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### The Genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology

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# The Genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology

Olivier Rieppel

## Abstract

*Placodus gigas* Agassiz, 1833, from the Muschelkalk of the Germanic Triassic, is recognized as the only valid species of its genus. *Placodus gracilis* Jurcsak, 1976 (pending a revision of the original material), and *Placodus impressus* Agassiz, 1833, are considered nomina dubia. An amended diagnosis based on homologies (synapomorphies) is provided for the genus *Placodus* and its only known species. The skeletal structure of *Placodus* is described, and the phylogenetic interrelationships of the genus are discussed. Placodonts originated along the northern coast of the Tethys, and early during their phylogeny split into two lineages, the Placodontoidea and Cyamodontoidea. *Placodus* immigrated into the Muschelkalk Basin through an eastern seaway (possibly the Silesian–Moravian Gate) during early Anisian time.

## Zusammenfassung

*Placodus gigas* Agassiz, 1833, aus dem Muschelkalk der Germanischen Trias wird als einziger Vertreter seiner Gattung anerkannt. *Placodus gracilis* Jurcsak, 1976 (eine Revision des Originalmaterials steht noch aus) und *Placodus impressus* Agassiz, 1833, werden zu nomina dubia erklärt. Eine erweiterte Diagnose für die Gattung *Placodus* fußt auf Homologie (Synapomorphie). Die Skelettmorphologie von *Placodus* wird beschrieben, und die phylogenetischen Verwandtschaftsbeziehungen der Gattung werden diskutiert. Die Placodontier erscheinen erstmals am Nordrand der Tethys, und spalten sich früh in zwei getrennte Entwicklungszweige, die Placodontoidea und die Cyamodontoidea. Die Gattung *Placodus* erreichte das Muschelkalkbecken durch eine östliche Pforte im frühen Anis.

## Introduction

Placodonts are a monophyletic clade of sauropterygian reptiles that are known from the late Early Triassic to the Rhaetian. They are found in deposits of coastal stretches along the western Tethys and of epicontinental seas in central Europe. The Placodonta comprise two major subclades, the armored Cyamodontoidea (Mazin & Pinna, 1993), and the Placodontoidea, with two genera, *Paraplacodus* from the Middle Triassic intraplatform basin facies in the Swiss Alps, and *Placodus* from Middle Triassic epicontinental deposits of Europe. The occurrence of teeth referable to *Placodus* in

the quarries at the Bindlacher mountain near Bayreuth and Oschenberg near Laineck was known since 1809 (Weiss, 1983). The first skull of *Placodus* was found in 1824 and figured by Münster (1830) as “specimen I” (the holotype of *Placodus gigas* [Nosotti & Pinna, 1989]; BSP AS VII 1208). Münster solicited Agassiz’s help in identifying the large, black, polished teeth. Agassiz attributed the remains to an as yet unknown genus of durophagous fish (Bronn, 1831), which he later named *Placodus* (Agassiz, 1833–1845). It was left to Owen (1858) to recognize the reptilian nature of that genus. Comparing *Placodus* to *Simosaurus*, Owen postulated sauropterygian affinities of placodonts.

He later (Owen, 1860) formalized this view by the inclusion of nothosaurs, pleiosaurs, and placodonts, as well as some other enigmatic fossils, in his Sauropterygia.

Whereas the original findings of *Placodus* were restricted to the upper Muschelkalk of the surroundings of Bayreuth in Bavaria, other material came from upper Muschelkalk outcrops in southern and southeastern Germany, from the upper Muschelkalk of Lunéville in eastern France, and from various localities in the lower Muschelkalk: Freyburg/Unstrut, eastern Germany (Meyer, 1851a; *Placodus antiquior* Huene, 1936); Rüdersdorf near Berlin; Jena (Meyer, 1851a); Gogolin in Upper Silesia (now Gorny Slask, Poland: Meyer, 1851b; Huene, 1905); Helgoland (Kruckow, 1979); and Winterswijk in the Netherlands (Oosterink, 1978). The occurrence of placodonts in the Triassic of Alesd, Romania (Jurcsak, 1976, 1977), indicates that the group reached the Muschelkalk Basin from the east, perhaps through the Silesian-Moravian Gate (Peyer & Kuhn-Schnyder, 1955; for a history of the Muschelkalk Basin, see Ziegler, 1982; Hagdorn, 1985).

## Systematic Paleontology

### Sauropterygia Owen, 1860

### Placodontia Zittel, 1887-1890 (also Seeley, 1889)

### Placodontoidea Nopcsa, 1923

### Placodontidae Cope, 1871

### *Placodus* Agassiz, 1833

TYPE SPECIES—*Placodus gigas* Agassiz, 1839, from the upper Muschelkalk (lower Ladinian, Middle Triassic) of Bayreuth, Bavaria.

DIAGNOSIS—Large sauropterygian; rostrum spatulate; three enlarged premaxillary teeth strongly procumbent and separated from maxillary molar teeth by a distinct diastema; three transversally expanded palatine tooth plates; nasals, frontals, and parietals fused in adult; jugal extends anteriorly beyond level of anterior margin of orbit; prefrontal and postfrontal in contact dorsal to orbit; internal nares confluent; pterygoid restricted to posterior position in dermal palate; pterygoid flanges distinct and longitudinally oriented; basioccipital tubers in complex ventral relation to dermal palate; “alisphenoid bridge” underlying olfactory tracts; dentary with large coronoid process; lateral exposure of coronoid bone restricted; mandibular symphysis elongate, formed by dentaries

and splenials; neural arches within dorsal region with elongated transverse processes and accessory hypophene-hypantrum articulations; neural canal high and rectangular; coracoids reduced; thyroid fenestra in pelvic girdle reduced; humerus expanded distally; entepicondylar foramen absent.

HORIZON AND LOCALITY—Lower Muschelkalk (upper lower Anisian), and lower to middle upper Muschelkalk (upper Anisian, lower Ladinian) of central and eastern Europe.

### *Placodus gigas* Agassiz, 1833

- 1830 no name, Münster, pp. 3-4, Pl. 1.  
1833- *Placodus gigas*, Agassiz, vol. 2, p. 218f.,  
1845 Pl. 70, Figs. 14-21.  
1833- *Placodus andriani*, Agassiz, vol. 2, p.  
1845 218f., Pl. 70, Figs. 8-13.  
1835 *Placodus gigas*, Bronn, p. 186, Pl. 13, Fig.  
13.  
1836 *Placodus* sp., Braun, p. 360f., figure on  
p. 361 (the specimen of *Placodus andriani* published by Agassiz, 1833-1845, and  
Münster, 1839).  
1839 *Placodus andriani*, Münster, p. 119.  
1839 *Placodus gigas*, Münster, p. 119.  
1840- *Placodus andriani*, Owen, Pl. 30, Figs.  
1845 2-4.  
1848 *Placodus gigas*, H.v. Meyer, p. 467.  
1851a *Placodus gigas*, H.v. Meyer, pp. 197-199,  
Pl. 33, Figs. 1-12.  
1851b *Placodus gigas*, H.v. Meyer, p. 241f., Pl.  
29, Figs. 51-54.  
1858 *Placodus bathygnathus*, Owen, p. 181f.,  
Pl. 11, Figs. 1-3.  
1858 *Placodus bombidens*, Owen, p. 180, Pl.  
9, Figs. 3-6.  
1858 *Placodus pachygnathus*, Owen, p. 179, Pl.  
10, Figs. 6-7.  
1861- *Placodus andriani*, H.v. Meyer, p. 57ff.,  
1863 Pl. 9.  
1861- *Placodus bathygnathus*, H.v. Meyer, pp.  
1863 57, 60-61.  
1861- *Placodus bombidens*, H.V. Meyer, pp. 57,  
1863 60-61.  
1861- *Placodus pachygnathus*, H.v. Meyer, pp.  
1863 57, 60-61.  
1862 *Placodus andriani*, Braun, p. 14.  
1862 *Placodus gigas*, Braun, pp. 8, 14.  
1863 *Placodus andriani*, Braun, p. 6.  
1863 *Placodus gigas*, Braun, p. 5.  
1863 *Placodus hypsicephalus*, Braun, p. 10.  
1863 *Placodus impressus* partim, Braun, p. 5.

1863	<i>Placodus quinomolaris</i> , Braun, p. 8	1907	<i>Placodus bombidens</i> , Jaekel, caption for Pl. 4.
1863	<i>Placodus aethiops</i> , H.v. Meyer, p. 180.	1907	<i>Placodus gigas</i> , Jaekel, caption for Pl. 4.
1863	<i>Placodus andriani</i> , H.v. Meyer, pp. 194–199, Pl. 30, Figs. 1–4, Pl. 31, Figs. 3–5, Pl. 35, Fig. 5.	1907	<i>Placodus hypsiceps</i> , Jaekel, caption for Pl. 4.
1863	<i>Placodus angustus</i> , H.v. Meyer, p. 180.	1907	<i>Placodus pachygnathus</i> , Jaekel, caption for Pl. 4.
1863	<i>Placodus bathygnathus</i> , H.v. Meyer, p. 180.	1907	<i>Placodus quinimolaris</i> , Jaekel, caption for Pl. 4.
1863	<i>Placodus bombidens</i> , H.v. Meyer, p. 180.	1911	<i>Placodus gigas</i> , F.v. Huene, p. 46, Fig. 52.
1863	<i>Placodus gigas</i> , H.v. Meyer, pp. 184–194, Pl. 25, Fig. 1, Pl. 26, Figs. 1, 2, Pl. 27, Figs. 1–3, Pl. 28, Figs. 1, 2, Pl. 29, Figs. 1–3.	1912	<i>Placodus gigas</i> , Broili, p. 147ff., figure on p. 151, Pl. 14.
1863	<i>Placodus hypsiceps</i> , H.v. Meyer, pp. 199–203, Pl. 29, Fig. 4.	1915	<i>Anemosaurus strunzi</i> , Drevermann, p. 403.
1863	<i>Placodus pachygnathus</i> , H.v. Meyer, p. 180.	1922	<i>Placodus gigas</i> , Drevermann, p. 98.
1863	<i>Placodus quinimolaris</i> , H.v. Meyer, pp. 203–205, Pl. 25, Figs. 2–4.	1928	<i>Placodus gigas</i> , Edinger, p. 311ff., Figs. A–C, Pl. 24.
1863	<i>Placodus rugosus</i> , H.v. Meyer, p. 180.	1928	<i>Placodus gigas</i> , Schmidt, p. 409f., Fig. 1149.
1887–	<i>Placodus andriani</i> , Zittel, p. 570.	1928	<i>Placodus andriani</i> , Schmidt, p. 410.
1890		1928	<i>Placodus hypsiceps</i> , Schmidt, p. 410.
1887–	<i>Placodus gigas</i> , Zittel, p. 570, Figs. 516, 517.	1928	<i>Placodus andriani</i> , Corroy, p. 124f.
1890		1928	<i>Placodus gigas</i> , Corroy, p. 124f.
1887–	<i>Placodus hypsiceps</i> , Zittel, p. 570, Fig. 515.	1931	<i>Placodus gigas</i> , Drevermann, p. 150.
1890		1933	<i>Placodus gigas</i> , Drevermann, p. 319ff., Pls. 1–16.
1887–	<i>Placodus quinimolaris</i> , Zittel, p. 570.	1933	<i>Placodus gigas</i> , F.v. Huene, p. 365ff., Figs. 1–5.
1890		1935	<i>Placodus gigas</i> , Peyer, p. 7ff.
1890	<i>Placodus andriani</i> , Lydekker, p. 5.	1936	<i>Placodus antiquior</i> , F.v. Huene, pp. 133–134, Figs. 24–25.
1890	<i>Placodus bathygnathus</i> , Lydekker, pp. 2–3.	1937	<i>Placodus gigas</i> , Gross, p. 6.
1890	<i>Placodus bombidens</i> , Lydekker, p. 5.	1938	<i>Placodus antiquior</i> , Schmidt, p. 62, Fig. 1149a.
1890	<i>Placodus gigas</i> , Lydekker, p. 2.	1940	<i>Placodus strunzi</i> , Romer & Price, p. 427.
1890	<i>Placodus hypsiceps</i> , Lydekker, pp. 2–3.	1943	<i>Placodus gigas</i> , F.v. Huene, p. 252, Fig. 1.
1890	<i>Placodus quinimolaris</i> , Lydekker, p. 4.	1946	<i>Placodus gigas</i> , Gregory, Fig. 32.
1896	<i>Placodus gigas</i> , Fraas, p. 14.	1947	<i>Placodus andriani</i> , Vialli, p. 111ff.
1902	<i>Anemosaurus</i> , F.v. Huene, p. 33, Pl. 4, Figs. 3, 4, Pl. 6, Fig. 4, Pl. 7, Fig. 6.	1947	<i>Placodus gigas</i> , Vialli, p. 111ff.
1903–	<i>Placodus andriani</i> , Frech, p. 17a, Pl. 14.	1949	<i>Placodus gigas</i> , F.v. Huene, p. 76ff., Figs. 1, 2, 3a.
1908		1951	<i>Placodus gigas</i> , Gregory, Figs. 13.18, 13.20.B.
1903–	<i>Placodus hypsiceps</i> , Frech, p. 17a, Pl. 14.	1955	<i>Placodus andriani</i> , Peyer & Kuhn-Schnyder, p. 472.
1908		1955	<i>Placodus antiquior</i> , Peyer & Kuhn-Schnyder, p. 472.
1905	<i>Anemosaurus strunzi</i> , F.v. Huene, p. 331, Figs. 1–13, Pls. 5–7.	1955	<i>Placodus gigas</i> , Peyer & Kuhn-Schnyder, pp. 460, 472, Figs. 1–6, 24.
1907	<i>Anemosaurus strunzi</i> , Case, pp. 33–34, 156.	1955	<i>Placodus hypsiceps</i> , Peyer & Kuhn-Schnyder, p. 472.
1907	<i>Placodus andriani</i> , Jaekel, caption for Pl. 4.		
1907	<i>Placodus aethiopi</i> , Jaekel, caption for Pl. 4.		
1907	<i>Placodus angustus</i> , Jaekel, caption for Pl. 4.		
1907	<i>Placodus bathygnathus</i> , Jaekel, caption for Pl. 4.		

- 1955 *Placodus quinimolaris*, Peyer & Kuhn-Schnyder, p. 472.
- 1956 *Placodus gigas*, F.v. Huene, p. 367, Figs. 410–413.
- 1967 *Placodus gigas*, Haas, p. 332.
- 1967 *Placodus gigas*, Westphal & Westphal, p. 249ff., Figs. 1–3.
- 1968 *Placodus gigas*, Peyer, p. 151, Fig. 94.
- 1968 *Placodus quinquemolaris*, Peyer, p. 151.
- 1974 *Placodus gigas*, Kuhn-Schnyder, p. 9, Fig. 8.
- 1974 *Placodus gigas*, Wild, p. 22, Fig. 6.
- 1975 *Placodus gigas*, Paton, p. 19.
- 1978 *Placodus gigas*, Wild, Fig. 7 (left).
- 1979 *Placodus andriani*, Kruckow, p. 65ff., Fig. 4.
- 1979 *Placodus antiquior*, Kruckow, p. 65.
- 1979 *Placodus gigas*, Kruckow, pp. 65–66.
- 1979 *Placodus hypsiceps*, Kruckow, p. 65.
- 1987 *Placodus gigas*, Sues, p. 138ff., Figs. 1–2.
- 1988 *Placodus gigas*, Westphal, p. 151ff., Figs. 1–9.
- 1989 *Placodus andriani*, Mazin, p. 726.
- 1989 *Placodus gigas*, Mazin, p. 726.
- 1989 *Placodus quinimolaris*, Marzin, p. 726.
- 1989 *Placodus gigas*, Pinna, p. 150ff., Figs. 1–3.
- 1989 *Placodus aethiops*, Nosotti & Pinna, p. 82, Fig. 23.4–5.
- 1989 *Placodus andriani*, Nosotti & Pinna, p. 33, Figs. 3, 5, 13, 21, Pl. 7.
- 1989 *Placodus angustus*, Nosotti & Pinna, p. 82, Fig. 23.6.
- 1989 *Placodus bathygnathus*, Nosotti & Pinna, p. 47, Fig. 10, Pl. 3.
- 1989 *Placodus bombidens*, Nosotti & Pinna, p. 47, Pl. 4.
- 1989 *Placodus gigas*, Nosotti & Pinna, p. 37, Figs. 16.1, 17–19, 20.1–3, 23, Pl. 5.2, 9, 10.
- 1989 *Placodus hypsiceps*, Nosotti & Pinna, p. 54, Fig. 15, Pl. 8.1.
- 1989 *Placodus pachygnathus*, Nosotti & Pinna, p. 47, Fig. 9.6–7, Pl. 43.2.
- 1989 *Placodus quinimolaris*, Nosotti & Pinna, p. 55, Fig. 16.2–4, Pl. 8.3.
- 1990 *Placodus andriani*, Pinna, p. 149, Fig. 1.
- 1990 *Placodus antiquior*, Pinna, p. 149, Fig. 1.
- 1990 *Placodus gigas*, Pinna, p. 149, Fig. 1.

**HOLOTYPE**—In 1830, Münster published a paper titled “Über einige ausgezeichnete fossile Fischzähne aus dem Muschelkalk bei Bayreuth.” Twenty-five copies of the brochure (four pages, one plate) were printed but never sold through the

book trade (Freyberg, 1972, p. 8). A skull of *Placodus* (collected in 1824: Weiss, 1983; “specimen I” of Münster, 1830) was figured in ventral view, but no name was given. The brochure was later referenced by Bronn (1831), who published Agassiz’s comments on the figured specimens. Again, no name was given. In the first volume of his “Poissons Fossiles” (1833–1845; p. 51), Agassiz commented on the brochure published by Münster, indicating that it figured the teeth of “*Placodus gigas* Agass.” This reference was entered in a revised version of the text, published in 1844, together with a note cancelling previous parts of the text (Brown, 1890). In the introduction to the first volume, Agassiz (1833–1845: p. xxxviii) listed as Triassic fishes *Placodus gigas* (no author) from the Muschelkalk of Lainéck near Bamberg, and Lunéville, and *Placodus andriani* Münster from the Muschelkalk of Bamberg (the latter two specimens come from the Oschenberg near Lainéck, not from Bamberg: Weiss, 1983, p. 28, and footnote 2, p. 25), as well as *Placodus münsteri*, *P. rostratus*, and *P. impressus* (see below). This list of Triassic fishes was originally published separately in 1840 and inserted into the first volume as part of a new introductory chapter in 1844 (Brown, 1890). In the first part to the second volume of “Poissons Fossiles,” published in 1833 (Brown, 1890; see also Owen, 1858, p. 169), Agassiz (1833, p. 15) defined the genus *Placodus* (“*Dents polygones, à angles arrondis, dont la surface est aplatie et entièrement lissée*”) and listed two species, *Placodus impressus* (a nomen dubium; see below) and *Placodus gigas*. The diagnosis of *Placodus gigas* (“*Dents à surfaces planes*”) is preceded by a reference to Münster’s (1830) brochure. Münster’s (1830) “specimen I” was figured by Agassiz (1833–1845) on Plate 70 (Figs. 14–21) published in April 1839 (Brown, 1890; Jeannet, 1928), and described in part 2 of volume 2 (17th delivery, published in 1843 according to Jeannet, 1928; the year of publication is 1844 according to Brown, 1890). Münster’s (1830) “specimen I” (Fig. 1) is therefore the holotype of *Placodus gigas* (Nosotti & Pinna, 1989). It is kept at the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich (bsp AS VII 1208).

**HORIZON AND LOCALITY**—Muschelkalk (from the lowermost lower Muschelkalk [Gogolin beds, Gogolin, upper Silesia] through the upper Muschelkalk [*spinulosus* biozone]), lower Anisian through lower Ladinian, Middle Triassic, central Europe (Hagdorn, 1993).



A



B

FIG. 1. Holotype of *Placodus gigas* Ag (BSP AS VII 1208; original of Münster, 1830, "specimen I"). Upper Muschelkalk, Bayreuth. A, Ventral view; B, dorsal view. Scale bar = 20 mm.

Diagnostic remains of *Placodus gigas* are restricted to the lower and upper Muschelkalk of the German Triassic. No material for *Placodus* has been reported from the middle Muschelkalk. Isolated placodont teeth have been reported from the Anisian and Ladinian of the Alpine Triassic (Furrer et al., 1992), but their specific identity remains unknown. Broili (1920) reviewed various isolated teeth from the uppermost Triassic or Rhaetic of the Austrian and Bavarian Alps and concluded that they belong to the genus *Cyamodus*. The same is true for isolated placodont teeth from the Rhaetic of the Swiss Alps (Furrer et al., 1992).

**DIAGNOSIS**—Same as for genus, of which this is the only known species.

**COMMENTS**—A single species has been described from the lower Muschelkalk, *Placodus antiquior* Huene, 1936. A total of six species have been described from the upper Muschelkalk, i.e., *Placodus andriani* Agassiz, 1833–1845, *Placodus bathygynathus* Owen, 1858, *Placodus bombidens* Owen, 1858, *Placodus hypsiceps* Meyer, 1863, *Placodus pachygynathus* Owen, 1858, and *Placodus quinimolaris* Braun, 1863. *Placodus aethiops*, *Placodus angustius*, and *Placodus rugosus* are "species" that were never described formally, but were men-

tioned in passing by Meyer (1863); the names were taken from labels written in Münster's handwriting and associated with isolated teeth that are not diagnostic at the species level. The genotypical species is *Placodus gigas* Agassiz, 1833.

Plate 70 of Agassiz (1833–1845), published in April 1839, figures the skull and isolated teeth of *Placodus andriani* (Pl. 70, Figs. 8–13; the specimen was collected in 1836: Weiss, 1983). The description of *Placodus andriani* followed in part 2 of volume 2 (17th delivery, published in 1843). Following the international rules of nomenclature, a species name is valid if published (before 1930) in a printed and generally available scientific publication as a binomen relating to a figure, as is the case for *Placodus andriani* on Plate 70 of Agassiz (1833–1845). Reference of *Placodus andriani* to Münster (1839, p. 119; see Kuhn, 1933) is erroneous. The holotype of *Placodus andriani* (Agassiz, 1833–1845, Plate 70, Fig. 8) is kept in the collections of the Oberfränkisches Erdgeschichtliches Museum, Bayreuth (BT, uncatalogued), and is an incomplete skull that is rather poorly preserved and prepared (Fig. 2). The length of the skull from the anterior margin of the rostrum (as preserved) to the posterior margin of the mandib-



FIG. 2. Holotype of *Placodus andriani* Ag (BR, uncatalogued; original of Agassiz, 1833–1845, Pl. 70, Fig. 8). Upper Muschelkalk, Bayreuth. A, Ventral view; B, dorsal view. Scale bar = 20 mm.

ular condyle of the quadrate is 163 mm on the right side and 172 mm on the left side. The only difference between this skull and the holotype of *Placodus gigas* is its slightly smaller size, recognized as ontogenetic variation by Braun (1862). The analysis of the size of the third (posteriormost) palatine tooth in a total of 50 articulated palatal dentitions indicates no significant size difference of *Placodus andriani* in comparison to other specimens referable to *Placodus* from the lower and upper Muschelkalk (Fig. 3). The holotype of *Placodus andriani* is not diagnostic. Braun (1862) suggested synonymizing *Placodus gigas* and *Placodus andriani* and keeping the latter species name, a procedure that would violate the rules of nomenclature.

*Placodus bathygnathus* (Owen, 1858, Pl. 11, Figs. 1–3; BMNH R-19677, now catalogued as *Placodus gigas*) was distinguished from *Placodus gigas* by

the absence of the lateral ledge of the dentary outside of the tooth row and by the relative length of the mandibular symphysis (Fig. 4). The species is based on a fragmentary left mandibular ramus with the two posteriormost tooth plates and the coronoid process present. The total length of the fragment is 134.5 mm and its maximal height is 85.5 mm. Meyer (1863) considered the species of questionable validity. As discussed by Lydekker (1890), the absence of the lateral ledge on the dentary is due to preparation; coarse preparation also resulted in perforation of the coronoid process. The relative length of the lower jaw symphysis is subject to ontogenetic variation, as discussed in more detail below. The holotype of *Placodus bathygnathus* is not diagnostic.

*Placodus bombidens* (Owen, 1858, Pl. 9, Figs. 3–6; BMNH R-1643) is based on a fragmentary left lower jaw (Fig. 5) that was suspected by Owen

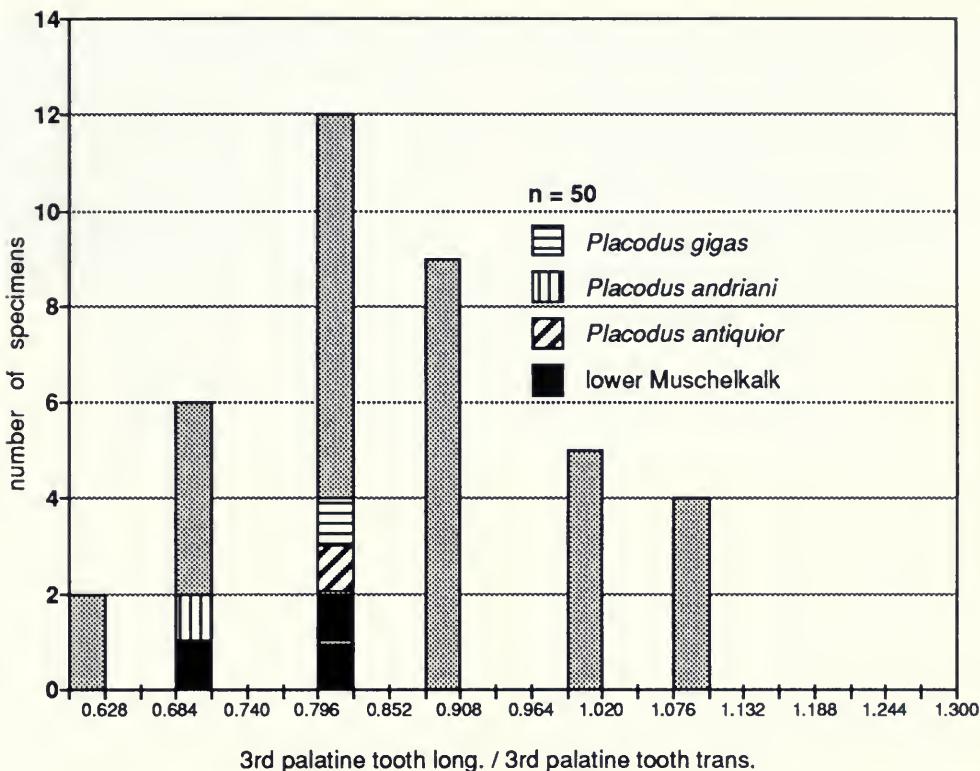


FIG. 3. Proportions of the third (posterior) palatine tooth plate in 50 articulated *Placodus* palatal dentitions.

himself (1858, p. 180) to be conspecific with *Placodus andriani*. The specimen shows little more than the three tooth plates, with a replacement tooth for the anteriormost tooth plate. The total length of the fragment is 135 mm. The specimen is not diagnostic of a separate species.

*Placodus pachygnathus* (Owen, 1858, Pl. 10, Figs. 6, 7; BMNH R-1641) consists of a very fragmentary lower jaw preserving parts of both rami (Fig. 6). The total length of the fragment is 123.5 mm. The specimen is not diagnostic of a separate species and was considered of questionable validity by

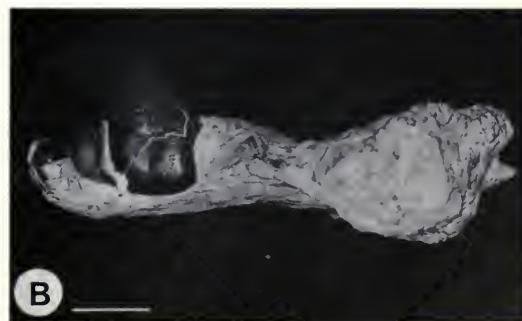


FIG. 4. Holotype of *Placodus bathygnathus* Owen (BMNH R-19677; original of Owen, 1858, Pl. 11, Figs. 1-3). Upper Muschelkalk, Bayreuth. A, Left lateral view; B, occlusal view. Scale bar = 20 mm.

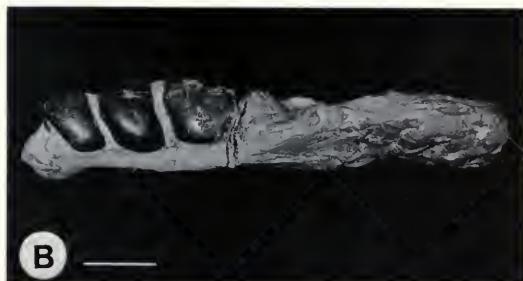
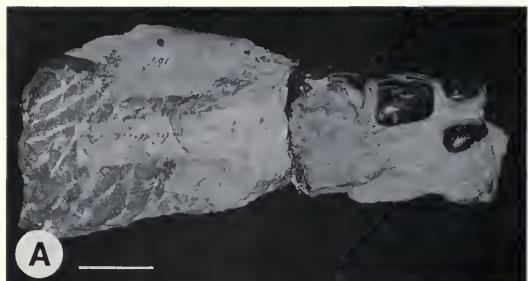


FIG. 5. Holotype of *Placodus bombidens* Owen (BMNH R-1643; original of Owen, 1858, Pl. 9, Figs. 3–6). Upper Muschelkalk, Bayreuth. A, Medial view; B, occlusal view. Scale bar = 20 mm.

Meyer (1863, p. 177). Lydekker (1890) synonymized *Placodus pachygnathus* with *Placodus gigas*.

*Placodus hypsiceps* was described as a valid species by Meyer (1863; erroneously referred to as *P. hypsicephalus* [nomen nudum] by Braun, 1863, p. 10; first described as a skull of *Placodus gigas* by Braun, 1862, p. 10), but considered a possible junior synonym of *Placodus gigas* by Lydekker (1890). The specimen is kept at the Oberfränkisches Erdgeschichtliches Museum, Bayreuth (BT, uncatalogued), and consists of the left half of a longitudinally split skull (Fig. 7). The specimen shows some morphological detail, which allows the identification of some derived characters shared with *Placodus gigas*. These include the anterior extent of the jugal, the anterior ascending process

of the maxilla, which defines most of the anteroventral margin of the external naris, and the exclusion of the frontal from the dorsal margin of the orbit by a contact of prefrontal with postfrontal. Traces of a suture between the nasals (if not due to breakage) may be indicative of subadult age, as are the relatively small palatal teeth. However, no suture between quadratojugal and squamosal can be identified in the posterior cheek region, indicating (early?) fusion of the two elements (see discussion below). The aberrant proportions considered diagnostic by Meyer (1863) are due to deformation of the skull during fossilization.

*Placodus quinimolaris* (Braun, 1863; Meyer, 1863, Pl. 25, Figs. 2–4) is kept at the Oberfränkisches Erdgeschichtliches Museum, Bayreuth (BT, uncatalogued), and consists of a very incomplete

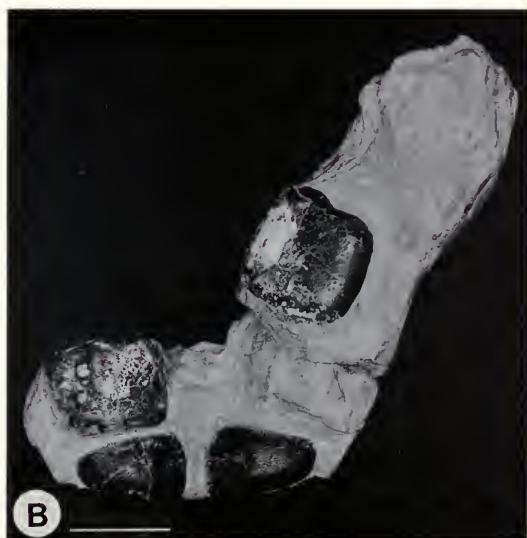


FIG. 6. Holotype of *Placodus pachygnathus* Owen (BMNH R-1641; original of Owen, 1858, Pl. 10, Figs. 6, 7). Upper Muschelkalk, Bayreuth. A, Left lateral view; B, occlusal view. Scale bar = 20 mm.



FIG. 7. Holotype of *Placodus hypsiceps* Meyer (BT, uncatalogued; original of Meyer, 1863, Pl. 24, Figs. 1–3; Pl. 29, Fig. 4). Upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

skull, comprising little more than the two palatines and maxillae and fragments of the right jugal (Fig. 8). Most skulls referable to *Placodus gigas* have four maxillary teeth, whereas *Placodus quinimolaris* has five. The species is listed as valid by Lydekker (1890). Jaekel (1907, Pl. 4) figured a

skull of *Placodus gigas* (kept at the Staatliches Museum für Mineralogie und Geologie Dresden, BA Tr 43) with five teeth on the right maxilla and four teeth on the left; and on that basis he synonymized *Placodus quinimolaris* with *Placodus gigas*. In the Dresden skull, the five teeth on the right maxilla



FIG. 8. Holotype of *Placodus quinimolaris* Braun (BT, uncatalogued; original of Meyer, 1863, Pl. 25, Figs. 2–4). Upper Muschelkalk, Bayreuth. Scale bar = 20 mm.



A



B

FIG. 9. *Placodus gigas* Ag (BA Tr 43; original of Jackel, 1907, Pl. 4). Upper Muschelkalk, Bayreuth. A, Skull, palatal view; B, right maxilla, occlusal view. Scale bar = 20 mm.

show an interesting size variation, in that the anteriormost tooth is significantly smaller than the posterior four teeth and situated somewhat more medially (Figs. 9, 10). This suggests that a fifth tooth has been added to the usual four maxillary teeth during late ontogeny, an argument supported by the fact that the Dresden skull is somewhat smaller than the holotype of *Placodus quinimolaris*, in which all five maxillary teeth are of more or less equal size. The first palatine tooth is 17.5 (17) mm long and 23 (23.9) mm wide in the Dresden skull, whereas that of *Placodus quinimolaris* is 20 mm long and 26 mm wide. The third palatine tooth is 24 (23.5) mm long and 32.5 (32.2) mm wide in the Dresden skull, whereas that of *Placodus quinimolaris* is 30 (32) mm long and 34 (36) mm wide. (Values in parentheses refer to the left side of the skull.) An undescribed skull of *Placodus gigas* kept at the Naturkundemuseum Erfurt (Er, coll. Wagner, #78/235) shows only three maxillary

teeth on the well-preserved right maxilla (Figs. 11, 12). The Erfurt skull is slightly smaller than the Dresden skull, its first palatine tooth being 15.5 (16) mm long and 19 (21) mm wide, the third palatine tooth being 23 (23) mm long and 27.5 (26) mm wide. However, the skull of a small individual kept at the Senckenberg Museum in Frankfurt am Main (SMF R-4038) is of similar size as the Erfurt skull, yet shows four teeth on the maxilla. Ontogeny therefore offers only a partial explanation for individual variation found in maxillary tooth counts in *Placodus*, ranging from three to five. Variation in tooth counts on the maxilla corroborates the synonymy of *Placodus quinimolaris* with *Placodus gigas*.

Whereas all material of *Placodus* from the upper Muschelkalk is referable to *Placodus gigas*, remains from the lower Muschelkalk have been referred to a separate species, *Placodus antiquior* (Huene, 1936; Peyer & Kuhn-Schnyder, 1955;

Kruckow, 1979; Pinna, 1990). The holotype of *Placodus antiquior* (Huene, 1936, Figs. 24a–c) from the Schaumkalk of Freyburg/Unstrut (upper lower Muschelkalk, Figs. 13, 14), as well as a fragmentary dentary (Huene, 1936, Figs. 25b; see also Huene, 1902, 1905) from the same locality and referred to the same species (Fig. 15), are kept at the Institut für Geologische Wissenschaften der Martin-Luther Universität, Halle (drawer M 5/1). Diagnostic characters of *Placodus antiquior* enumerated by Huene (1936, p. 134) are (as compared to *Placodus gigas*): relatively smaller size of the first palatine tooth plate; different shape of the orbit; narrow frontal bridge between the orbits; and different shape of the upper temporal fossa, which is also relatively shorter. In view of the very incomplete preservation of the skull, only two of these characters can be critically evaluated—the proportions of the first palatine tooth and the shape of the orbit. The left orbit shows a thickened anterior edge and a slightly angulated anterodorsal corner as in *Placodus gigas*, and, as in the latter species, the jugal extends anteriorly to a level in front of the anterior margin of the orbit. Again, the maxilla forms an anterior ascending process that defines the anteroventral margin of the external naris. There is no indication of the relative size and shape of the upper temporal opening, or of the relative width of the frontal bridge between the orbits. The teeth of *Placodus antiquior* (holotype and left dentary) do not differ in any significant degree from those of other remains of *Placodus* from either the lower or the upper Muschelkalk. In particular, the proportions (length/width) of the first palatine tooth in *Placodus antiquior* are very closely comparable to those of the holotype of *Placodus andriani* and *Placodus gigas* (Fig. 16). Similarly, the proportions of the tooth plates on the left dentary attributed to *Placodus antiquior* by Huene (1936) fall squarely into the range of variability of *Placodus gigas* jaws from the upper Muschelkalk (Fig. 17). *Placodus antiquior* turns out to be another junior synonym of *Placodus gigas*. Naming a different species for *Placodus* remains from the lower Muschelkalk reflects a general tendency of earlier authors to separate taxa from the lower and upper Muschelkalk for stratigraphic rather than morphological reasons. Synonymy of *Placodus antiquior* with *Placodus gigas* indicates that the taxon persisted throughout the Muschelkalk, although no *Placodus* material has yet been recorded from the middle Muschelkalk.

Two species of *Placodus* have been described

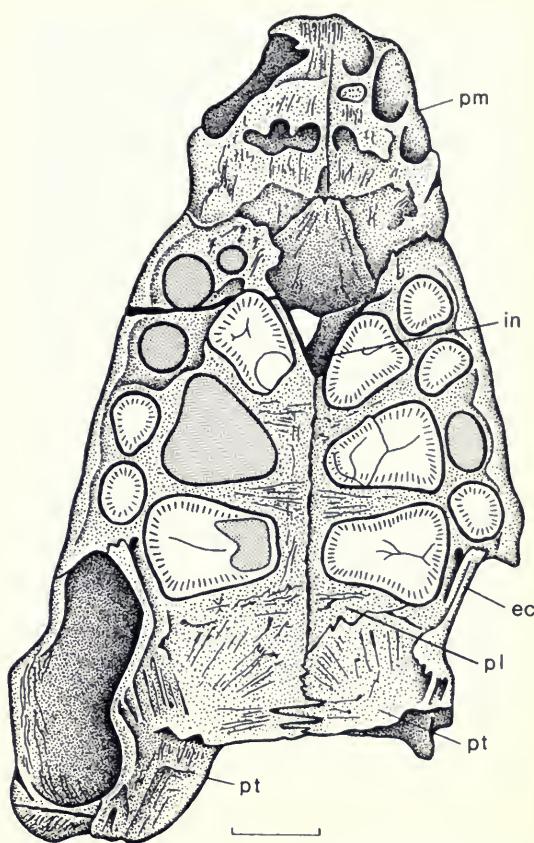


FIG. 10. *Placodus gigas* Ag (BA Tr 43; original of Jaekel, 1907, Pl. 4). Upper Muschelkalk, Bayreuth. Scale bar = 20 mm. Abbreviations: ec, ectopterygoid; in, internal naris; pl, palatine; pm, premaxilla; pt, pterygoid.

from deposits other than the Germanic Muschelkalk. If valid as a species, *Placodus impressus* would represent the geologically earliest placodont. Agassiz (1833–1845) described the species from the top of the Lower Triassic (upper Buntsandstein) of Zweibrücken (Saarland, Germany) on the basis of isolated teeth. Owen (1858, p. 171) commented: “The character on which *Placodus impressus* Agassiz is differentiated, ‘une impression ou une sorte de sillon longitudinal qui se voit au milieu de la couronne,’ is one common to the newly-formed crushing teeth of all placodonts.” Lydekker (1890, p. 5) listed *Placodus impressus* as unrepresented in the British Museum (Natural History), but these collections today include five maxillary teeth (BMNH R-1328-9, with a maximal diameter of 12–14 mm) identified as *Placodus impressus*. An old museum label refers to these teeth as *Placodus andriani*, in better accordance with their provenience from the

**A****B**

FIG. 11. *Placodus gigas* Ag (Er 78/235). Upper Muschelkalk, Bayreuth. A, Skull, palatal view; B, skull, dorsal view. Scale bar = 20 mm.

upper Muschelkalk of Bayreuth. Peyer and Kuhn-Schnyder (1955, p. 480) tentatively identified four teeth of the original material of *Placodus impressus* described by Agassiz (1833) as those of *Sargodon tomicus*, the remaining fifth tooth as a possible cyamodont. *Placodus impressus* is a nomen dubium.

In 1973, Jurcsak reported the discovery of an elongated placodont tooth ( $13 \times 5.5$  mm) from the Triassic (Anisian) of Aleșd near Oradea, which he identified as a tooth of *Paraplagodus*. In 1976, Jurcsak described a lower jaw fragment from the same locality, which he referred to the genus *Placodus*, questioning whether it represented a juvenile individual or a new but small species ("*Placodus gracilis?*," Jurcsak, 1976, p. 75), close to *Paraplagodus* (Jurcsak, 1978, p. 41). In the figure caption (Jurcsak, 1976, Figs. 13–15; see also Jurcsak, 1982, Fig. 16), the specimen is referred to as "*Placodus gracilis* n.sp." To judge from the figures, however, the specimen does not represent *Placodus* or, indeed, a placodont. The mandibular symphysis is narrow, and there are five slender anterior teeth with a narrow cylindrical base and broken tips; three anterior teeth are strongly procumbent.

*Placodus* shows an elongated symphysis and two chisel-shaped anterior teeth, separated from posterior crushing teeth by a wide diastema. An elongated symphysis, and a wide diastema separating two conical and procumbent anterior teeth from the posterior crushing teeth, are also characteristic of *Paraplagodus* (Peyer, 1935). *Placodus gracilis*, therefore, is a nomen dubium, pending a revision of the original material. However, the occurrence of placodonts (mostly Cyamodontoidae, perhaps also Placodontoidae) in the Triassic (Anisian) of Transylvania is documented by other material (Jurcsak, 1977, 1978, 1982), all of which is too fragmentary to be diagnostic at the genus or species level.

### Skeletal Morphology of *Placodus gigas*

#### Skull

The skull of *Placodus gigas* is known from a number of specimens, most of which are incom-

plete to a variable degree. The best specimen is the acid-prepared skull BT 13 from the Oberfränkisches Erdgeschichtliches Museum in Bayreuth (Figs. 18, 19), recently described by Sues (1987). It will also form the basis of this description, supplemented by the other material listed in the Appendix.

The durophagous habits of *Placodus* are reflected by the robust skull. The premaxillae form a spatulate rostrum, which is set off from the remainder of the skull by a distinct constriction of the snout at the level of the anterior margin of the external nares. The premaxillae form short posterior (nasal) processes that meet the nasal in between the two external nares (i.e., not projecting beyond the posterior margin of the external nares). The premaxillary-maxillary suture extends from the anterolateral corner of the external naris in a lateroventral direction. The dorsal surface of the premaxilla is pierced by numerous small nutritive foramina, but also by larger foramina located immediately in front of the external naris as well as further anteriorly, close to the anterior margin of the premaxilla. Shallow grooves extending from those foramina indicate the course of nerves (branches of the medial ethmoidal nerve: Sues, 1987) and blood vessels that have supplied the snout (Fig. 20).

The maxilla of *Placodus* is a massive element with a well-developed ascending process providing lateral cover for the preorbital region of the skull and defining the posterior margin of the external naris. The anterior end of the maxilla is deeply bifurcated (Fig. 19C). The lateral anterior process meets the premaxilla in an anterolaterally trending suture. The medial anterior process of the maxilla extends medial to the premaxilla along the ventral and anteroventral margin of the external naris, meeting the nasal in the anterior margin of the external naris. Posteriorly, the maxilla does not quite reach the level of the posterior margin of the orbit.

The nasals are fused along the dorsal midline of the skull (Fig. 19A). Anteriorly, the nasal forms slender processes that line the dorsal margin of the external naris, thus embracing the posterior (nasal) processes of the premaxillae. Laterally, the nasal forms relatively slender lateral processes that extend onto the lateral surface of the prefacial skull, entering between the ascending process of the maxilla and the prefrontal. Posteriorly, the nasal extends in between well-defined anterolateral processes of the frontal to about the level between the first and second third of the longitudinal diameter

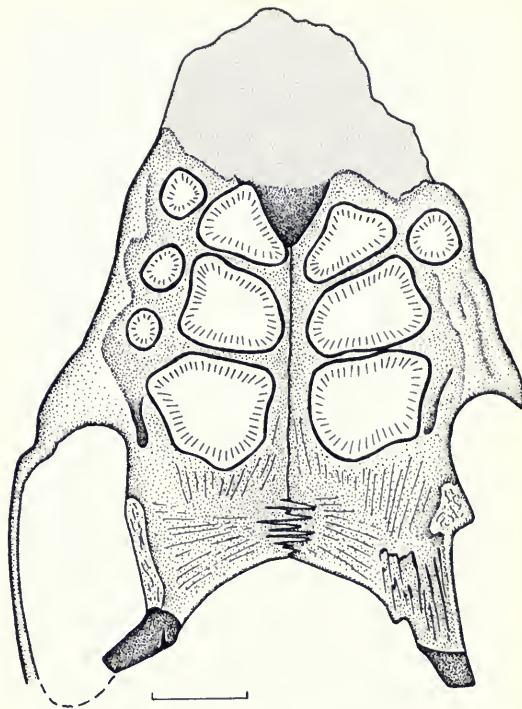


FIG. 12. *Placodus gigas* Ag (Er 78/235). Upper Muschelkalk, Bayreuth. Skull in palatal view. Scale bar = 20 mm.

of the orbit. The posterior part of the nasal is broad, and terminates in a slightly concave posterior suture with the frontal.

The frontals again are fused along the dorsal midline of the skull, a longitudinal ridge indicating the line of fusion (the frontals remain separate in the skull BSP 1925 I 16, described by Broili, 1912). The frontal is a relatively broad plate, embracing the posterior end of the nasal with relatively short anterolateral processes, whereas equally short but well-defined posterolateral processes embrace the anterior end of the parietal. In the specimen described by Broili (1912, Pl. 14, Figs. 1–4; BSP 1968 I 75), the frontal and parietal meet in a deeply interdigitating suture, and posterolateral processes of the frontal are not distinct (Fig. 21).

The prefrontal is a large element and defines the anterodorsal, anterior, and anteroventral margin of the orbit. The anterodorsal corner of the orbit is developed into a thickened ridge. Dorsally, the prefrontal meets the postfrontal in the dorsal margin of the orbit. Ventrally, the prefrontal is in extensive contact with the jugal. Medially, the prefrontal forms a relatively narrow descending process that contacts the palatine and thus defines the

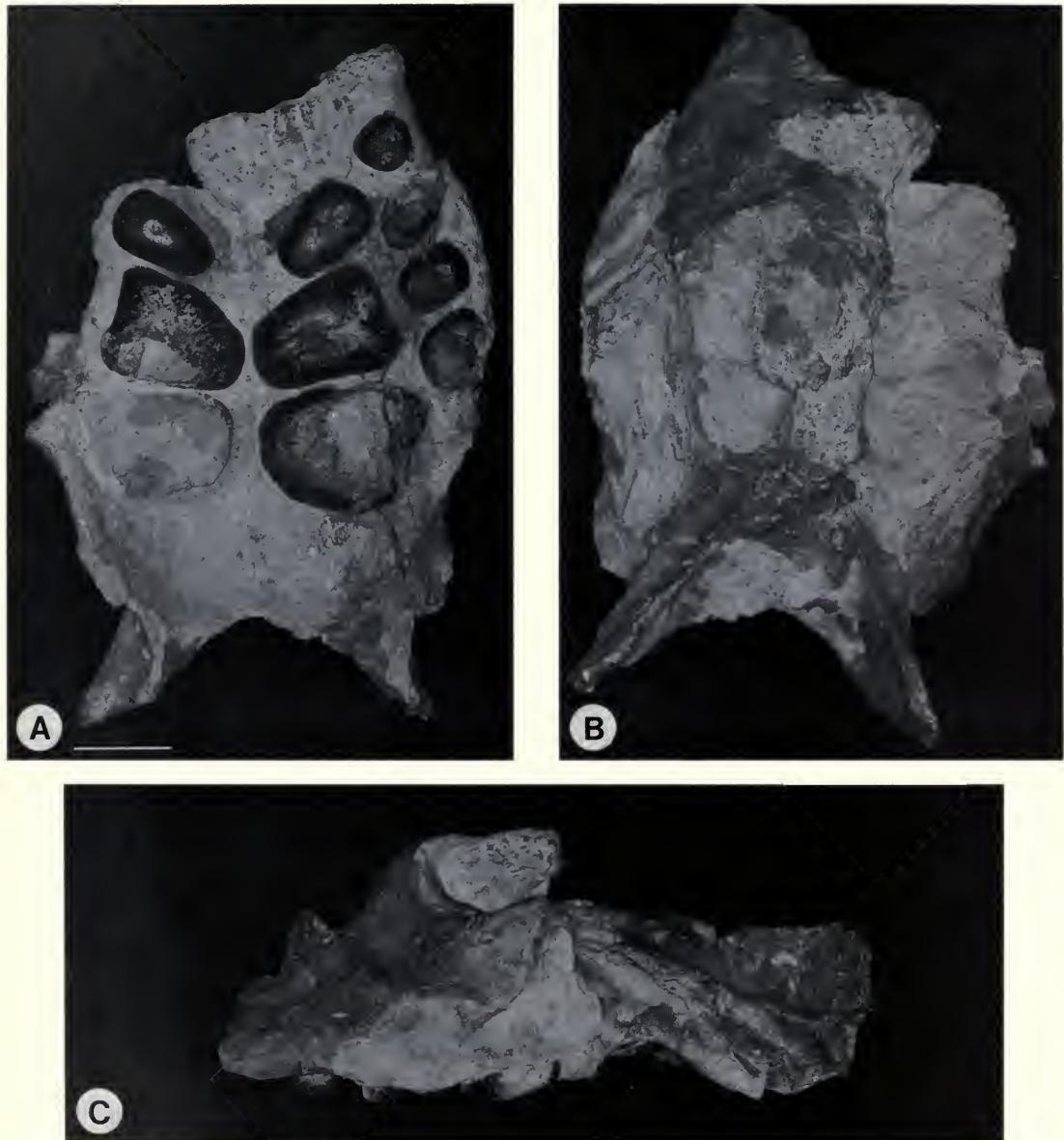


FIG. 13. Holotype of *Placodus antiquior* Huene (Ha, M5/1; original of Huene, 1936, Figs. 24a-c). Schaumkalk (upper lower Muschelkalk), Freyburg/Unstrut. A, Ventral view; B, dorsal view; C, left lateral view. Scale bar = 20 mm.

anterior wall of the orbit. This descending process of the prefrontal is pierced by the large lacrimal foramen (also seen in SMF R-4126). A lacrimal is absent in *Placodus*.

The postfrontal defines the posterodorsal margin of the orbit as well as part of the anterior margin of the upper temporal fossa. A tapering ventral process forms a broadly overlapping con-

tact with the postorbital along the caudal margin of the orbit.

The postorbital defines the posterior and posteroventral margin of the orbit. The element is broadly exposed in the dorsal part of the dermal covering of the temporal region, extending posteriorly to a level slightly behind the midpoint of the upper temporal region. In its dorsal part, the

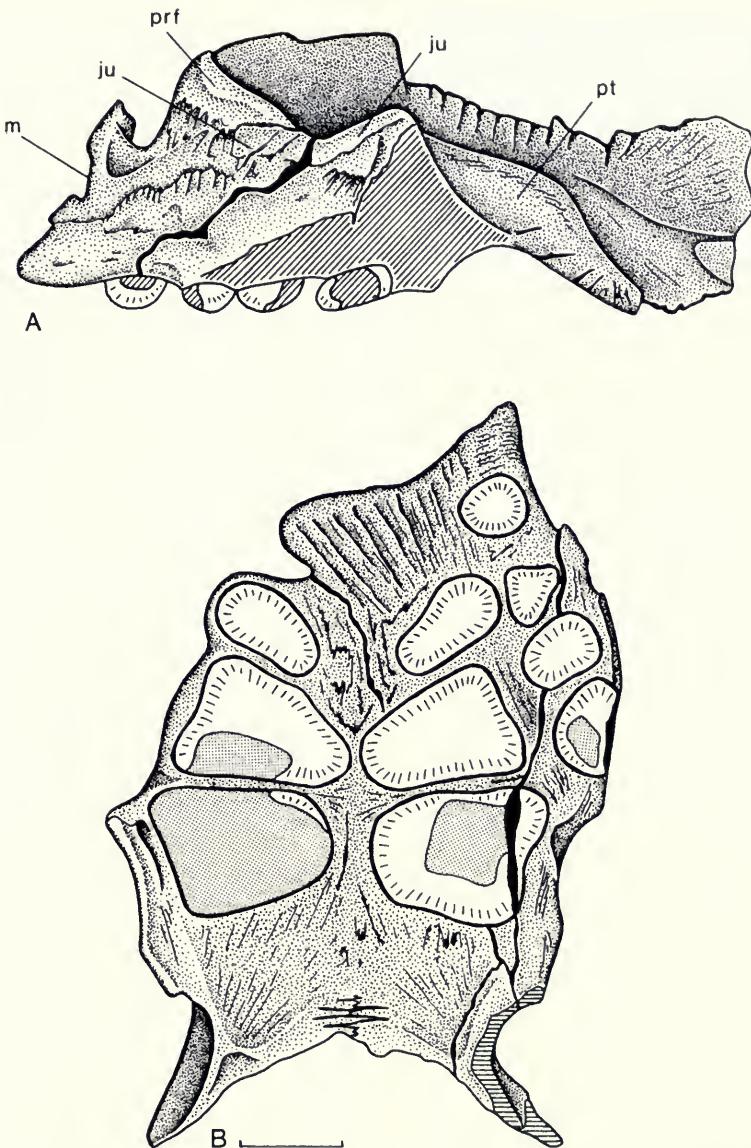


FIG. 14. Holotype of *Placodus antiquior* Huene (Ha, M5/1; original of Huene, 1936, Figs. 24a-c). Schaumkalk (upper lower Muschelkalk), Freyburg/Unstrut. A, Skull, left lateral view; B, skull, palatal view. Scale bar = 20 mm. Abbreviations: ju, jugal; m, maxilla; prf, prefrontal; pt, pterygoid.

postorbital forms a distinct spine that projects into the posterodorsal corner of the orbit. Anteroventrally, the postorbital forms a distinct step in the lower margin of the orbit. Between this step and the posterodorsal spine, the postorbital forms a shallow depression that extends backward as a shallow groove across the temporal arch in a posterodorsal direction.

The jugal is a large element that is broadly exposed in the anterior ventral part of the temporal

arch, extending posteriorly to the same level as the postorbital. Anteriorly, it narrows as it lines the dorsal margin of the maxilla and defines part of the ventral margin of the orbit. A narrow anterior process of the jugal extends between maxilla and prefrontal to a level well in front of the anterior margin of the orbit.

The interpretation of the posterior temporal region of the skull of *Placodus* remains controversial to the present day. Broili (1912) believed the qua-

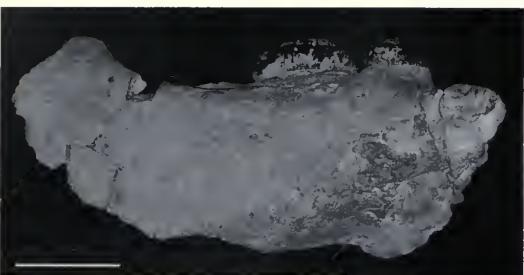


FIG. 15. Fragmentary dentary, referred to *Placodus antiquior* (Ha, M5/1; original of Huene, 1936, Fig. 25b). Scale bar = 20 mm.

dratojugal to be absent in *Placodus*, or fused to the squamosal; the squamosal would define most of the lateral, the posterior, and the posteromedial margin of the upper temporal fossa and would extend ventrally to cover the quadrate in lateral view. Huene (1911) had been unable to identify a suture line in the posterior part of the upper temporal arch that would separate the squamosal from the quadratojugal (his supratemporal and squamosal). The hatched line indicated by Huene (1911) was eventually confirmed as the suture between quadratojugal and squamosal by Sues (1987), a

claim that was disputed by Pinna (1989). Following the latter author, the squamosal would be restricted to the posterior and posteromedial margin of the upper temporal fossa, whereas the quadratojugal would be of extraordinary size and would enter the posterolateral margin of the upper temporal fossa. This interpretation of the temporal region of the skull of *Placodus* was influenced by a comparison with Nosotti and Pinna's (1993a) reconstruction of the sutural pattern in *Cyamodus*. A critical discussion of the cranial anatomy of *Cyamodus* is beyond the scope of this paper, although personal inspection of the skulls of *Cyamodus kuhnschnyderi* (Nosotti & Pinna, 1993a; SMNS 15855 and SMNS 16270) did not convince me that the quadratojugal does, indeed, broadly enter the dorsal margin of the upper temporal fossa. In SMNS 16270, both temporal arches have been largely replaced with resin; only their posterior part is preserved and encrusted with osteoderms. In SMNS 15855, the contact between postorbital and squamosal appears identifiable in the dorsal margin of the upper temporal arch, and the contours of the quadratojugal can be followed on the medial surface of the temporal arch along its ventral margin. As far as it can be identified, this sutural pattern

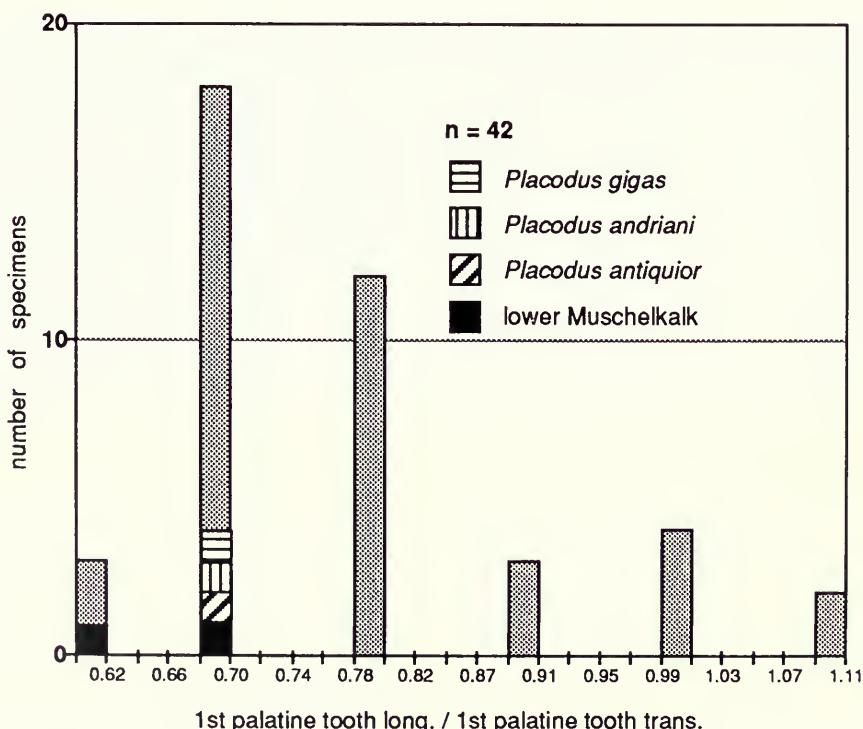


FIG. 16. Proportions of the first (anterior) palatine tooth plate in 42 articulated *Placodus* dentitions.

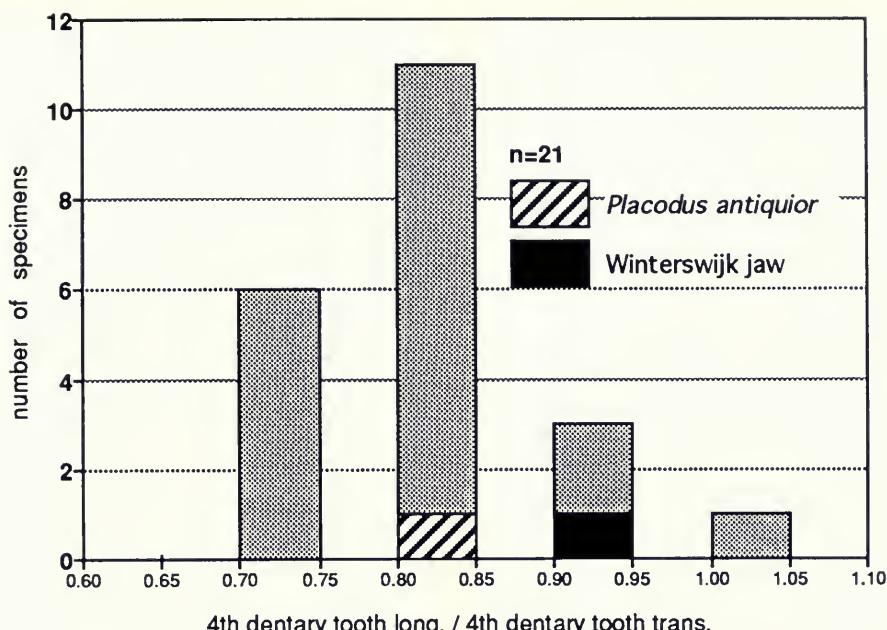


FIG. 17. Proportions of the fourth (posterior) dentary tooth plate in 21 articulated *Placodus* dentitions.

corresponds to the sutures observed in the temporal arch of *Macroplacus raeticus* (Schubert-Klempnauer, 1975), with the squamosal defining the entire posterior and most of the lateral margin of the upper temporal fossa, while the quadratojugal remains restricted to the ventral aspect of the posterior part of the temporal arch (Fig. 22). These observations contradict Nosotti and Pinna's (1993a) reconstruction of the temporal region in *Cyamodus* and renders the genus obsolete as a model for the reconstruction of temporal sutures in *Placodus*. Whereas ridges appear to indicate a squamosal-quadratojugal suture on the occiput of *Placodus*, as drawn by Sues (1987) and accepted by Pinna (1989), there is no unequivocal evidence for the lateral termination of the squamosal at the posterolateral corner of the upper temporal fossa, as reconstructed by Pinna (1989). A shallow groove seems to restrict the squamosal to that position on the left side of skull BT 13, but no such groove or suture is distinct on the right side. In addition, a fragmentary skull (SMNS 59434; Fig. 23) shows a well-preserved posterolateral margin of the upper temporal fossa, but no indication of a squamosal-quadratojugal suture as indicated by Pinna (1989).

However, I agree with Pinna (1989) that the suture line separating the squamosal from the quadratojugal as drawn by Sues (1987) is erroneous. Sues (1987) probably took the lower edge of the

shallow depression extending from the orbit across the temporal arch in a posterodorsal direction as a suture. The absence of such a suture can be established beyond doubt by microscopical inspection of the bone surface and by the use of bone surface ornamentation as a guide to the suture pattern (Fig. 24). The absence of a squamosal-quadratojugal suture as indicated by Sues (1987) is furthermore well demonstrated by the holotype of "*Placodus hypsiceps*" (Fig. 25), by the skull described by Broili (1912, BSP 1968 I 75) (Fig. 26), and by the fragmentary skull SMNS 59434. Unequivocal evidence for the presence of a quadratojugal in *Placodus* is missing. The bone may be absent or fused with the squamosal, as postulated by Broili (1912).

The parietals are fused in BT 13 (paired in BSP 1968 I 75) and form a relatively broad parietal skull table. The frontoparietal suture is somewhat obscured in BT 13 by partial fusion of the bones and by a break that traverses the skull at that level. The lateral margins of the parietal are concave, as they define the medial margin of the upper temporal fossa. Posteriorly, the parietal skull table is deeply excavated. The pineal foramen lies somewhat in front of the center of the skull table in BT 13 (in BSP 1968 I 75, the pineal foramen lies close to the deeply interdigitating frontoparietal suture; Fig. 21).

The dermal palate of *Placodus* is completely

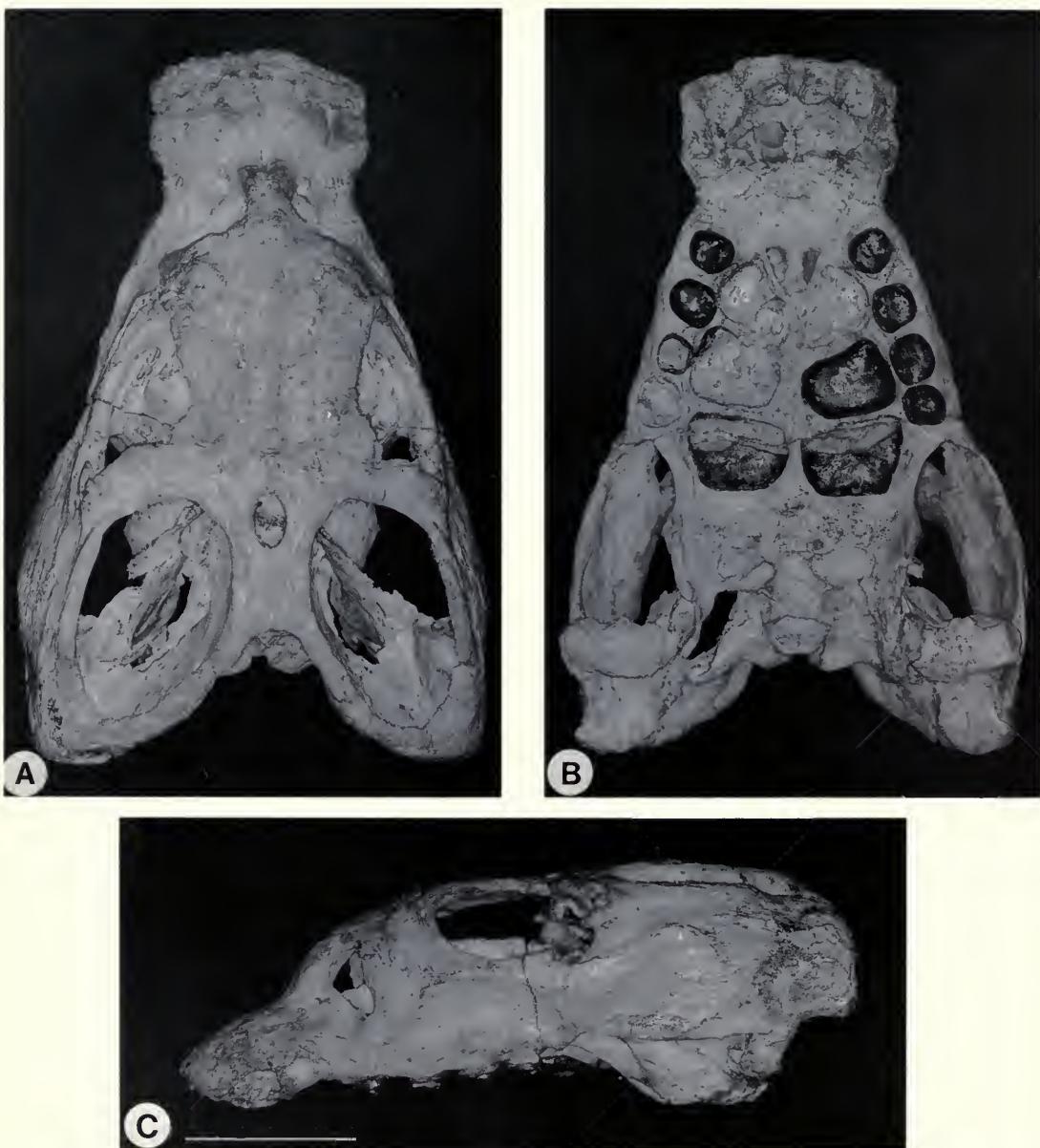


FIG. 18. *Placodus gigas* Ag (BT 13, original of Sues, 1987). Upper Muschelkalk, Bayreuth. A, Skull, dorsal view; B, skull, ventral view; C, skull, left lateral view. Scale bar = 50 mm.

closed except for the confluent internal nares (Figs. 18, 19). The internal nares are separated at a somewhat deeper level by the fused vomer, which meets the premaxillae anteriorly. The broad palatines have expanded anteriorly at a level below the original position of the internal nares, partially obscuring the latter in ventral view, thus forming the posterior and lateral margins of the single medial opening for the internal nares. Lateral to that

opening, the palatine meets the premaxilla between the vomer (medially) and the maxilla (laterally).

The palatines have also expanded posteriorly in correlation with the development of large crushing tooth plates (see below). The palatines meet in an extended ventromedial suture and restrict the pterygoids to a posterior position entirely behind the level of the anterior margin of the subtemporal

fossa. As a consequence thereof, the pterygoids remain widely separated from the maxilla. The anteromedial margin of the subtemporal fossa is formed by the narrow ectopterygoid, which posteriorly extends into the anterior part of the pterygoid flange. The pterygoids meet in an interdigitating ventromedial suture (their posterior edges are incomplete in BT 13). Posteriorly, the pterygoid extends into a deep quadrate ramus that forms a prominent pterygoid flange oriented more or less longitudinally and serves as the area of origin for the large pterygoideus musculature.

The occipital view of the skull shows a broad occipital exposure of the parietal and squamosal. Ridges indicate a supposed suture between squamosal and quadratojugal as indicated by Sues (1987) and Pinna (1989) (see discussion above). The parietal meets the supraoccipital in an extended suture enclosing a small foramen at the anterolateral corners of the supraoccipital (a vascular foramen according to Sues, 1987). The occiput of *Placodus* is deeply concave, and shows slender yet distinct paroccipital processes formed by the exoccipital and opisthotic (Fig. 27). Small posttemporal fossae are bordered ventrally by the paroccipital processes, dorsally by the parietal and squamosal. The distal tips of the paroccipital processes terminate freely and seem to have been capped by cartilage (intercalary cartilage, an epihyal derivative [Bellairs & Kamal, 1981]) in life, connecting the paroccipital process to the dorsal part of the quadrate close to the junction of quadrate, squamosal, and pterygoid. The deep quadrate ramus of the pterygoid establishes an interdigitating sutural contact with the posteromedial aspect of the quadrate along the latter's entire height.

The splanchnocranum is represented by the ossified epipterygoid and quadrate. The latter bone is deeply concave posteriorly, in dorsal contact with the squamosal and in anteromedial contact with the pterygoid. It is covered in lateral view by the squamosal (see the discussion of the quadratojugal above). The mandibular condyle is broad transversely and subdivided to fit the saddle-shaped articular facet of the lower jaw.

The epipterygoid of *Placodus* is a distinct element with a broad base, sutured to the dorsolateral aspect of the pterygoid and reaching the posteriorly expanded palatine with its anterior portion. The anteromedial margin of the epipterygoid is lined by an ascending process, which Broili (1912) interpreted as part of the palatine but which more probably is part of the pterygoid. The dorsal part of the epipterygoid is narrower than its base, and

contacts the prootic and/or the descending flange of the parietal (the two elements are difficult to distinguish in this region in BT 13). The cavum epipterum opens anteriorly through a gap located between the clinoid process of the basisphenoid medially and the pterygoid process lining the anteromedial edge of the epipterygoid laterally.

The basicranium of *Placodus* deserves special discussion, because morphological relations have changed significantly due to the posterior expansion of the palatines. As can be seen in an occipital view of the skull (Fig. 27), the basioccipital condyle is formed by the basioccipital only; the exoccipitals do not meet on the dorsal surface of the occipital condyle. The occipital condyle is pierced by a distinct notochordal pit. The exoccipital is pierced by one large foramen for the passage of the hypoglossal nerve into the jugular foramen (SMF R-359 and R-4038). A well-defined jugular foramen (metotic foramen) is located between the exoccipital and the opisthotic. Ventrally, the opisthotic appears fused with large tubers extending ventrolaterally from the basicranium in front of and below the occipital condyle (Fig. 28). These tubers have been described as basipterygoid processes by Sues (1987), but they are a composite structure, formed by the basioccipital posteriorly and the basisphenoid anteriorly, and are better termed palatobasal tubers (Broili, 1912; Zanon, 1989; Nosotti & Pinna, 1993b). The basioccipital-basisphenoid suture can be identified on the anterolateral aspect of these palatobasal tubers (Fig. 27A; see also Nosotti & Pinna, 1993b), extending dorsally into the anteroventral corner of the fenestra ovalis. Accordingly, the basioccipital broadly participates in the formation of the ventral margin of the fenestra ovalis.

The palatobasal tubers articulate with the posterior and medial aspects of the diverging quadrate rami of the pterygoids. In posterior view, the basisphenoid is exposed between the palatobasal tubers and above the pterygoids (Fig. 28B; see also Nosotti & Pinna, 1993b). The cranoquadrate passage extends between the pterygoid and the dorsolateral aspect of the palatobasal tubers into the posteroventral part of the cavum epipterum deep to the epipterygoid. Before entering the cranoquadrate passage, the internal carotid must have given rise to the stapedial (temporal) artery, which entered the temporal region through a distinct slit-like gap between the quadrate ramus of the pterygoid laterally and the otic capsule, as well as the descending flange of the parietal medially (Fig. 19A). The otic capsule is composed of the prootic

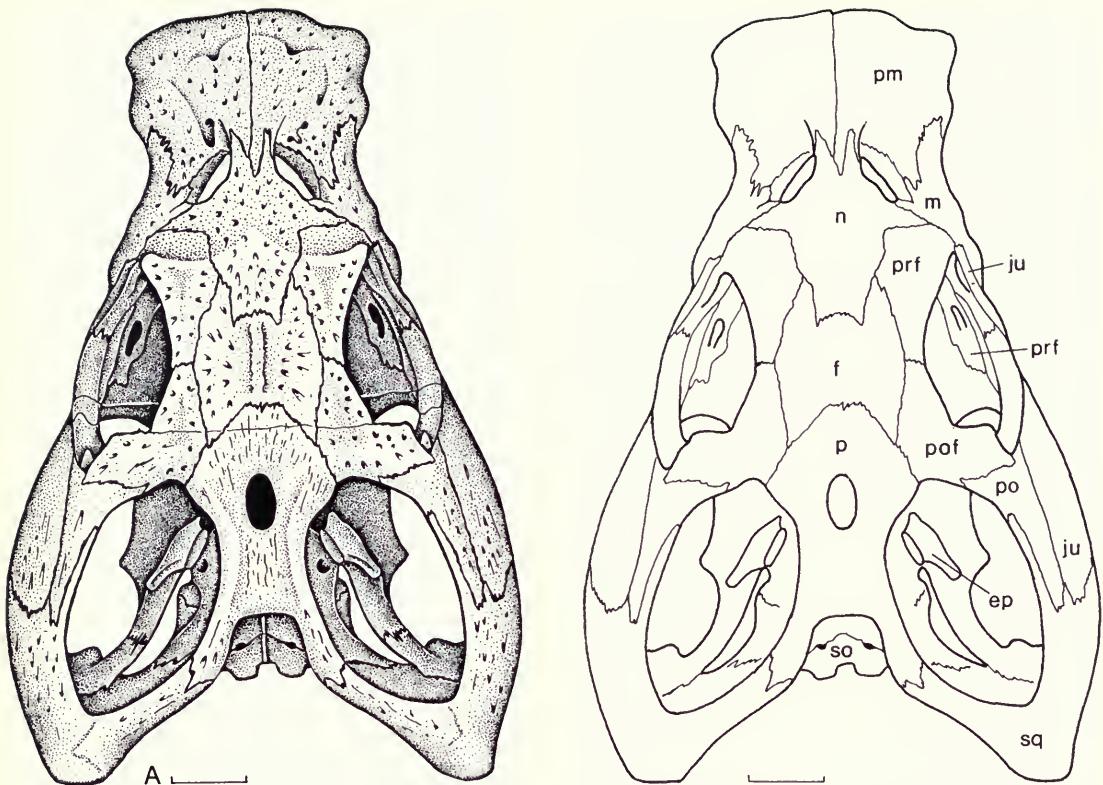


FIG. 19. *Placodus gigas* Ag (BT 13, original of Sues, 1987). Upper Muschelkalk, Bayreuth. A, Skull, dorsal view; B, skull, palatal view; C, skull, left lateral view. Scale bar = 20 mm. Abbreviations: bo, basioccipital; bs, basisphenoid; ep, epipterygoid; f, frontal; ju, jugal; m, maxilla; n, nasal; op, opisthotic; pm, premaxilla; p, parietal; pl, palatine; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; v, vomer.

anteriorly and the opisthotic posteriorly. Its medial wall remains unossified. Details of the course of the *facialis* nerve are difficult to identify in the skull BT 13. SMF R-4038 (original of Edinger, 1928) shows a rather large opening in the lateral wall of the otic capsule, the irregular shape of which suggests an original subdivision of the foramen by a horizontal bony bridge now lost. If that interpretation is correct (and it corresponds to Edinger's, 1928, reconstruction of the roots of the *facialis* nerve), then the dorsal part of the opening would correspond to the vestibular fenestra and the ventral portion would serve as the exit of the *facialis* nerve through a foramen located immediately anteroventral to the vestibular fenestra. The trigeminal nerve preserved its classic relations to the epipterygoid (Goodrich, 1930), the Gasserian ganglion being housed in a deep prootic incisure situated in front of the prootic and epipterygoid and limited dorsally by the "alisphenoid bridge" (Broili, 1912).

The "alisphenoid bridge" is an autapomorphic character of *Placodus*; its precise derivation remains obscure at this time. It appears to be an ossification of the primary braincase, forming a transverse bony bridge in front of the prootics and underlying the tractus olfactorii. An alternative interpretation would be to compare the bony bridge to an ossified subiculum infundibuli (Bellairs & Kamal, 1981), but the space between it and the dermal skull roof appears to be too narrow to accommodate the cerebral hemispheres.

#### Lower Jaw

The lower jaw of *Placodus* is characterized by a much elongated symphysis accommodating the roots and replacement teeth for the strongly procumbent incisors. The dentaries always contribute to the mandibular symphysis with a deeply interdigitating suture. The degree to which they do so

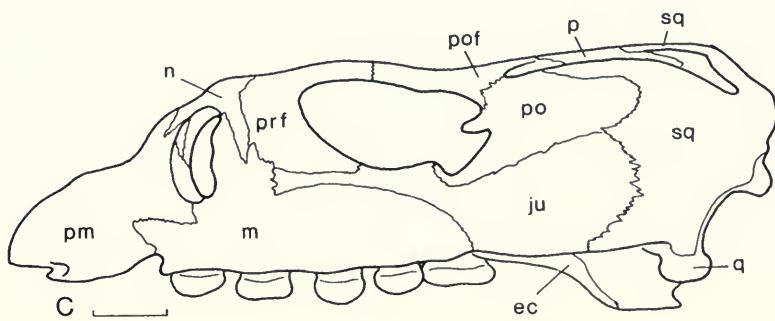
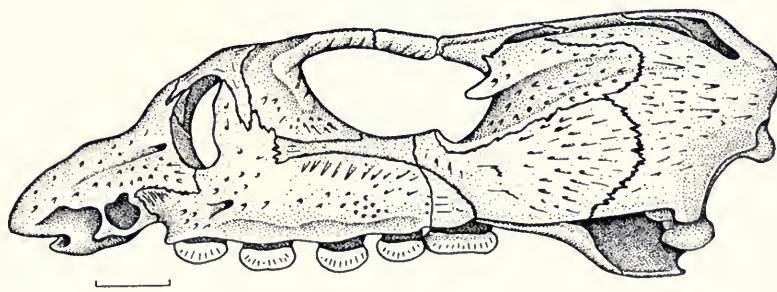
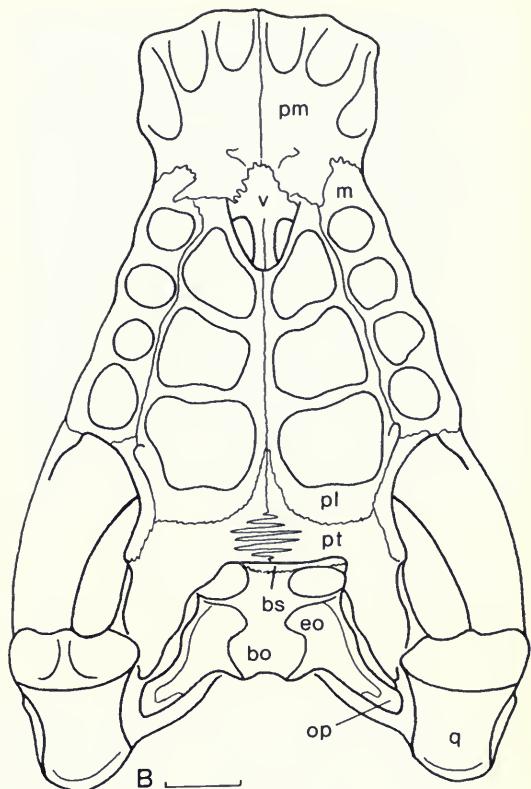
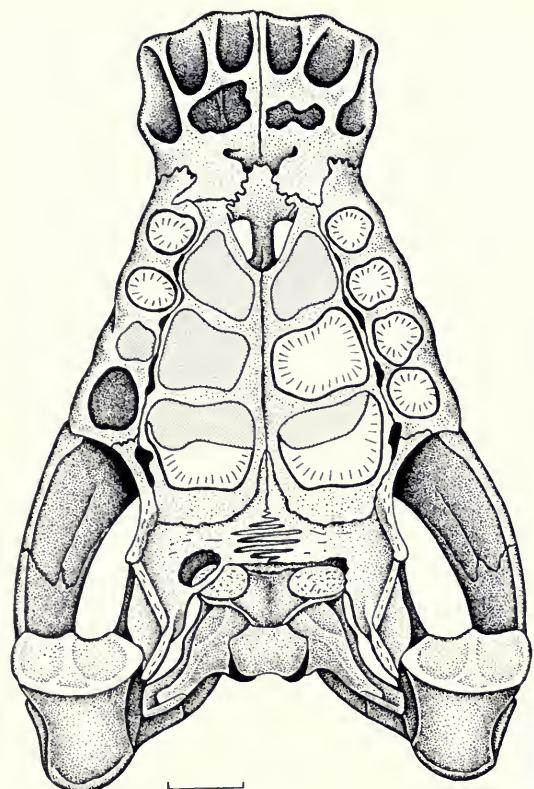




FIG. 20. *Placodus gigas* Ag (BT 13, original of Sues, 1987), premaxillary rostrum in dorsal view. Upper Muschelkalk, Bayreuth. Scale bar = 10 mm.

is variable, however. In SMF R-1035 and SMF R-4112 (Fig. 29A), the dentaries remain separate from one another in their anterior part (i.e., between the alveoli for the incisors), whereas in other jaws (such as SMF R-4110 [Fig. 29B] and BSP AS VII 1208) the dentaries are in contact with each other up to the anterior margin of the mandibular symphysis. The degree to which the anterior parts of the dentaries fuse may be subject to late ontogenetic variation because the posterior crushing teeth are somewhat larger in SMF R-4110 (with fully fused dentaries), as opposed to SMF R-4112 (see discussion of dentition below). Behind the symphysis and lateral to the posterior crushing teeth, the dentary develops a broad lateral shelf for the insertion of the superficial jaw adductor muscle fibers. Posteriorly, the dentary extends into a large ascending process that covers most of the lateral surface of the high coronoid process.

The broad splenial closes Meckel's canal medially, gaining a ventral and, anteriorly, a narrow ventrolateral exposure on the lower jaw. Anteri-

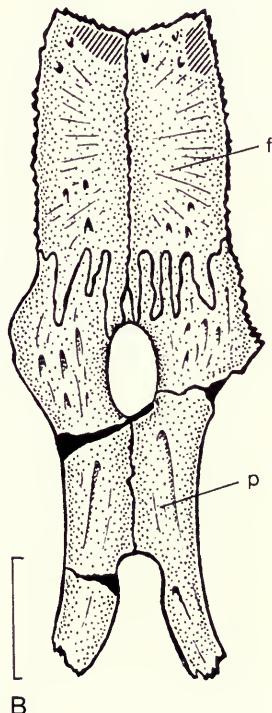


FIG. 21. *Placodus gigas* Ag (BSP 1968 I 75; original of Broili, 1912, Pl. 14, Figs. 1-4). Upper Muschelkalk, Hegnabrunn near Kulmbach. A, Skull, dorsal view; B, frontal and parietal bones, dorsal view. Scale bar = 20 mm. Abbreviations: f, frontal; p, parietal.

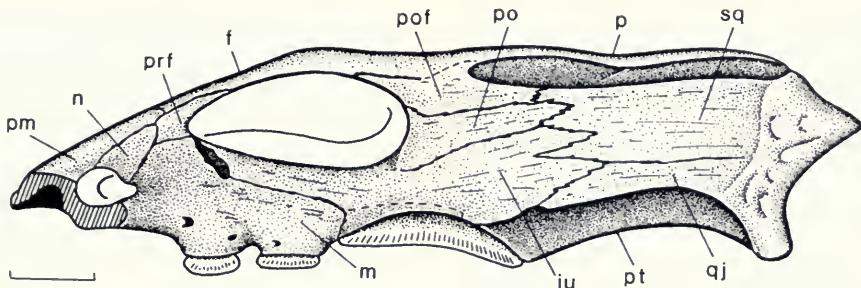


FIG. 22. *Macroplacus raeticus* Schubert-Klempnauer (holotype, BSP 1967 I 324; original of Schubert and Klempnauer, 1975, Pls. 4, 5). Rhaetic (upper Triassic), Hinterstein near Hindelang, Bavarian Alps. Scale bar = 20 mm. Abbreviations: f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; qj, quadratojugal; sq, squamosal.

orly, the splenials of the two mandibular rami meet in an interdigitating medioventral suture behind the dentaries, thus contributing to the anteroposterior elongation of the mandibular symphysis. Posteriorly, the splenial meets the prearticular and angular in a suture enclosing a large mylohyoid foramen.

The coronoid process of *Placodus* is very high, but incompletely preserved in most specimens except for that described by Drevermann (1933), the original of which is on permanent exhibit and hence inaccessible for detailed investigation. The dentary forms a large posterodorsal process that covers most of the lateral surface of the coronoid process, meeting the surangular posteriorly (Fig. 30). The coronoid bone has a very limited lateral exposure on the coronoid process (Huene, 1936, 1943). The element is largely restricted to the anteromedial aspect of the coronoid process, defining

the anterior margin of the deep adductor fossa. This is a derived (autapomorphic) character of *Placodus*, contrasting with the broad lateral exposure of the coronoid in *Paraplatodus* and in cyamodontids (Drevermann, 1928) (Fig. 31). The adductor fossa in the lower jaw of *Placodus* is wide and deep, allowing an anterior expansion of the jaw adductor musculature into Meckel's canal (m. intramandibularis: see Rieppel, 1990, for a discussion). A fragmentary jaw (SMF R-365) shows a vertically oriented bony ridge projecting from the dorsal surface of the angular into the floor of the adductor fossa; it must have intersected the intramandibular muscle, thereby providing an improved area for fiber insertion.

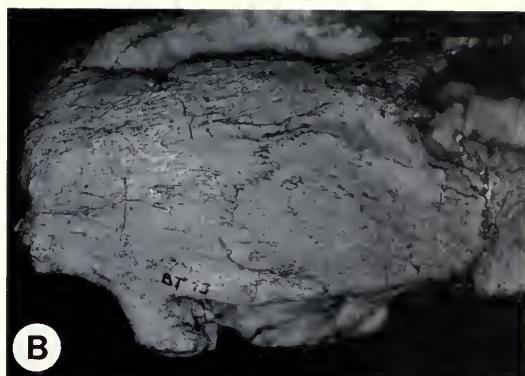
The surangular covers the posterolateral aspect of the coronoid process, from where it extends in an anteroventral direction between the dentary and the angular. The angular is a broad, cup-shaped



FIG. 23. *Placodus gigas* Ag (SMNS 59434), incomplete skull, right lateral view. Upper Muschelkalk, Bayreuth. Scale bar = 20 mm.



A



B

FIG. 24. *Placodus gigas* Ag (BT 13, original of Sues, 1987). Upper Muschelkalk, Bayreuth. A, Posterior (temporal) region of skull in left lateral view; B, posterior (temporal) region of skull in right lateral view. Scale bar = 20 mm.

element that wraps around the posteroventral part of the lower jaw. The retroarticular process is well developed and covered by the large articular-prearticular medially and dorsally. The prearticular meets the angular in a suture that runs along the laterodorsal edge of the retroarticular process.

#### Dentition

*Placodus* is characterized by strongly procumbent, chisel-shaped anterior teeth, separated by a diastema from the posterior crushing teeth. The

premaxillae of *Placodus* each bear three incisors (Braun, 1836). The maxillae bear four rounded crushing teeth in most specimens, with variation ranging from three to five ("*Placodus quinimolaris*"). The palatines are expanded posteriorly and bear three large tooth plates each, which increase in size from front to back.

Each dentary bears two strongly procumbent incisors opposing the premaxillary incisors. Three large tooth plates are typically situated on the broad posterior part of the dentary, separated from the incisors by a distinct diastema. The posteriormost tooth plate is the largest, and is positioned im-

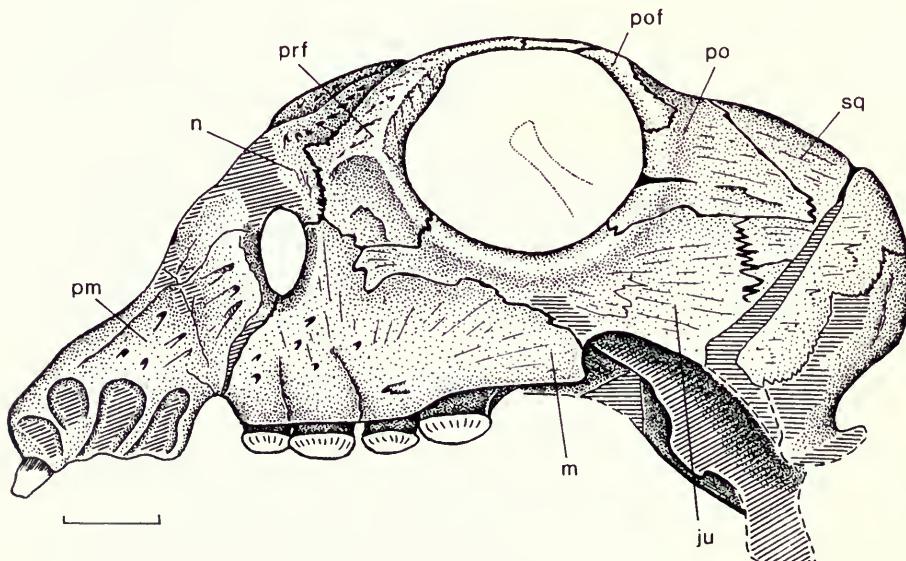


FIG. 25. Holotype of *Placodus hypsiceps* Meyer (BT, uncatalogued; original of Meyer, 1863, Pl. 24, Figs. 1–3; Pl. 29, Fig. 4). Upper Muschelkalk, Bayreuth. Scale bar = 20 mm. Abbreviations: ju, jugal; m, maxilla; n, nasal; premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; sq, squamosal.

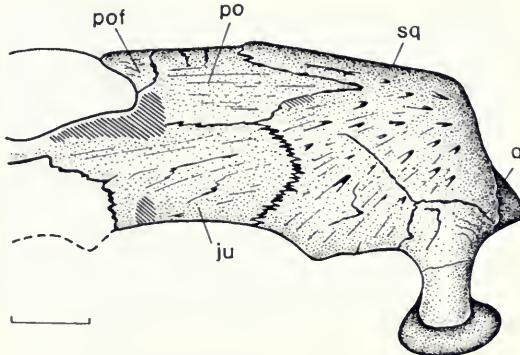


FIG. 26. *Placodus gigas* Ag (BSP 1968 I 75; original of Broili, 1912, Pl. 14, Figs. 1–4). Upper Muschelkalk, Hegnabrunn near Kulmbach. Posterior (temporal) region of skull in left lateral view. Scale bar = 20 mm. Abbreviations: ju, jugal; po, postorbital; pof, postfrontal; q, quadrate; sq, squamosal.

mediately in front of the coronoid process, where the load arm relative to the force arm is shortest. The crushing tooth plates on the dentary are typically much larger than the maxillary teeth, and occlude against the medial part of the latter as well as the lateral aspect of the palatine tooth plates.

Variation of maxillary tooth counts was discussed in the systematic section above, with respect to the questionable validity of *Placodus quinimolaris*. Variation of tooth counts can also be seen in the posterior dentition of the lower jaw, with three large tooth plates being the norm. In a number of individuals, a distinctly smaller and rounded (fourth) crushing tooth is positioned immediately in front of the (three) large dentary tooth plates. Such is the case in a fragmentary dentary from the lower Muschelkalk of Winterswijk (Oosterink, 1978; Fig. 1 in this paper), as well as in several specimens from the upper Muschelkalk (BSP 1968 I 76, SMF R-363, SMF R-1035, SMF R-4110, SMNS 58021, SMNS 17572). Late ontogenetic addition of a fourth tooth to the posterior dentary tooth row is suggested by a comparison of SMF R-4112 and SMF R-4110 (Fig. 32). The first specimen (SMF R-4112) is smaller than the second (transverse diameter of fourth dentary tooth plate: 27.5 [25] mm), the anterior parts of the dentaries remain separate, and only three tooth plates are located on the dentary. SMF R-4110 is somewhat larger (transverse diameter of fourth dentary tooth plate: 31.5 [33.2] mm), the anterior parts of the dentary have completely fused, and a fourth element has been added to the posterior dentary tooth row on the left lower jaw ramus. It should be noted, however, that of a total of 24 articulated dentary

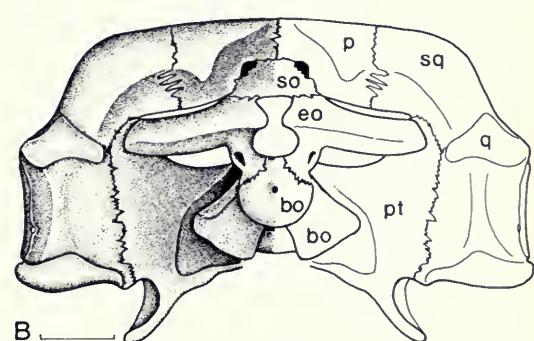
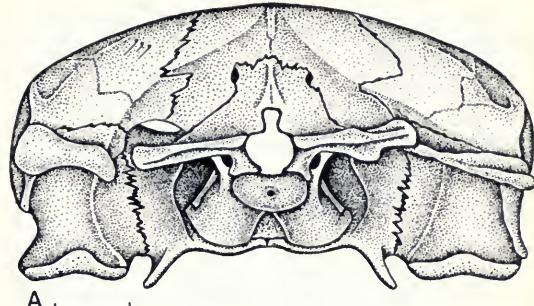


FIG. 27. *Placodus gigas* Ag, occipital view of skull. A, BT 13 (original of Sues, 1987), upper Muschelkalk, Bayreuth; B, BSP 1968 I 75 (original of Broili, 1912, Pl. 14, Figs. 1–4), upper Muschelkalk, Hegnabrunn near Kulmbach. Scale bar = 20 mm. Abbreviations: bo, basisoccipital; eo, exoccipital; p, parietal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal.

dentitions, the seven specimens that show four posterior dentary teeth span the entire size range (Fig. 33). They include the smallest specimen of all, the right dentary from the lowermost Muschelkalk of Winterswijk (Fig. 34). Conversely, the two largest available jaws bear only three dentary tooth plates. As is the case with maxillary teeth (see discussion above), ontogeny offers only a partial explanation of the variation of tooth counts in the posterior dentary tooth row.

Tooth replacement in *Placodus* was shown by Broili (1912) to be by vertical succession. This is documented by many specimens, including sections, for the maxillary, palatine, and posterior dentary teeth. In the maxillary, palatine, and posterior dentary bones, the replacement teeth develop directly above, or below, the functional tooth. Transverse sections through the palatines, as well as parasagittal sections through the maxilla and/or dentary, show replacement teeth at different stages of maturation. The limited material available indicates that at least the large tooth plates

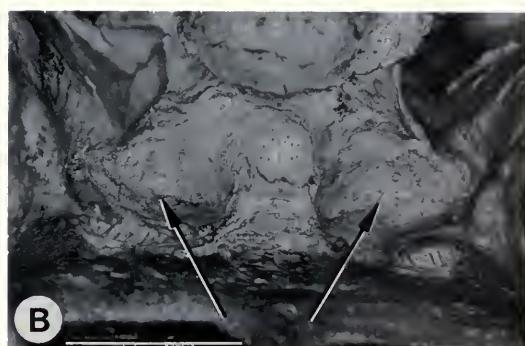
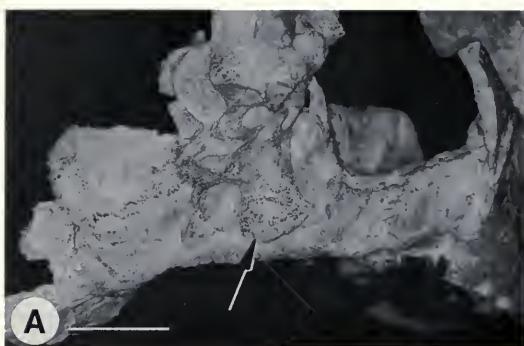


FIG. 28. *Placodus gigas* Ag., basioccipital tubers. A, Right posterolateral view (SMF R-4038; original of Edinger, 1928, Pl. 24, Fig. 1), upper Muschelkalk, Bayreuth; B, posterior view (BT 13; original of Sues, 1987), upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

on the palatines and dentaries are replaced one by one, maintaining the dentition in a continuously functional condition.

The anterior chisel-shaped incisors show horizontal tooth replacement, which, due to the strongly procumbent position of the functional teeth, mimics vertical replacement. Replacement teeth for the premaxillary (BMNH R-41096, Fig. 35A; SMNS 18641) and anterior dentary teeth (BSP AS VII 1209, Fig. 35B) develop in a position posterior (medial morphologically) to the functional tooth, within a replacement pit that will eventually migrate anteriorly (morphologically laterally) in completion of the replacement cycle.

In his description of the skull BT 13, Sues (1987)

described a slitlike infraorbital fenestra (Fig. 36A). In fact, this specimen shows similar openings all along the maxillary-palatine suture, each positioned lateral to a palatine tooth plate. The posterior foramen (the infraorbital fenestra of Sues, 1987), located lateral to the posterior palatine tooth plate, is also well developed in a fragmentary skull (SMNS 18641), which shows that the opening has no connection to the floor of the orbit. In the holotype of *Placodus gigas* (BSP AS VII 1208), the replacement for the left posterior palatine tooth plate can be seen through the foramen (Fig. 36B). I therefore concur with G. Pinna (pers. comm.) that the foramina located lateral to the palatine tooth plates (including the infraorbital fenestra of

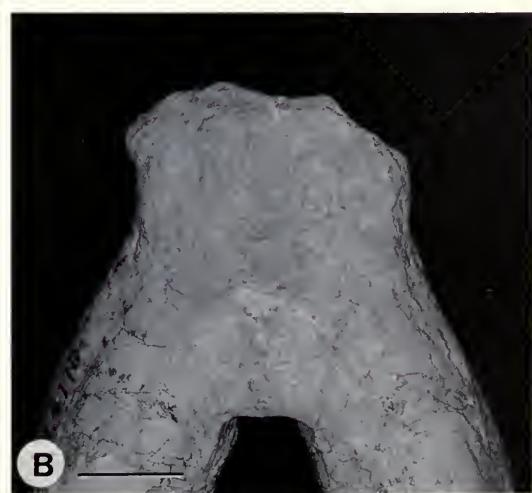
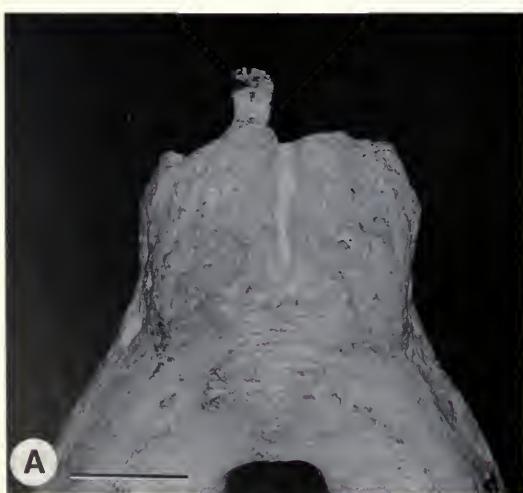


FIG. 29. *Placodus gigas* Ag., mandibular symphysis, ventral view. A, SMF R-4112 (original of Huene, 1936, Fig. 23a), upper Muschelkalk, Bayreuth; B, SMF R-4110 (original of Huene, 1936, Fig. 23a), upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

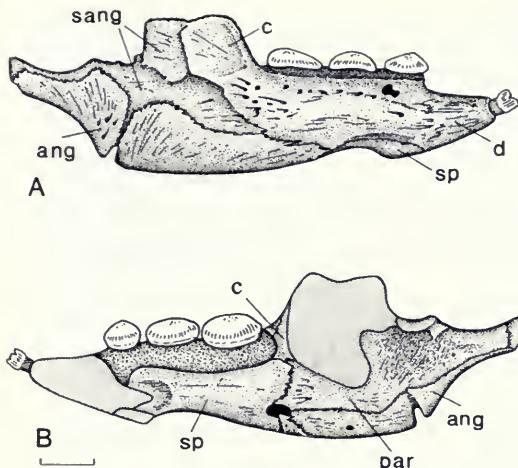


FIG. 30. *Placodus gigas* Ag., right lower jaw ramus (SMF R-4112). Upper Muschelkalk, Bayreuth. A, Right lateral view; B, medial view (partially reconstructed). Scale bar = 20 mm. Abbreviations: ang, angular; c, coronoid; d, dentary; par, prearticular; sang, surangular; sp, splenial.

Sues, 1987) are, in fact, dental lamina openings relating to the development of replacement teeth for the palatal and maxillary dentition.

### Postcranial Skeleton

The postcranial skeleton of *Placodus* has been described in a beautifully illustrated monograph by Drevermann (1933; published posthumously). The functional anatomy of the skeleton of *Placodus* has been dealt with by Vogt (1983). The following description will be based mainly on Drevermann's (1933) specimen unless otherwise noted.

The vertebral column of *Placodus* comprises 8 cervicals, 20 dorsals, 3 sacrals, and 40–50 caudals. The vertebrae are characterized by a deeply amphicoelous and notochordal centrum (Fig. 37). The neural canal is high and almost rectangular in cross section. The pedicles of the neural arch sit on narrow ridges, which define the neural canal on the dorsal surface of the centrum. The neurocentral suture remains visible throughout the vertebral column, but the neural arch rarely separates from the centrum during fossilization. The transverse processes are slender and elongate throughout the dorsal region. Intervertebral articulations are strengthened by the development of hypophene and hypantrum (Figs. 37, 38). These are weakly developed in the cervical region, but distinct

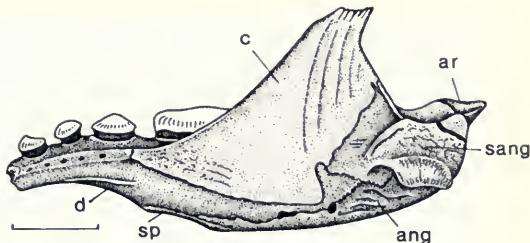


FIG. 31. *Cyamodus* sp., lower jaw (SMF R-4040; original of Drevermann, 1928, Pl. 23, Figs. 3a-d); upper Muschelkalk, Bayreuth. Scale bar = 20 mm. Abbreviations: ang, angular; ar, articular; c, coronoid; d, dentary; sang, surangular; sp, splenial.

throughout the dorsal region and absent in the caudal region. The hypophene is a posterior projection on the neural arch, situated just above the neural canal but below the postzygapophyses; it articulates with the hypantrum, a groove located below the prezygapophyses of the succeeding vertebra. The hypophene-hypantrum articulation differs fundamentally in its topological relations from the zygosphenes-zyganostrum articulation of other sauropterygians (eosaurophterygians: Rieppel, 1994a). The zygosphenes is an anterior projection of the neural arch located above the prezygapophyses. It articulates with the zygantrum on the posterior surface of the preceding vertebra, again dorsal to the postzygapophyses.

The centra of the cervical vertebrae are keeled ventrally. If present, the rudimentary hypophene and hypantrum do not engage in intervertebral articulation. The articular surfaces of the pre- and postzygapophyses show a tendency toward increased inclination along an anteroposterior gradient. In the third cervical vertebra, the articular surface of the prezygapophysis is inclined by approximately 20° from the horizontal (facing dorsomedially), in the seventh element, the inclination has increased to approximately 35° from the horizontal. The first cervical rib is associated with the axis. The cervical ribs are dichotomous and carry a free anterior process in addition to tuberculum and capitulum. The diapophysis is formed by the base of the neural arch facing ventrolaterally, and develops into a distinct free-ending transverse process in the last cervical. The parapophysis, facing laterally, develops into a distinct projection close to the anterior margin of the centrum in the posterior cervical vertebrae.

Hypophene and hypantrum are prominently developed and engage in intervertebral articulation in the first dorsal. The diapophysis expands

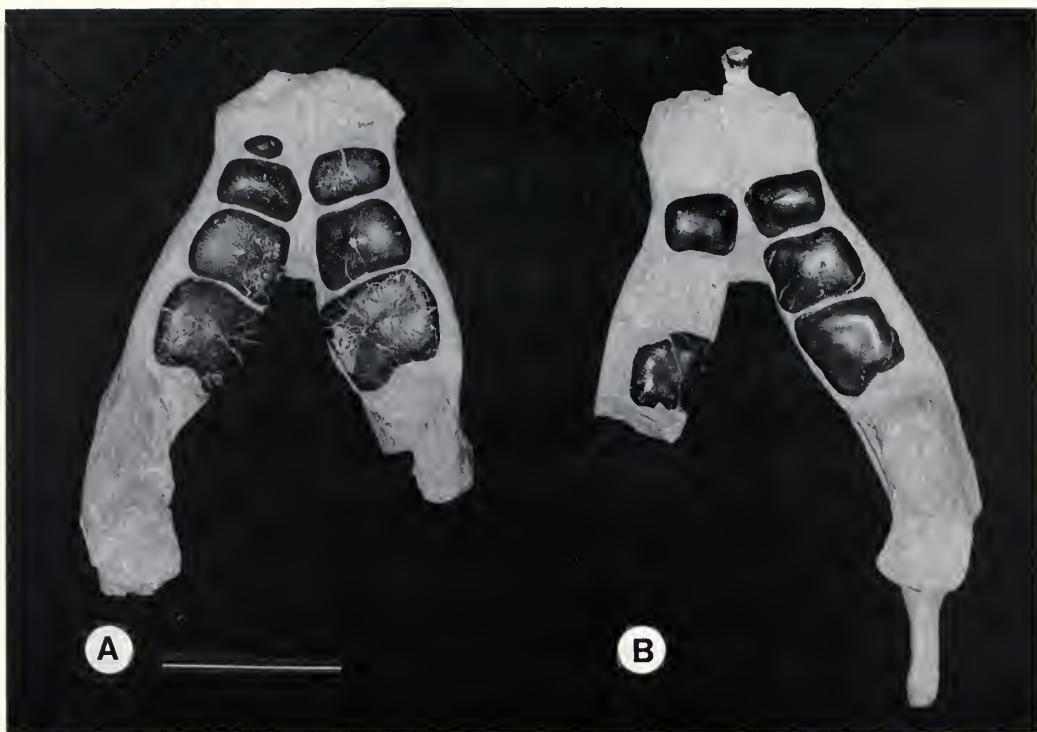


FIG. 32. *Placodus gigas* Ag., lower jaw, occlusal view. A, SMF R-4110 (original of Huene, 1936, Fig. 23a), upper Muschelkalk, Bayreuth; B, SMF R-4112 (original of Huene, 1936, Fig. 23a), upper Muschelkalk, Bayreuth. Scale bar = 50 mm.

into elongated transverse processes in the anterior dorsal region, whereas all traces of the parapophysis are lost on the second dorsal element. The dorsal ribs are holocephalous. The trend toward increased inclination of the articular surface of pre- and postzygapophysis continues into the posterior dorsal region, where it becomes reversed. In the eighth dorsal vertebra, the articular surface of the prezygapophysis is inclined by approximately 45° from the horizontal (facing dorsomedially), in the 13th element, the inclination has increased to approximately 55° from the horizontal, but in the 15th dorsal, the inclination has decreased to approximately 30° from the horizontal. In the 18th dorsal vertebra, the inclination of the articular surfaces has decreased to approximately 15° from the horizontal, whereas in the sacral vertebrae, the inclination of the articular surfaces of pre- and postzygapophyses is approximately 10–15° from the horizontal.

The sacrum of *Placodus* comprises three vertebrae, but Drevermann's (1933, Pl. 9, Figs. 49a–c) specimen shows an interesting partial sacraliza-

zation of the last dorsal ("lumbar") vertebra. Gradual reduction in the length of transverse processes starts with the 16th dorsal element. The last dorsal vertebra retains a short transverse process on the left side but shows a deep and only weakly projecting articular facet on its right side. Expansion of the articular facet across the neurocentral suture onto the centrum is characteristic of sacral vertebrae. The sacral ribs are not fused to the sacral vertebrae, and are characterized by distinct proximal and distal expansions. The distal expansion is least expressed in the first sacral rib, and most distinct in the third sacral rib.

The proximal caudal vertebrae show an increased inclination of the articular surfaces of the pre- and postzygapophyses again, approximately 35° from the horizontal in the first element and approximately 55° from the horizontal in the third element. Caudal ribs are not fused to their respective centrum and may have extended to the 10th or 12th element; the ribs of the first caudal vertebra trend in an anterior direction (toward the ilium) and show a distal expansion, as do the sacral

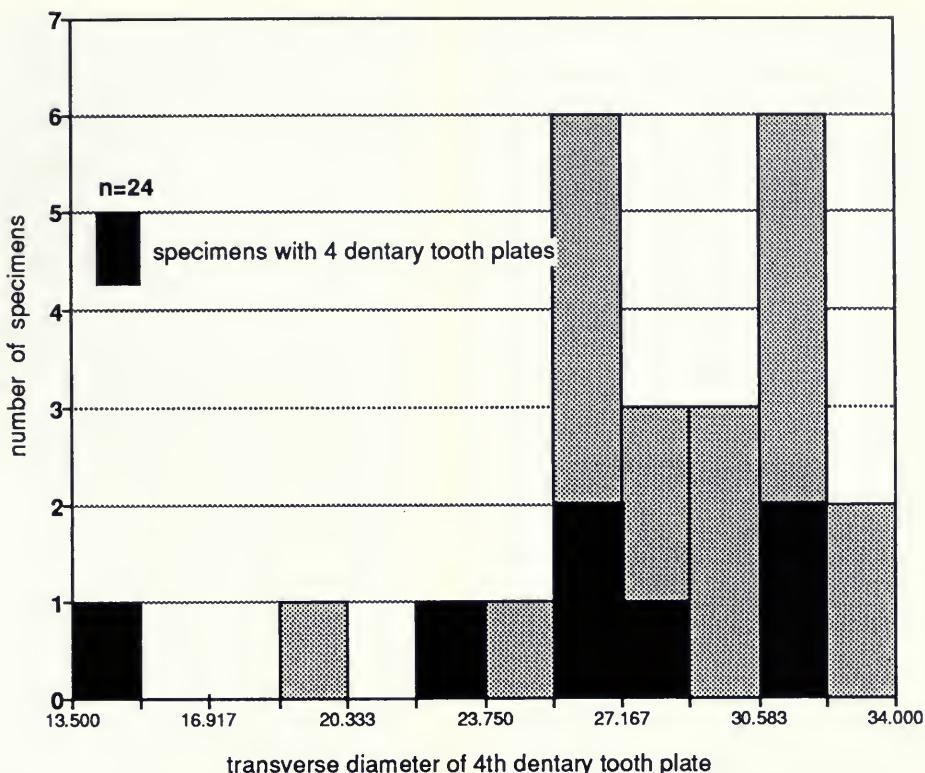


FIG. 33. Size distribution of the fourth (posterior) dentary tooth plate in 24 articulated *Placodus* dentitions.

ribs. The morphology of the ilium indicates, however, that only three pairs of functional sacral ribs are present.

Associated with the axial skeleton is a row of dermal ossifications capping the expanded dorsal tips of the neural spines. The gastral ribs form a solid ventral rib cage. Each gastral rib is composed of five elements, of which the medioventral one is less angulated and without the distinct anterior tip seen in other sauropterygians.

The interclavicle of *Placodus* retains a reduced posterior stem, which may be differentiated as a posterior tip only (Fig. 39). The clavicles are curved elements, and the two limbs enclose an angle of approximately 110°. The anteromedial ramus of the clavicle wraps around the anterior aspect of the interclavicle. Anteromedially, the clavicle tapers to a blunt tip and fails to meet its counterpart in an anteroventral suture (Fig. 40). The posterior ramus of the clavicle is applied against the medial surface of the platelike scapula, a sauropterygian synapomorphy. The scapula and coracoid of *Placodus* are platelike elements, with the coracoid foramen located between the two bones (Fig. 40).

The dorsal wing of the scapula is distinctly less reduced than in other sauropterygians, which retain a narrow posterodorsal process only.

Storrs (1991, 1993) described the "central fenestration" of the pectoral girdle as a sauropterygian synapomorphy. The "central fenestration" is not obvious in *Placodus*, due to failure of the coracoids



FIG. 34. *Placodus gigas* Ag (Museum Freriks, #20784); incomplete dentary. Lower Muschelkalk, Winterswijk. Scale bar = 10 mm.



A

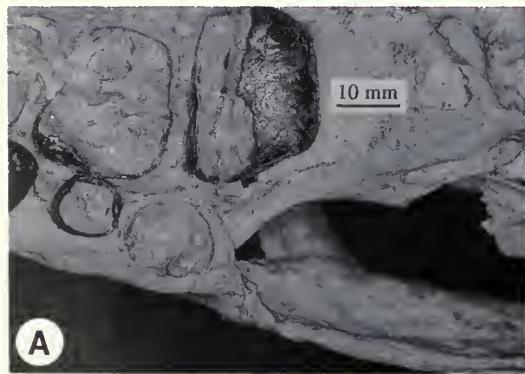


B

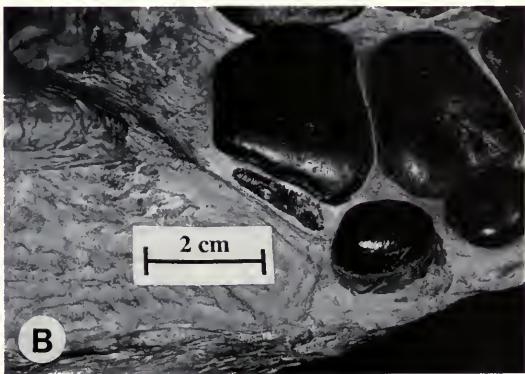
FIG. 35. *Placodus gigas* Ag. A, Premaxillary rostrum, occlusal view (BMNH R-41096, original of Seeley, 1890, Pl. 14), upper Muschelkalk, Bayreuth; B, lower jaw, occlusal view (BSP AS VII 1209, original of Agassiz, 1833–1845, Pl. 20, Fig. 14; Meyer, 1863, Taf. 32, Figs. 1–3; Zittel, 1887–1890, Fig. 517), upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

to meet in the midline. Storrs (1991) attributed this condition to a reduction of the coracoids, a reasonable proposition in view of the other apomorphic similarities in the pectoral girdle shared

by *Placodus* and other sauropterygians. The test of congruence remains inconclusive with respect to this character because the systematic position of placodonts as sister-group to the Eosauopter-

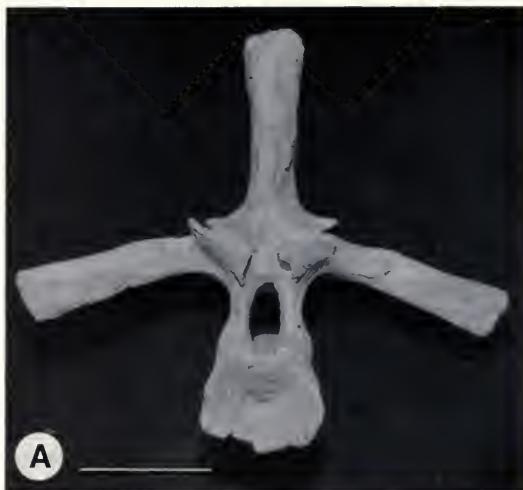


A

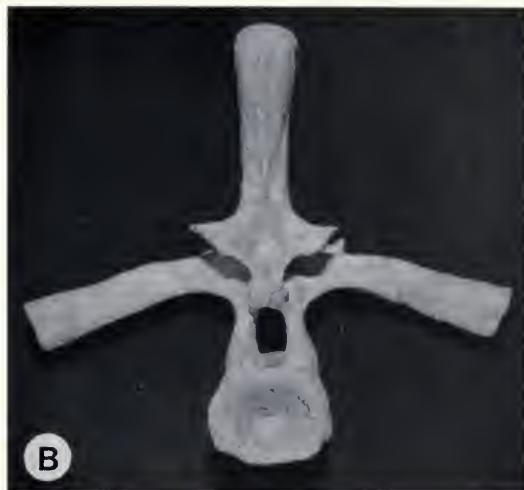


B

FIG. 36. *Placodus gigas* Ag, dental lamina foramen for third (posterior) palatine tooth plate. A, BT 13 (original of Sues, 1987), upper Muschelkalk, Bayreuth; B, BSP A VII 1028 (original of Münster, 1830, "specimen I," holotype), upper Muschelkalk, Bayreuth. Scale bar = 10 mm.



A



B

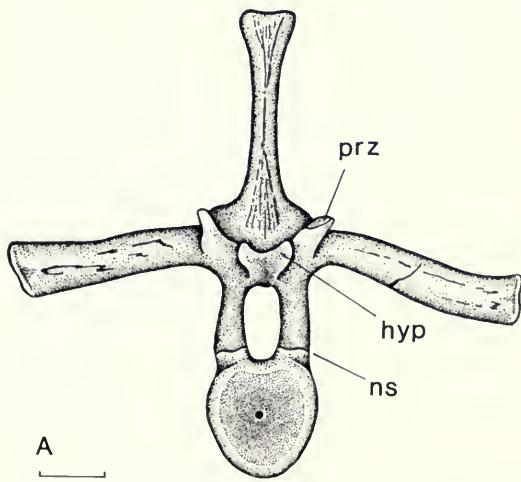
FIG. 37. *Placodus gigas* Ag, dorsal vertebra (GMF R-2003). Upper Muschelkalk, Bayreuth. A, Anterior view; B, posterior view. Scale bar = 20 mm.

ygia (Rieppel, 1994a) does not change whether pectoral fenestration is coded as present or absent (see below).

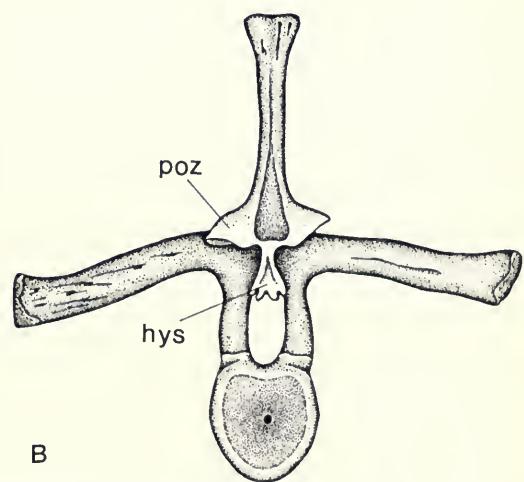
The pelvic girdle shows an ilium that resembles those of other sauropterygians rather closely (Fig. 41), whereas the pubis and ischium are again plate-like elements of rounded contours (Drevermann, 1933). The ilium shows a reduced iliac blade, which retains a preacetabular tip. On its medial surface, three articular facets are developed for the three functional sacral ribs. In sauropterygians, a thyroid fenestra is commonly observed in the pelvic

girdle; in *Placodus*, this fenestra is present but reduced by the platelike morphology of the ischium and pubis. The obturator foramen is an open slit.

The partial humerus referred to *Placodus* by Drevermann (1933) is, in fact, the distal end of a left humerus of *Nothosaurus* (R. Wild, pers. comm.; see also Rieppel, 1994a, Fig. 60). Humerus structure in *Placodus* and *Cyamodus* was discussed by Vogt (1983). The humeri of these two genera are very similar, and their identification is largely based on absolute size (*Cyamodus* tends to be larger) and stratigraphy (in the uppermost upper Muschel-



A



B

FIG. 38. Placodontia, isolated dorsal vertebra (SMNS 59825). Upper Muschelkalk, Hegnabrunn near Kulmbach. A, Anterior view; B, posterior view. Scale bar = 20 mm. Abbreviations: ns, neurocentral suture; hyp, hypantrum; hys, hypophene; poz, postzygapophysis; prz, prezygapophysis.



FIG. 39. Placodontia, isolated interclavicle (SMNS 59824). Upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

kalk, i.e., above the *spinosus* biozone, *Placodus* is absent, whereas remains of *Cyamodus* are quite common [Hagdorn, 1993]). The humerus of *Placodus* and *Cyamodus* shows a concave preaxial, an angulated postaxial margin, and a marked distinct distal expansion that is rather flat (Fig. 42A). An ectepicondylar groove is distinct, but no ectepicondylar notch or entepicondylar foramen is present. The distal humeral condyles are not separated from one another. Among disarticulated material from the Germanic Muschelkalk, placodont humeri are easily distinguished from the

humerus of *Simosaurus* by the ratio length/distal width (Table 1). The placodont humeri differ from the *Nothosaurus* humerus by the absence of the entepicondylar foramen, and the distal expansion as expressed by the ratio minimal width/distal width (although a narrow overlap exists in that ratio for the two genera).

The radius and ulna, as well as the manus, remain incompletely known for *Placodus*. A single proximal carpal ossification has been identified (probably the ulnare), but more may have been present. The phalangeal formula most probably was 2-3-4-5-3 (or 4) (Gross, 1937).

The femur of *Placodus* is known from well-preserved specimens (Fig. 42B), including the right femur of the specimen described by Drevermann (1933). The bone is slender and rather straight, and characterized by a well-developed trochanter separated from the proximal articular head by a distinct intertrochanteric fossa. The tibia is slightly longer but distinctly broader than the fibula, with a straight preaxial and a slightly concave postaxial margin. The concave preaxial margin of the slender fibula results in the formation of a narrow spatiuum interosseum. Two proximal tarsal os-

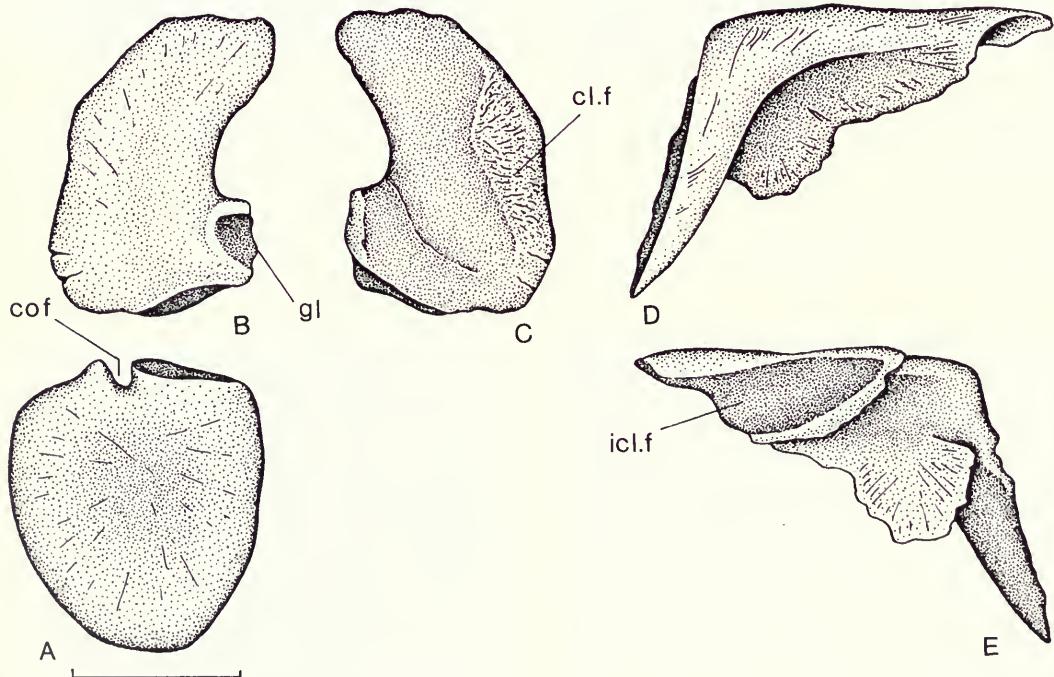


FIG. 40. *Placodus gigas* Ag, pectoral girdle (SMF R-1035, cast of original of Drevermann, 1933). A, Left coracoid, lateral view; B, left scapula, lateral view; C, left scapula, medial view; D, left clavicle, dorsal view; E, left clavicle, ventral view. Scale bar = 50 mm. Abbreviations: cl.f, clavicular facet; cof, coracoid foramen; gl, glenoid facet; icl.f, interclavicular facet.

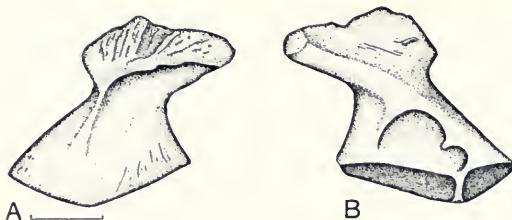


FIG. 41. *Placodus gigas* Ag, ilium (SMF R-1035, cast of original of Drevermann, 1933). A, Lateral view; B, medial view. Scale bar = 20 mm.

fications are preserved, the astragalus and calcaneum. Both elements form simple rounded ossifications. Of the four preserved metatarsals, the third appears to be the longest (Drevermann, 1933). The phalangeal formula for the pes remains unknown.

### The Systematic Position of the Genus *Placodus*

Diapsid affinities of placodonts were first recognized by Sues (1987), but the precise relationships of the Placodontia within the Neodiapsida were not determined (see also Carroll & Currie, 1991). Later, a sister-group relationship of Placodontia and Sauropterygia ("Euryapsida") was postulated by Rieppel (1989) and Zanon (1989), whereas placodonts were found to be nested within the Eusauropterygia by Storrs (1991, 1993). Other authors have invoked a close relationship of placodonts to the Ichthyosauria (Mazin, 1982; Pinna, 1989).

A recent analysis of phylogenetic interrelationships of Triassic stem-group Sauropterygia (Rieppel, 1994a, including a total of 29 taxa and 94 characters) confirmed the diapsid affinities of *Placodus* and showed the Placodontia to be the sister-group of all other Sauropterygia (Eosauropterygia, new taxon) (Fig. 43), nested within crown-group diapsids (Sauria). Diapsid, neodiapsid, and saurian synapomorphies shared by *Placodus* include (see Rieppel, 1994a, for a complete discussion of diagnostic characters): presence of the upper temporal fenestra; exclusion of lacrimal from external naris (preceding the loss of the lacrimal in sauropterygians); quadrate concave posteriorly; absence of caniniform teeth on maxilla; absence of teeth on pterygoid flange; presence of a retroarticular process; absence of cervical intercentra; absence of dorsal intercentra; loss of cleithrum; loss



FIG. 42. *Placodus gigas* Ag, stylopodium. A, Left humerus (SMNS 59827; original of Vogt, 1983, Fig. 2b), upper Muschelkalk, Hagnabrunn near Kulmbach; B, right femur (SMNS, uncatalogued, coll. M. Wild # 1798; original of Vogt, 1983, Fig. 2c), upper Muschelkalk, Bayreuth. Scale bar = 20 mm.

of supraglenoid buttress; acetabulum circular; presence of thyroid fenestra; femoral shaft slender; intertrochanteric fossa reduced; anterior femoral condyle not larger than posterior condyle and of subequal extent distally; loss of distal tarsals 1 and 5. At the level of crown-group diapsids (Sauria), a number of characters must be interpreted as reversals in *Placodus* (and in eosauropterygians where present), such as the closure of the lower temporal region in the skull (see discussion of *Paraplatodus*

TABLE 1. Proportions of the humerus in *Cyamodus/Placodus* ( $n = 9$ ), *Nothosaurus* ( $n = 35$ ), and *Simosaurus* ( $n = 9$ ).

	Length/ Distal width	Proximal width/ Distal width	Minimal width/ Distal width
<i>Cyamodus/Placodus</i>	2.7–3.5	0.6–1.0	0.4–0.6
<i>Nothosaurus</i>	3.3–4.8	0.7–1.2	0.6–0.9
<i>Simosaurus</i>	4.2–5.9	0.8–1.2	0.5–0.7

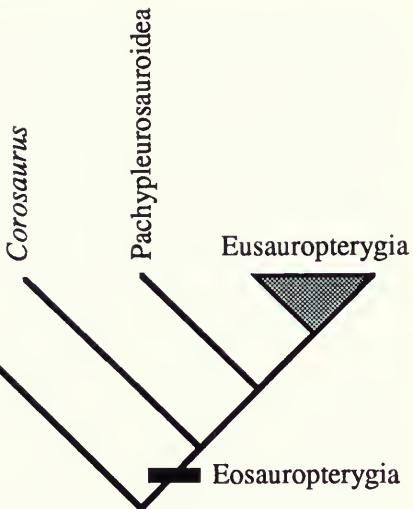


FIG. 43. Phylogenetic relationships of the Placodontia (after Rieppel, 1994a).

below), the lateral covering of the quadrate by the squamosal (quadratojugal?), the reduced thyroid fenestra in the pelvis, the notochordal vertebrae, and the loss of the hooked fifth metatarsal. Controversial characters such as the infraorbital fenestra have been coded as either present (reduced) or absent for *Placodus* with no effect on its position as sister-group of the Eosauropterygia.

The monophyly of the Sauropterygia, including the Placodontia and the Eosauropterygia, is again supported by a number of synapomorphies such as loss of lacrimal; akinetic palate; clavicles applied to the medial surface of the scapula; clavicles positioned anteroventrad to interclavicle; coracoid foramen enclosed between scapula and coracoid; pectoral fenestration present; three (or more) sacral ribs; posterior process on interclavicle reduced or absent; humerus angulated or "curved"; humerus with reduced epicondyles; radius and ulna of approximately equal length; iliac blade reduced. Again, controversial characters such as the pectoral fenestration have been coded as either present (reduced) or absent for *Placodus* with no effect on its position as sister-group of the Eosauropterygia.

The position of Placodontia nested within the Sauria as sister taxon of the Eusauropterygia (*sensu* Tschanz, 1989) was postulated by Storrs (1991, 1993), but was not confirmed in the analysis referred to above. Storrs's (1991, 1993) concept of Nothosauriformes is supported by some characters such as the elongated mandibular symphysis,

the constricted snout, the elongation of the postorbital skull correlated with an increased size of the upper temporal opening, humerus morphology, and equal length of radius and ulna where known. However, this hypothesis is not the most parsimonious one over the whole data matrix of 94 characters (defined in Rieppel, 1994a), and it creates a number of conflicting character interpretations. The elongated mandibular symphysis includes the splenial in *Placodus*, but not in other sauropterygians. The temporal region is greatly expanded in cyamodontoids, but not in *Placodus* or in *Paraplagodus*. Both placodonts and eosauropterygians have developed an akinetic palate, but closure of the dermal palate was effected in fundamentally different ways in the two groups (Sues, 1987): by expansion of the palatines in placodonts and by expansion of the pterygoids in eosauropterygians (*Corosaurus*, pachypleurosaur, and eusauropterygians). Pachypleurosaur and eusauropterygians have an essentially closed, platelike occiput, whereas *Placodus* retains distinct paroccipital processes. The basioccipital tubers show a complex relation to the dermal palate in both *Placodus* and eusauropterygians (Zanon, 1989; the character is unknown for pachypleurosaur), but the details of these structural relations are different in the two groups. The basioccipital tubers are directed ventrally in *Placodus*, with the cranoquadrate passage extending between them and the pterygoids; in eusauropterygians, the basioccipital tubers are directed laterally and relate to the "eustachian foramen" (Rieppel, 1994b). Differences are also observed in the postcranial skeleton. The dorsal vertebrae of *Placodus* are characterized by a hypophene-hypantrum articulation, which is the reverse of the topographical relations of the zygosphenes-zigantrum articulation seen in pachypleurosaur and eusauropterygians. The scapula of pachypleurosaur and eusauropterygians has a narrow dorsal wing that receives the clavicle on its anterior and medial surface; the scapula in *Placodus* is a broad, platelike element that receives the scapula on its medial surface only.

Ichthyosaur relationships of Placodontia have been postulated by Mazin (1982) and Pinna (1989), mainly on the basis of the configuration of the temporal bones. In view of the controversies still surrounding the interpretation of the temporal region in the skulls of placodonts (see discussion above) and ichthyosaurs, the use of this character complex in support of a sister-group relationship of ichthyosaurs and placodonts seems highly tenuous. Nevertheless, the potential for ichthyosaur

affinities to placodonts seems indicated by the fact that a heterodont dentition, including posterior crushing teeth, may be plesiomorphic at the level of the Ichthyosauria (Mazin, 1981, 1982), and hence a shared derived character of placodonts and ichthyosaurs. Independent evidence indicates that ichthyosaurs may be related to lepidosaurs (Massare & Callaway, 1990), which is also the relationship postulated for Sauropterygia (Rieppel, 1994a). Finally, eosaurophterygians, placodonts, and ichthyosaurs share a derived pattern of ossification of proximal limb bones and vertebral centra (Moodie, 1908; Haas, 1967). In view of the strong support for a monophyletic Sauropterygia (including Placodontia and Eosaurophterygia), the analysis of ichthyosaur interrelationships will ultimately have to be placed within this wider context. Future analysis may well show ichthyosaurs, placodonts, and eosaurophterygians to be a monophyletic radiation of lepidosauromorphs invading the Mesozoic sea.

The Placodontia (Fig. 44) have been divided into the nonarmored placodonts (Placodontoidea), comprising the genera *Placodus* and *Paraplagodus*, and the armored placodonts (Cyamodontoidea), comprising the genera *Cyamodus*, *Henodus*, *Placochelys*, *Protenodontosaurus*, *Psephoderma*, and perhaps the problematic genus *Saurosphargis* (Peyer & Kuhn-Schnyder, 1955; Mazin & Pinna, 1993). Among these, *Paraplagodus* (Peyer, 1931, 1935; Kuhn-Schnyder, 1942) has been portrayed as the relatively most plesiomorphic placodont because of its relatively plesiomorphic dentition. The material is generally incomplete and difficult to work with, yet, in spite of its importance, the most complete specimen discovered so far has been described only in a preliminary fashion (Kuhn-Schnyder, 1942) and is currently not available for detailed study. The genus shows the characteristic placodont dentition with anterior procumbent teeth and posterior crushing teeth separated by a distinct diastema, as well as the characteristic placodont humerus morphology (see description above). The dorsal ribs show a distinct posterior broadening of their proximal part, an autapomorphy of *Paraplagodus*. The best preserved skull of *Paraplagodus* (BSP 1953 XV 5) is crushed in lateral view, but it allows the identification of some structural detail. The skull (Figs. 45, 46) has rather high contours, as does that of *Placodus*, and the premaxillaries form a broad and projecting snout, bearing three pointed and strongly procumbent teeth on either side. Seven maxillary teeth were reconstructed by Peyer (1935); one

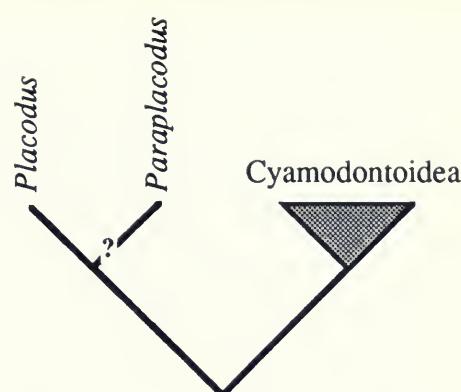


FIG. 44. Interrelationships within the Placodontia.

exposed replacement tooth indicates vertical tooth replacement. One tooth has been displaced into the posteroventral corner of the orbit, an observation taken as evidence of the presence of an infraorbital fenestra by Zanon (1989). The most interesting observation is the presence of a boomerang-shaped jugal defining the posteroventral margin of the orbit, correlated with a deep embayment of the lower cheek region (Pinna, 1989; Zanon, 1989). Because of extensive breakage, the configuration of the temporal bones in the temporal arch cannot be unequivocally ascertained beyond the observation of a sutural contact at about the midpoint of the dorsal margin of the upper temporal arch. The two bones meeting at that point are the postorbital (anteriorly) and the squamosal (posteriorly), which therefore show similar relations as in *Placodus* (but see Pinna, 1989, for a different interpretation of *Placodus*). The relatively high skull, the broad snout, and the enlarged, strongly procumbent premaxillary teeth are shared derived characters, placing *Paraplagodus* into the Placodontoidea. In view of the position of Sauropterygia (including placodonts) nested within crown-group diapsids (Sauria), the deep embayment of the lower temporal region in the skull of *Paraplagodus* supports the hypothesis of a secondary closure of the cheek region in *Placodus* (Sues, 1987; the cheek generally shows a ventral embayment in cyamodontoids).

Meyer (1863; see also Braun, 1862) already drew the distinction between placodontoids (his "Macrocephali") and cyamodontoids (his "Platycephali"), thereby capturing a number of essential characteristics separating the two clades. The skull of cyamodontoids is rather low and broad, characterized by flaring upper temporal arches. The

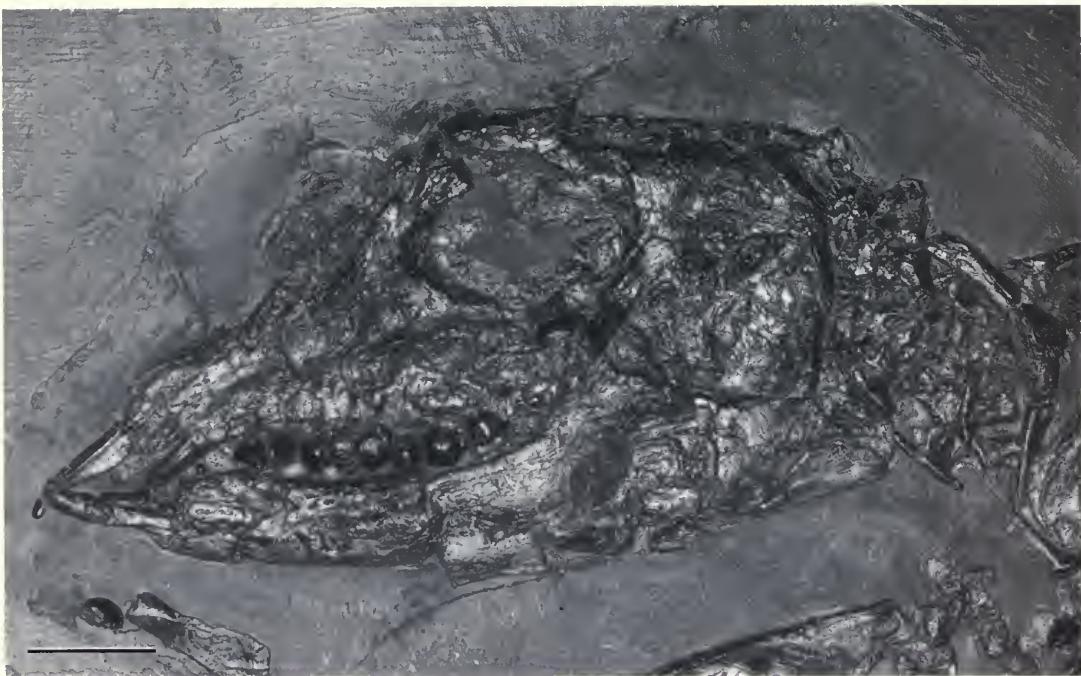


FIG. 45. *Paraplatodus broili* Peyer, skull (BSP 1953 XV 5). Grenzbitumenzone, Monte San Giorgio, Switzerland. Scale bar = 20 mm.

premaxillary rostrum is short and pointed (except in *Henodus*) and furnished with small teeth, or it is edentulous. The maxillary and palatine dentition is reduced, and only the posterior palatine teeth are expanded into distinctly enlarged tooth plates (except in *Henodus*; see also Mazin, 1989). More recently, Nosotti and Pinna (1993b) have added to the list of cyamodontoid synapomorphies. In cyamodontids (Fig. 47), the opisthotic, rather than the basioccipital, forms a complex articulation with the dermal palate, and the temporal artery reached the temporal musculature through a restricted “pteroccipital” foramen piercing the paroccipital process between the squamosal and the opisthotic (in *Placodus*, the temporal artery passes through a slitlike gap between the quadrate ramus of the pterygoid and the otic capsule). In contrast to *Placodus*, the epipterygoid is broad dorsally in cyamodontids (cf. *Cyamodus rostratus* [Kuhn-Schnyder, 1965]; *Cyamodus kuhnschnyderi* [Nosotti & Pinna, 1993a]), possibly a plesiomorphic feature, but the extensive dermal body armor is another indisputable synapomorphy of the Cyamodontoidea. A proper cladistic analysis of placodont interrelationships must await a detailed revision of cyamodontoid taxa.

### Stratigraphy, Paleobiogeography, and Paleoecology of the Genus *Placodus*

The Placodontia are restricted to the Middle and Upper Triassic (lower Anisian through Rhaetian) of the western Tethyan Province (Pinna, 1989). With *Placodus impressus* Agassiz being a nomen dubium (Peyer & Kuhn-Schnyder, 1955), the earliest occurrence of the genus *Placodus* is documented from the lowermost Muschelkalk (lower Gogolin Beds [“Chorzower Schichten”], *Dadocrinus* biozone) of Gogolin, Upper Silesia (Wysogorski, 1904; Huene, 1936). A number of teeth referable to *Placodus* indicate the occurrence of the genus in classic deposits of the lower Muschelkalk in the eastern part of the Muschelkalk Basin (Rüdersdorf near Berlin, Freyburg/Unstrut, and Jena [Meyer, 1851a,b]; additional material includes BSP 1959 XIII 25; SMNS 13666a, 15992, and uncatalogued material; as well as uncatalogued teeth in the stratigraphic collection of the Bundesamt für Geowissenschaften und Rohstoffe, Berlin, and in the Institut für Geowissenschaften, Martin-Luther-Universität, Halle/Saale). The skull of *Placodus “antiquior”* described by Huene (1936)

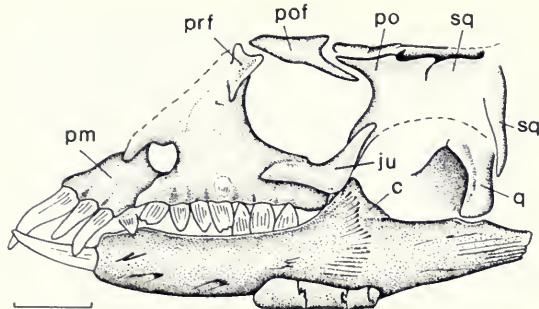


FIG. 46. *Paraplagodus broili* Peyer, skull (BSP 1953 XV 5). Grenzbitumenzone, Monte San Giorgio, Switzerland. Scale bar = 20 mm. Abbreviations: c, coronoid; ju, jugal; pm, premaxilla; po, postorbital; pof, postorbital frontal; prf, prefrontal; q, quadrate; sq, squamosal.

comes from the upper lower Muschelkalk (Schaumkalk) of Freyburg/Unstrut.

Early northward expansion of *Placodus* within the Muschelkalk Basin is documented by teeth from the lower Muschelkalk (*Wellenkalk*) of Helgoland (Kruckow, 1979); early westward dispersal is documented by the occurrence of the genus in the lower Muschelkalk of Württemberg (Aach: SMNS, uncatalogued; Bödigheim: SMNS 30006; Dittighausen: SMNS, uncatalogued; Freudenstadt: SMNS 593790; Lambach-Sulzbach: SMNS 56313; Sondershausen: SMNS 13665), and by the occurrence of *Placodus* in the lowermost Muschelkalk of Winterswijk, Netherlands (Oosterink, 1978). (An isolated neural arch from the Lower Triassic of Sulzbach [Alsace, France] was tentatively referred to an unspecified placodont by Huene [1936], but the specimen is not diagnostic.)

The history of the Muschelkalk Basin, most recently reviewed by Haggdorn (1985, 1991; see also Ziegler, 1982), indicates that basal deposits in the west are geologically younger than those in the eastern part of the basin (Haggdorn, 1991). Analysis of the invertebrate fauna indicates an initial immigration into the Muschelkalk Basin from the east, through the East Carpathian Gate (Kozur, 1974; Ziegler, 1982, 1988; Haggdorn, 1985, 1991; Urlich & Mundlos, 1985), following a relative sea-level rise in early Anisian times that induced the Muschelkalk transgression. Westward dispersal followed a second sea-level rise during the lower Anisian. A similar paleobiogeographic history may be hypothesized for the genus *Placodus*.

Interpreting *Paraplagodus* from the Middle Triassic intraplatform basin facies of the southern Alps (Anisian–Ladinian boundary) as a “primi-

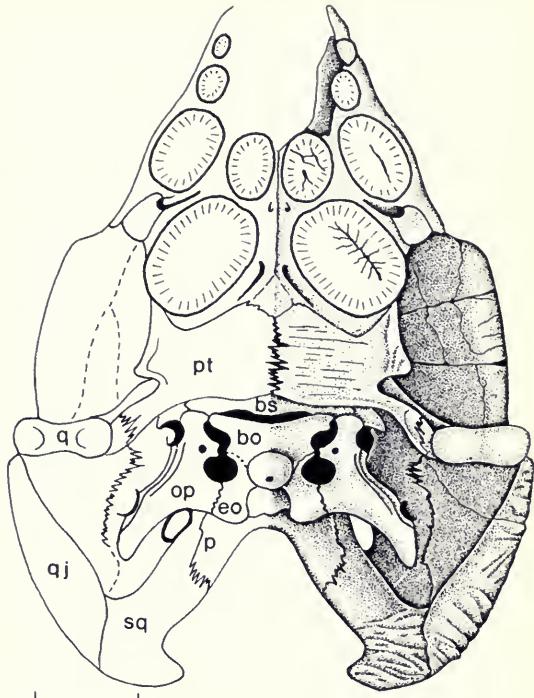


FIG. 47. *Placochelys placodonta* (MB R. 1765; original of Jaekel, 1907, Pl. 3, Fig. 1); skull in ventral view. Lower Keuper, Hungary. Scale bar = 20 mm. Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; op, opisthotic; p, parietal; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal.

tive” placodont, Peyer and Kuhn-Schnyder (1955) postulated a center of placodont origin along the northwestern coast of the Tethys from where they would have migrated into the Germanic Muschelkalk Basin; a similar hypothesis has been advanced by Mazin (1986a). This hypothesis would be supported if *Paraplagodus* could be shown to be the sister taxon of *Placodus* plus Cyamodontoidea. However, the three-taxon statement involving *Paraplagodus*, *Placodus*, and the Cyamodontoidea remains unresolved at the present time because of the lack of critical data on the skeletal anatomy of *Paraplagodus* and the Cyamodontoidea.

In contrast, Pinna (1990; see also Pinna & Mazin, 1993) postulated a placodont origin in the European epicontinent sea habitat, referring to the fact that the earliest placodonts appear at the top of the Lower Triassic or early Middle Triassic of epicontinent deposits, already differentiated into an armored and nonarmored lineage. The taxa

cited by Pinna (1990) in support of his hypothesis are "*Placodus impressus*" (nomen dubium), *Placodus* "antiquior" (junior synonym of *Placodus gigas*), *Cyamodus tarnowitzensis*, *Negevodus ramonensis*, *Saurosphargis voltzi*, and *Psephosaurus mosis*.

Of these, *Negevodus ramonensis* (Haas, 1975, Mazin, 1986b) from the Middle Triassic of Israel is a labyrinthodont (Zanon, 1991). *Saurosphargis voltzi* (Huene, 1936) from the lower Gogolin beds of Upper Silesia (now Poland) is an incomplete specimen of highly problematic affinity (the holotype and only known specimen was lost during World War II). The skull and dentition of *Saurosphargis* are unknown; elongate transverse processes indicate placodont affinities, and the posterior expansion of the midregion of the dorsal ribs (forming broad and blunt uncinate processes) recalls the rib morphology of *Paraplagodus*. The classification of *Saurosphargis* as cyamodontoid incertae sedis (Peyer & Kuhn-Schnyder, 1955) is not supported by shared derived characters. *Cyamodus tarnowitzensis* (Gürich, 1884; the holotype and only known specimen was lost during World War II) is from the Karchowice beds of Tarnowiskie, Poland (former Tarnowitz, Upper Silesia), which belong in the uppermost lower Muschelkalk (upper Pelsonian, lower Illyrian), and hence are somewhat younger than the Gogolin beds that have yielded *Placodus* (Szulc, 1991). Nevertheless, *Cyamodus tarnowitzensis* documents the early occurrence of *Cyamodus*, along with *Placodus*, in the eastern Muschelkalk Basin. *Psephosaurus mosis* (Brotzen, 1957; and the incompletely preserved *Psephosaurus picardi*) is a cyamodontoid from the lower Muschelkalk of Wadi Ramon, Israel (Member B of Brotzen's *Beneckeia* beds, corresponding to Kozur's, 1974, "assemblage zone" with *Beneckeia buchi* of the lowermost lower Muschelkalk). The occurrence of a cyamodontoid in the lower Anisian of Israel expands the geographic range of the early occurrence of placodonts eastward, and the question arises whether placodonts reached the Muschelkalk Basin from the east or expanded from the Muschelkalk Basin toward the east. Again, cladistic analyses testing these alternative hypotheses are currently lacking. Placing placodonts into the wider context of sauropterygian interrelationships supports the hypothesis of an eastern origin, however.

Currently available evidence indicates that the Placodontia represent the sister-group of the Eosauropterygia, which are known from the Middle

Triassic of China (Young, 1958, 1959, 1960, 1965) and Europe, and from the upper Lower Triassic of the western United States (Storrs, 1991). The hypothesis of an eastern rather than a western Tethyan center of origin of the Sauropterygia, including placodonts and eosauropterygians, could account for their known fossil distribution by eastward expansion into the eastern Pacific Province, and westward expansion into the western Tethyan Province. The occurrence of cyamodontoids and placodontoids in Triassic (Anisian) deposits of Transylvania (Alesd, Oradea [Jurcsak, 1976, 1977, 1982]) would seem to support the assumption that placodonts invaded the central and western European epicontinental seas from the east, perhaps through the Silesian-Moravian Gate (Jurcsak, 1982; Szulc, 1991). However, the proper assessment of the paleobiogeographic history of the Placodontia must await greater cladistic resolution of the group than is currently available.

The known distribution of placodonts is restricted to coastal stretches of the western Tethyan Province (intraplatform basin facies) and to shallow epicontinental seas. The paleoecology of *Placodus* was most recently reviewed by Vogt (1983) and Westphal (1988). The skeletal structure of *Placodus* clearly indicates a durophagous inhabitant of coastal stretches and shallow seas. The anterior teeth were suited to picking up hard-shelled invertebrate prey from the substrate; prey species were crushed between the posterior molar teeth. Nerve foramina and grooves on the maxillae and premaxillae indicate sensitive innervation of the spatulate rostrum. The high skull, high coronoid process, and posterior position of crushing teeth combine to maximize bite force (Vogt, 1983). Huene (1933) reports a statistical correlation of *Placodus* teeth with accumulations of the brachiopod *Terebratula* in the upper Muschelkalk of Bayreuth, a correlation that is not observed in Württemberg (H. Hagdorn, pers. comm.; Westphal, 1988). An interesting observation is the mutual exclusion of *Placodus* and *Cyamodus* in these deposits (Huene, 1933). The trunk of *Placodus* must have been rather rigid, with respect to the increasing inclination of zygapophyseal articulations in anteroposterior direction, the differentiation of hypantrum and hypophene, and the massive gasteral rib cage. Main propulsion may have been generated by the front limbs (characterized by a robust and distally expanded humerus) and by the tail (characterized by almost horizontal zygapophyseal articulations; see also Vogt, 1983).

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## Appendix: Material Included in This Study

### Institutional Abbreviations

Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin (BGR; only type material or otherwise published and figured specimens are catalogued in this institution. Other specimens are referred to by drawers. The prefix S specifies the stratigraphic collection. Each cabinet has two rows of drawers [left and right] numbered from top to bottom); The Natural History Museum, London: BMNH; Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich: BSP; Naturkundemuseum Erfurt: Er; Institute für Geologische Wissenschaften der Martin-Luther Universität, Halle: Ha; Senckenberg Museum, Frankfurt a.M.: SMF; Staatliches Museum für Mineralogie und Geologie, Dresden: BA Tr; Staatliches Museum für Naturkunde, Stuttgart: SMNS; Muschelkalk Museum Ingelfingen, Sammlung H. Hagdorn: SHG; Oberfränkisches Erdgeschichtliches Museum, Bayreuth: BT.

## Material

*Cyamodus*: SMNS 15855, 16270 (upper Muschelkalk, Tiefenbach near Crailsheim; skulls); SMNS 59825 (upper Muschelkalk, Hegnabrunn; dorsal vertebra); SMNS 15937 (upper Muschelkalk, Heldenmühle near Crailsheim; humerus); SMNS 17872 (upper Muschelkalk, Heldenmühle near Crailsheim; humerus); SMNS 18057 (upper Muschelkalk, Heldenmühle near Crailsheim; humerus); SMNS coll. M. Wild #1070 (upper Muschelkalk, Unterrodach. Original of Vogt, 1983, Fig. 2d); SMNS uncatalogued (upper Muschelkalk, Zuffenhausen—Stuttgart);

### *Placodus gigas*:

PARTIALLY ARTICULATED SKELETON—SMF R-1035 (upper Muschelkalk, Steinsfurt near Heidelberg; original of Drevermann, 1931, 1933).

SKULLS OR SKULL FRAGMENTS—BMNH R-1642, upper Muschelkalk, Bayreuth (original of Owen, 1858, Pl. 10, Figs. 2–5); BMNH R-35868, upper Muschelkalk, Bayreuth; BMNH R-41096, upper Muschelkalk, Bayreuth (original of Seeley, 1889); BSP AS VII 1208, upper Muschelkalk, Bayreuth (holotype of *Placodus gigas*); BSP AS VII 1211, upper Muschelkalk, Bayreuth; BSP 1968 I 75, upper Muschelkalk, Hegnabrunn near Kulmbach (original of Broili, 1912, Pl. 14, Figs. 1–4); BT, uncatalogued, upper Muschelkalk, Bayreuth (holotype of *Placodus andriani*, *Placodus hypsiceps*, *Placodus quinimolaris*, and several skull fragments); BT 13, upper Muschelkalk, Bayreuth; BA Tr 43, upper Muschelkalk, Bayreuth; Er 78/235, upper Muschelkalk, Bad Sulza; Er 78/235a, upper Muschelkalk, Bad Sulza; Ha, uncatalogued, lower Muschelkalk, Freyburg/Unstrut (holotype and assigned material of *Placodus antiquior*); SMF R-359 a, b, upper Muschelkalk, Bayreuth (original of Broili, 1912; Edinger, 1928); SMF R-360, upper Muschelkalk, Bayreuth (original of Broili, 1912, p. 151); SMF R-366, upper Muschelkalk, Bayreuth; SMF R-1035, upper Muschelkalk, Bayreuth; SMF R-4038, upper Muschelkalk, Bayreuth (original of Edinger, 1928); SMF R-4038, upper Muschelkalk, Bayreuth; SMF R-4162, upper Muschelkalk, Bayreuth; SMNS 12679, upper Muschelkalk, Münster; SMNS 18641, upper Muschelkalk, Crailsheim; SMNS 59434, upper Muschelkalk, Bayreuth;

LOWER JAWS OR FRAGMENTS THEREOF—BMNH R-1641, upper Muschelkalk, Bayreuth (holotype of *Placodus pachygynathus*); BMNH R-1643, upper Muschelkalk, Bayreuth (holotype of *Placodus bombidens*); BMNH R-19677, upper Muschelkalk, Bayreuth (holotype of *Placodus bathygynathus*); BSP

1925 I 16, upper Muschelkalk, Bayreuth; BSP 1968 I 76, upper Muschelkalk, Hegnabrunn near Kulmbach; BSP AS VII 1209, upper Muschelkalk, Bayreuth; Er 78/278, upper Muschelkalk, Bad Sulza; Ha, uncatalogued, lower Muschelkalk, Freyburg/Unstrut; SMF R-359, upper Muschelkalk, Bayreuth; SMF R-362, upper Muschelkalk, Bayreuth; SMF R-363, upper Muschelkalk, Bayreuth; SMF R-364, upper Muschelkalk, Bayreuth; SMF R-365, upper Muschelkalk, Bayreuth (original of Drevermann, 1933, p. 334); SMF R-367, upper Muschelkalk, Bayreuth; SMF R-368, upper Muschelkalk, Bayreuth; SMF R-492, upper Muschelkalk, Bayreuth; SMF R-4110, upper Muschelkalk, Bayreuth; SMF R-4112, upper Muschelkalk, Bayreuth; SMNS 17572, upper Muschelkalk, Stengelberg; SMNS 58021, upper Muschelkalk, Lauchringen; SMNS uncatalogued, coll. M. Wild #98, upper Muschelkalk, Hegnabrunn near Kulmbach.

VERTEBRAE—SMF R-576, R-578, R-579, R-2000, R-2003, upper Muschelkalk (dorsal vertebrae); SMF R-2001, upper Muschelkalk, Bayreuth (two cervical vertebrae); SMNS 53006, lower Muschelkalk, Bödigheim (caudal vertebra); SMNS 59370, lower Muschelkalk, Freudenstadt (dorsal vertebra); SMNS coll. M. Wild #81, upper Muschelkalk, Bindlach (sacral vertebra).

HUMERUS—SMF R-672, upper Muschelkalk, Bayreuth (possibly *Cyamodus*, R. Wild, in litt., 3 November 1977); SMNS 15891, upper Muschelkalk, Tiefenbach near Crailsheim; SMNS 59827, upper Muschelkalk, Hegnabrunn near Kulmbach (original of Vogt, 1983, Fig. 2b); SMNS uncatalogued, coll. M. Wild #1365, upper Muschelkalk, Hegnabrunn near Kulmbach).

FEMUR—SMF R-86, upper Muschelkalk, Bayreuth; SMF R-88, upper Muschelkalk, Bayreuth; SMF R-760, upper Muschelkalk, Bayreuth (proximal end only); SMNS uncatalogued, coll. M. Wild #1789, upper Muschelkalk, Bindlach near Bayreuth.

ISOLATED TOOTH PLATES—BMNH R-1328-9, upper Muschelkalk, Bayreuth; BGR X-06153, upper Muschelkalk, Tarnowitz, Upper Silesia (original of Meyer, 1851b, Pl. 29, Fig. 51); BGR X-06154, upper Muschelkalk, Rybina, Upper Silesia (original of Meyer, 1851, Pl. 29, Fig. 52); BRG S 55-R 14, upper Muschelkalk, Rüdersdorf near Berlin; BRG S 55-R 15, upper Muschelkalk, Rüdersdorf near Berlin; BRG S 55-L 02, lower Muschelkalk, Rüdersdorf near Berlin; BRG S 54-R 02, upper Muschelkalk, Jena; BRG S 54-R 09, lower Muschelkalk, Freyburg/Unstrut; BRG S 54-L 09, lower Muschelkalk, Jena; BRG S 56-R 02, lower Mu-

schelkalk, Rüdersdorf near Berlin; BRG S 56-R 03,  
lower Muschelkalk, Rüdersdorf near Berlin; BRG  
S 56-L 11, lower and middle Muschelkalk, Rüd-  
ersdorf near Berlin; BSP 1959 XIII 25, lower Mu-  
schelkalk, Freyburg/Unstrut; SMNS 13666a, lower

Muschelkalk, Jena; SMNS 15992, lower Muschel-  
kalk, Jena; SMNS 56313, lower Muschelkalk, Lam-  
bach-Sulzbad; SMNS 13665, lower Muschelkalk,  
Sondershausen.

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