquadrate passage (SHISHKIN 1987, textfig. 4b, indicated by ccq) has been restored so that no part of the ascending ramus of the pterygoid is visible.

Pectoral girdle, Interclavicle. – The strange shape of the interclavicle as described by E. FRAAS (1896, textfig. 1) may not be correct. The specimen appears to have been antero-posteriorly reversed by E. FRAAS and is not complete. Its anterior border may have been more normally plagiosaurid in shape and all plagiosaurs lack the usual temnospondyl posterior extension of the interclavicle. The shelf associated with that border in heavily armoured plagiosaurs is missing in E. FRAAS's specimen.

Clavicle. – Of the several partial clavicles of *P. granulosum* known none has a complete dorsal process so there is no direct evidence for the absence of a complex between the dorsal process and its associated cleithrum. Comparison of these clavicles with plagiosaurs which do have a complex indicates that the latter have a dorsal process which bears a deep posterior notch extending dorsally from the base of the process. This notch is absent in clavicles of *P. granulosum* and for this reason I consider the complex was absent. Also, there are no known complexes associated with pectoral girdles with reticulate ornament (HELLRUNG, pers. com. 1994).

### 3. Systematic palaeontology

#### Order Temnospondyli

#### Superfamily Plagiosauroidea SHISHKIN 1987

#### Family Plagiosauridae ABEL 1919

#### Subfamily Plagiosterninae SHISHKIN 1986

#### Genus *Plagiosternum* E. FRAAS 1896

#### *Plagiosternum granulosum* (E. FRAAS 1889)

- partim \*1889 *Mastodonsaurus granulosus* E. FRAAS. – E. FRAAS, pp. 94–100, pl. 6.  
 1896 *Plagiosternum granulosum* E. FRAAS. – E. FRAAS, p. 5, textfig. 1.  
 1913 *Plagiosternum granulosum* E. FRAAS. – E. FRAAS, pp. 277–282, textfig. 1, pl. 17, figs. 1–3.  
 1911 *Plagiosternum*. – JAEKEL, p. 110, fig. 123.  
 1919 *Plagiosternum granulosum* E. FRAAS. – ABEL, p. 292, fig. 221.  
 1922 *Plagiosternum granulosum* E. FRAAS. – HUENE, pp. 410–418, figs. 13–24.  
 1927 *Plagiosternum granulosum*. – BROILI, p. 19, fig. on p. 19.  
 1928 *Plagiosternum granulosum* E. FRAAS. – CORROY, p. 112.  
 1931 *Plagiosternum granulosum* E. FRAAS. – SCHMIDT, pp. 33–37, pl. 4, figs. 21–25.  
 1935 *Plagiosternum granulosum* E. FRAAS. – SÄVE SÖDERBERGH, pp. 57–58, fig. 28.  
 1937 *Plagiosternum granulosum* E. FRAAS. – NILSSON, pp. 47–50, fig. 12.

1986 *Plagiosternum*. – SHISHKIN, pp. 41–43.

1987 *Plagiosternum granulosum*. – SHISHKIN, pp. 18, 44, fig. 45b.

Lectotype: Left clavicle (SMNS 11824) described and figured by E. FRAAS 1889: 99, pl. 6, fig. 1; designated herein.

Referred material:

SMNS 13168: Partial skull, E. FRAAS (1913, textfig. 1).

SMNS 56614: Partial skull, this paper, figs. 1–5.

SMNS, without number: Left pterygoid including part of the ascending ramus, figured as a right pterygoid HUENE (1922, textfig. 17).

SMNS, without number: Skull fragments, including several pterygoids.

SMNS 8733: Interclavicle, figured by E. FRAAS (1896, textfig. 1).

SMNS 8675: Interclavicle, described by E. FRAAS (1913: 280).

SMNS 11830: Vertebral centra, E. FRAAS (1889, pl. 6, fig. 12), HUENE (1922, figs. 22–24).

Diagnosis. – Species of the Plagiosterninae with reticulate ornament of dermal bones. The skull is distinct from other species of the Plagiosterninae in the following derived characters:

- Frontal and parietal bones take part in the margin of the orbit.
- Prefrontal and postfrontal bones absent.
- Supratemporal bone absent.
- Exoccipital sutures with the pterygoid on the palatal surface.
- Pterygoids meet the palatine bones.
- Cheek fenestra (SHISHKIN 1987) absent.

Remarks. – All studied material of *P. granulosum* was recovered from the Upper Muschelkalk Grenzbonebed in the region of Crailsheim, Germany.

The syntype material (E. FRAAS 1889: 94–100, pl. 6, figs. 1–14) is a collection of disassociated cranial and postcranial material, some of which is mastodontosaurid. The lectotype designated herein is the most complete bone within the syntype material and shows well the reticulate ornament of dermal bones characteristic of the species.

### Other *Plagiosternum* species

(*Plagiosternum nanum* SCHMIDT, 1931; M. Triassic, Hochstedt, Germany; type material undeterminable.)

*Plagiosternum danilovi* SHISHKIN 1986; M. Triassic (Ladinian), southern Cis-Urals, Russia.

*Plagiosternum paraboliceps* (SHISHKIN 1986) (= *Plagiorophus paraboliceps* KONZHUKOVA 1955); M. Triassic (Upper Anisian? – Lower Ladinian), southern Cis-Urals, Russia.

### Acknowledgments

I would like to thank Dr. Rupert Wild of the Staatliches Museum für Naturkunde in Stuttgart for allowing me to borrow *Plagiosternum granulosum* SMNS 56614, and for his hospitality while I worked in that institution, and the Museum itself for accommodation. The Paleontological Institute, Moscow kindly allowed me access to its plagiosaur collection, and Dr. Igor Novikov translated the taxonomic sections of SHISHKIN (1987). Photographs were taken by the La Trobe University Reprography Unit.

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