The Cranial Anatomy of *Placochelys placodonta* Jaekel, 1902, and a Review of the Cyamodontoidea (Reptilia, Placodonta)

Olivier Rieppel
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The Cranial Anatomy of *Placochelys placodonta* Jaekel, 1902, and a Review of the Cyamodontoidea (Reptilia, Placodonta)

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The Cranial Anatomy of *Placochelys placodonta* Jaekel, 1902, and a Review of the Cyamodontoidea (Reptilia, Placodonta)

Olivier Rieppel

Abstract

The skull of *Placochelys placodonta* Jaekel is described in detail and compared with all other cyamodontoid skulls kept in public repositories. Cladistic analysis based on a character set derived from cyamodontoid skull anatomy results in a reconstruction of placodont interrelationships as follows: *(Paraplacodus (Placodus ((Henodus, Cyamodus) (Macroplacus (Protenodontosaurus (Placochelys, Psephoderma)))))))*. The monophyly of the Cyamodontoidea is very robust, supported in particular by a suite of derived braincase characters. On the basis of present evidence, *Henodus* is the sister taxon of *Cyamodus*, and the monophyletic genus *Cyamodus* includes *C. hildegardis*. The monophyly of placochelyids, including *Placochelys* and *Psephoderma*, is strongly supported also.

A detailed comparison of skull anatomy provides no basis for a hypothesis of close phylogenetic relationships of turtles and cyamodontoid placodonts. Any similarities between the two clades, particularly with respect to the development of extensive dermal armor, must be convergent.

The historical paleobiogeography of cyamodontoid placodonts can largely be understood as a sequence of vicariance events that involved an early bifurcation establishing separate clades in the Germanic Basin and on the Eurasian carbonate platform. Subsequent vicariance established separate clades in the northern Alpine Triassic and in the southern Alps on the Hungarian platform, with further subdivision of the clades within the latter.

Introduction

Cyamodontoid placodonts are a clade of marine reptiles that occurs in shallow epicontinental and nearshore deposits of Middle and Upper Triassic age throughout the western Tethyan faunal province. The earliest cyamodontoid placodont to appear in the fossil record is *Cyamodus tarnowitzensis* Gürich, 1884, a skull (now lost) from the Karchowice Beds of Tarnowskie Gory, Poland (formerly Tarnowitz in Upper Silesia), which belong to the uppermost lower Muschelkalk (lower Illyrian, lower Anisian). Another early occurrence is a skull fragment (Brotzen, 1957; Rieppel, Mazin, & Tchernov, 1999) of a cyamodontid from the lower Muschelkalk of Makhtesh Ramon, Negev, Israel (Middle Member of the Gevanim Formation, upper Bithynian, upper lower Anisian: Druckman, 1974). The latest occurrences of cyamodontoids are from the Rhaetian of the northern (*Psephoderma*: Meyer, 1858a, b; Broili, 1921; *Macroplacus*: Schubert-Klemptauer, 1975) and southern (*Psephoderma*: Osswald, 1930; Boni, 1946 [1947], 1947 [1948]; Pinna, 1975, 1976a, b; 1978, 1979; Pinna & Nosotti, 1989) Alpine Triassic and from the Rhaetian of England (Meyer, 1858a, b; Storrs, 1994; see also Pinna, 1990a). Other localities that have yielded cyamodontoid placodonts are in the Anisian of Transylvania (Jurcsak, 1982; Huza et al., 1987); the upper Muschelkalk and Keuper of southern Germany (*Cyamodus rostratus*, *Cyamodus muensteri*, and *Cyamodus “laticeps”* from the upper Anisian [Agassiz, 1833–45; Münster, 1839; Owen, 1858;
Cyamodus kuhnschnyderi from the lower Ladinian [Nosotti & Pinna, 1993a]; Pseudosaurus suevicus from the upper Ladinian [Fraas, 1896]; Henodus chelops from the Carnian [Huene, 1936]) and of the Lorraine, France (Corroy, 1928; Rieppel & Hagdorn, 1999); the Ladinian of the southern Alps (Cyamodus hildegardis, Peyer, 1931a); the middle Carnian of the Tre Venezie area of northeastern Italy (Pinna & Zucchi Stolfi, 1979; Dalla Vecchia, 1993; Protodontosaurus italicus, Pinna, 1990b); the Ladinian of northeastern Spain (Rieppel and Hagdorn, 1998); and Middle Triassic (?Anisian, Ladinian) localities on the northern Gondwanan shelf (Haas, 1959, 1975; Gorce, 1960; Beltan et al., 1979; Vickers-Rich et al., 1999).

Cyamodontoid placodonts were a widespread and taxonomically diverse group characterized by the development of extensive dermal armor, which enhanced their chances of representation in the fossil record. In its most derived condition, this dermal armor consisted of a solid carapace, linked to a ventral armor by a lateral dermal body wall (Haas, 1969). This resulted in a remarkably turtle-like appearance of cyamodontoid placodonts, so much so that, based on his study of the cranial anatomy and dermal armor of Placochelys placodonta, Jaekel (1902a, b, 1907) proposed a derivation of turtles from cyamodontoids. The hypothesis of a relationship of turtles to placodonts was later rejected by Gregory (1946), who noted that convergent evolution is remarkable in these two groups, especially with regard to the dermal armor.

The more recent finding that turtles may be the sister-group of Sauropterygia among crown-group Diapsida (Rieppel & deBraga, 1996; deBraga & Rieppel, 1997; Rieppel & Reisz, 1999) has brought cyamodontoid placodonts back into focus. Although a broad-based analysis of turtle relationships over a wide range of taxa confirmed that the similarities shared by turtles and cyamodontoids are convergent (Rieppel & Reisz, 1999), a more in-depth analysis of the cranial anatomy of cyamodontoid placodonts and its comparison with that of turtles appears desirable in the attempt to discover further similarities or differences between the two groups. Placochelys placodonta was selected as primary focus for this project not only because Jaekel (1902a, b, 1907) based his hypothesis of a turtle–placodont relationship on this taxon, but also because it represents one of the best-preserved cyamodontoid skulls. The cranial anatomy of Placochelys placodonta will also be compared in detail with the cranial anatomy of all other cyamodontoids for which skull material is available in an effort to analyze the phylogenetic interrelationships within the Cyamodontidea. This will provide the necessary framework for the identification of the basal cyamodontoid skull morphology and the analysis of evolutionary changes of skull morphology within this group of fascinating reptiles.

Material Included in This Study

The following is a list of material included in the present study. Institutional abbreviations are: BMNH: British Museum (Natural History), now The Natural History Museum, London; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; FAFl, Magayar Alami Földtani Intézet (Geological Institute of Hungary, Budapest); GPIP, Geologisch-Paläontologisches Institut, Universität Tübingen; HU-Pal., Paleontological Collections, Department of Evolution, Systematics and Ecology, Hebrew University, Jerusalem; MB.R., Museum für Naturkunde der Humboldt Universität, Berlin, fossil reptile collection; MBSN, Museo Brembano di Scienze Naturali, San Pellegrino; MFSN, Museo Friuliano di Storia Naturale, Udine; MNS, Museo Civico di Scienze Naturali “E. Gaiffi,” Bergamo; MSNM, Museo Civico di Storia Naturale di Milano; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; SMF, Senckenberg Museum, Frankfurt a.M.; SMNS, Staatliches Museum für Naturkunde, Stuttgart; ST, Museo della Vicaria di S. Lorenzo, Zogno (Bergamo, Italy); UMO, Urvelt-Museum Oberfranken, Bayreuth.

Cyamodus hildegardis Peyer, 1931a: PIMUZ T4763 (holotype), T4768 (original of Peyer, 1935, Pl. 46, Figs. 1a–c, and Pinna, 1992, Fig. 6), T4771 (original of Pinna, 1992, Fig. 7), T2796 (original of Kuhn-Schnyder, 1959, Pl. I, and Pinna, 1992, Fig. 8).

Cyamodus “laticeps” (Owen, 1858): BMNH R 1644 (holotype).

Cyamodus kuhnschnyderi Nosotti and Pinna, 1993a: SMNS 15855 (holotype), SMNS 16270 (paratype); MHI 1294 (incomplete skull).

Cyamodus muensieri (Agassiz, 1839): BSP AS VII 1210 (holotype, original of Münster, 1830, skull no. II; Meyer, 1863, Pl. 31, Figs. 1–2).

Cyamodus rostratus (Münster, 1839): UMO BT
748 (holotype, original of Drevermann, 1928; Kuhn-Schnyder, 1965a).

Cyamodus cf. rostratus: SMNS 17403 (incomplete skull, original of Nosotti and Pinna, 1993b, Fig. 3); UMO BT 2172 (isolated lower jaw, original of Drevermann, 1928, Pl. 23, Fig. 2); SMF R-4040 (isolated lower jaw, original of Drevermann, 1928, Pl. 23, Figs. 3a–d, and of Rieppel, 1995a, Fig. 31).


Placochelyanus stoppanii Osswald, 1930: BSP AS I 1457 (holotype).

Placochelys alpis sordidae Broili, 1921: BSP 1921.1.3 (holotype).

Placochelys placodonta Jaekel, 1902b: FAFI Ob/2323/Vt.3. (holotype); MB.R. 1765 (paratype).


Psephoderma alpinum H. v. Meyer, 1858: BSP AS I 8 (holotype, carapace); MSNM V471 (skull; referred specimen); MSNB 4884a–b (juvenile skull, original of Pinna, 1979).


fc.st facet (on quadrato) receiving the shaft of the stapes
f.jug jugular foramen
f.l lacrimal foramen
f.pdl posterior dental lamina foramen
f.pin pineal foramen
f.trig trigeminal foramen
f.vest vestibular (oval) fenestra
in internal naris
ju jugal
m maxilla
mc Meckel’s canal
n nasal
op opisthotic
p parietal
pl palatine
pm premaxilla
po postorbital
pof postfrontal
pq.rc palatoquadrate cartilage recess
pra prearticular
prf prefrontal
pro prootic
pt pterygoid
pt.f posttemporal fenestra
pto.f pteroccipital foramen
q quadrate
qj quadratojugal
sang surangular
so supraoccipital
sp splenial
sq squamosal
sq.bt squamosal buttress (receiving the distal end of the paroccipital process)
stc sella turcica
v vomer

List of Abbreviations Used in the Figures

ang angular
ar articular
bo basioccipital
c coronoid
c.ce canal for internal carotid
d dentary
ds dorsum sellae
eo exoccipital
ep epipterygoid
ep.o epiotic ossification
f frontal
f.cc foramen for cerebral carotid
f.ch.t. chorda tympani foramen

The Cranial Anatomy of Placochelys placodonta

Remains of Placochelys placodonta were first collected in 1899 by Desiderius Laczkó in the Alsó Keuper (upper Middle Triassic) of Jeruzalemhegy (Jerusalem mountain) near Veszprém, a small town in west central Hungary, located on the south slopes of the Bakony Mountains overlooking Lake Balaton. Subsequent collecting efforts yielded two skulls, several carapace fragments, and scattered remains of the postcranial skeleton. The new genus and species was described by Jaekel in 1902, who subsequently presented the material in a comprehensive mono-
graph (Jaekel, 1907). The holotype (skull, specimen I of Jaekel, 1907) is three-dimensionally preserved (Fig. 1), but was incompletely prepared at the time of its original description. A cast of the holotype in its original condition, that is, as described by Jaekel (1902a, b, 1907), is kept at the Geological Institute of Hungary. The second skull (Fig. 2) is dorsoventrally compressed and was figured in ventral view only by Jaekel (1907, Pl. III).

The holotype was later sent to Frankfurt a.M. for further preparation by Christian Strunz, because Fritz Drevermann planned to study the specimen in greater detail. Strunz separated the lower jaw from the cranium and fully exposed the braincase. Drevermann never got around to describing the specimen, but it was briefly dealt with in a publication by Huene (1931). The figures published by Huene (1931) are erroneous in many details, as will be discussed below. In his monograph, Jaekel (1907) made only passing reference to the second skull, which later received no further attention other than a photograph included in Kuhn-Schnyder (1965b, Fig. 8) and Müller (1968, Fig. 235).

Parts of the postcranial remains of Placochelys placodonta were lost during World War II (Westphal, 1975). The material now missing comprises the following elements illustrated by Jaekel
Fig. 2. Skull of Placochelys placodonta Jaekel (paratype, MB.R. 1765): A, dorsal view; B, ventral view. Scale bar = 20 mm.

(1907): Pl. V, Figs. 2–7; Pl. VI, Fig. 4; Pl. VII, Figs. 3, 5–6, 8, 10–11; Pl. VIII, Figs. 1–18. Casts of the right femur (BMNH R 4070, 4074) and of the left humerus (BMNH R 4069) are kept at The Natural History Museum, London.

Measurements of the Holotype

The anterior tip of the rostrum is broken in the holotype. All measurements are given as pre-

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<td>posterior maxillary tooth</td>
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<td>anterior palatine tooth</td>
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<tr>
<td>posterior palatine tooth</td>
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served in the fossil. Measurements in parentheses are those of the right side of the skull. Measurements for the maxillary and palatine tooth plates are given in Table 1.

Tip of rostrum to occipital condyle: 118.3 mm
Tip of rostrum to mandibular condyle of quadrate: 119.2 (116.4) mm
Tip of rostrum to posterior margin of skull table: 112.8 mm
Maximal length of skull: 148 mm
Tip of rostrum to anterior margin of external naris: 21.2 (20.5) mm
Tip of rostrum to anterior margin of internal naris: 32.0 (32.0) mm
Tip of rostrum to anterior margin of orbit: 39.1 (38.5) mm
Tip of rostrum to anterior margin of upper temporal fossa: 83.5 (82.1) mm
Longitudinal diameter of external naris: 12.5 (13.0) mm
Transverse diameter of external naris: 9.8 (10.0) mm
Longitudinal diameter of internal naris: 7.1 (7.0) mm

Table 1. Measurements of maxillary and palatine tooth plates of Placochelys placodonta (holotype, MAI Ob/2323/Vi.3). All measurements in mm; approximate values in parentheses.
Transverse diameter of internal naris: 4.3 (4.1) mm
Longitudinal diameter of orbit: 26.1 (27.4) mm
Transverse diameter of orbit: 27.4 (24.8) mm
Longitudinal diameter of upper temporal fossa: 52.1 (51.5) mm
Transverse diameter of upper temporal fossa: 32.9 (32.4) mm
Distance from external naris to orbit: 7.0 (7.0) mm
Distance from orbit to upper temporal fossa: 18.5 mm
Bony bridge between external nares: 6.3 mm
Bony bridge between internal nares: 4.0 mm
Bony bridge between orbits: 10.6 mm
Bony bridge between upper temporal fossae: 8.2 mm

Morphological Description of the Skull

All cyamodontoid placodonts with the exception of *Henodus* (Huene, 1936) have a skull with a broadly expanding temporal region and a narrow, tapering rostrum. Proportions vary from a rather short and blunt rostrum in *Cyamodus* (Nosotti & Pinna, 1996) to a very elongate, narrow rostrum in *Psephoderma* (Pinna & Nosotti, 1989; see also further discussion below). *Placochelys* is intermediate between these two extremes, with an elongate and narrow rostrum formed by the premaxillae (Fig. 3A). The tip of the rostrum is broken in the holotype, and the rostrum is altogether missing in MB.R. 1765. The rostrum is sufficiently well preserved in the holotype, however, to allow the conclusion that the premaxilla of *Placochelys* was edentulous. In ventral view, distinct longitudinal grooves can be seen running from the anterior margins of the external nares anteriorly up to the broken tip of the rostrum. These grooves are delineated laterally by the maxilla (in their posterior part) and by the premaxilla (in their anterior part), and medially by a raised ventral crest running along the medial edge of each premaxilla.

The premaxilla broadly enters the anterior and lateral margin of the external nares. It forms a distinct (autapomorphic) posterior process that extends backward from the posteroventral corner of the external nares to a level slightly behind the anterior margin of the orbit, embraced both dorsally and ventrally by the maxilla (Fig. 4A). A comparable process is not observed in other cyamodontoid taxa. Dorsomedially, the premaxilla meets the nasal between the two external nares in a posteroLaterally trending suture.

In ventral view (Fig. 3B), the contact of the premaxilla with the maxilla posterolaterally and the vomer posteriorly is obscured by paint covering the bone surface. In dorsal view, however, the anterior end of the maxilla can be seen to expand medially to form most of the dermal floor of the external naris. The ventral outline of the anterior end of the maxilla has been reconstructed accordingly (broken lines in Fig. 3B), which indicates that the maxilla met the vomer along the anterior margin of the external naris, excluding the premaxilla from the latter.

The maxilla forms a slender anterior process that runs along the ventrolateral margin of the rostrum to a level well in front of the anterior margin of the external naris (Fig. 4A). It remains separated from the lateral margin of the external naris by the posterior process of the premaxilla. The maxilla expands medially below and deep to this posterior process of the premaxilla, as it forms most of the floor of the external naris. Between the external nares and the orbit, the maxilla forms a distinct ascending process with a pointed dorsal tip wedged in between the nasal anteriorly and the prefrontal posteriorly. The maxilla narrowly enters the anteroventral margin of the orbit, but further posteriorly it is excluded from the ventral margin of the orbit by the anterior process of the jugal. The posterior end of the maxilla forms an essentially vertical and deeply interdigitating suture with the jugal at a level somewhat in front of the posterior margin of the orbit but behind the level of the midpoint of the longitudinal diameter of the orbit. The lateral surface of the maxilla shows five to seven superior labial foramina (Fig. 4A).

In ventral view (Fig. 3B), the maxilla is seen to enter the anterolateral margin of the internal naris. It contacts the vomer anteromedially in front of the external naris (the suture between the two bones is distinct at the anterior margin of the internal naris), and the palatine lateral to the external naris. The maxilla remains excluded from the anterior margin of the subtemporal fossa by a lateral process of the palatine, which contacts the jugal. Each maxilla carries three tooth plates, of which the posteriormost one is distinctly larger than the two anterior ones (Table 1). In contrast to the holotype, MB.R. 1765 shows a distinct dental lamina foramen located on the palatine-maxillary suture posteromedial to the posterior maxillary tooth plate.
The nasals are paired, triangular elements that define the posteromedial margin of the external nares. They meet each other along the dorsal midline of the skull, separating the premaxilla from the frontal (Fig. 3A). The anterior tips of the nasals lie at a level behind the anterior margin of the external nares. In the holotype, a narrow but deep cleft separates the nasals from one another posteriorly, exposing the underlying frontal. Given the overall solid ossification of the skull and the tendency for the sutures to fuse in the dermal skull roof, it seems unlikely that the narrow cleft between the nasals reflects incomplete ossification of these latter elements. In no other cyamodontoid skull are the posterior parts of the nasals separated by a deep cleft exposing the underlying frontal. The posterolateral margin of the nasal runs from the posterior margin of the external naris in a posteromedial direction, contacting the ascending process of the maxilla, the anterior margin of the prefrontal, and the short anterolateral process of the frontal. The anterolateral process of the frontal therefore remains separated from the ascending process of the maxilla by the nasal and prefrontal (Fig. 3A).

The prefrontal is a rather small element located at the anterodorsal margin of the orbit. A medial ventral process forms the anteromedial margin of the orbit. The location of the lacrimal foramen cannot be identified unequivocally in *Placochelys*. The anteroventral corners of the orbits are not preserved in MB.R. 1765. The anteroventral margin of the right orbit is subject to breakage in the holotype. In the left orbit of the holotype, the prefrontal is seen to extend further down than in *Cyamodus kuhnschnyderi* and *Protenodontosaurus*, where the prefrontal remains excluded from the lacrimal foramen (Nosotti & Pinna, 1996, 1998; see further discussion of the latter two taxa below). In *Placochelys* the medial ventral process of the prefrontal reaches the maxilla and closely approaches the anterior process of the jugal without quite reaching it (Fig. 3A). The position of the lacrimal foramen is again obscured by breakage and compression. However, this break might pass through an area of weakness indicating the position of the lacrimal foramen, in which case the prefrontal might have entered its dorsal margin. Breakage likewise obscures the location of the foramen for the passage of the infraorbital division of the maxillary branch of the trigeminal nerve (infraorbital foramen sensu Oelrich, 1956) in the anteroventral corner of the orbit. However, *Placochelys* does not show a distinct groove running along the anteroventral margin of the orbit, identified as "basiorbital furrow" in *Cyamodus kuhnschnyderi* by Nosotti and Pinna (1996).

The frontals are paired in *Placochelys*, as in all other cyamodontoids. Short anterolateral processes of the frontal are embraced between the prefrontals and nasals. These anterolateral processes of the frontal are shorter (i.e., less well developed) in *Placochelys* than in some other cyamodontoids. The concave lateral margin of the frontal broadly enters the dorsal margin of the orbit between the prefrontal and the postfrontal. A massive break running obliquely through the skull table and the right postorbital arch obscures sutural details of the frontoparietal suture. However, a posterolateral lappet of the frontal is clearly identifiable on the left side of the skull, indicating that the frontoparietal suture was located at a level between the posterior margin of the orbit and the anteroposterior margin of the temporal arch (Fig. 3A).

The postfrontal is a broad element that defines the posterodorsal margin of the orbit. Its ventral process tapers off along the posterior margin of the orbit but remains separated from the jugal by the postorbital. The posterior process is rather broad and extends backward to about the level of the anterior margin of the temporal fossa; it remains narrowly excluded from the anteromedial margin of the upper temporal fossa by a contact of the postorbital with the parietal. Posteriorly the postfrontal meets the parietal in an interdigitating suture, which slightly trends in an anteromedial direction. The medial margin of the postfrontal is more or less straight. The posterolateral margin of the postfrontal is deeply concave and angled in *Placochelys*, as it also is in *Cyamodus kuhnschnyderi* (Nosotti & Pinna, 1996), but unlike in *Cyamodus rostratus* (Kuhn-Schnyder, 1965a), *Protenodontosaurus*, or *Psephoderma*, where this bone has a less concave and more evenly curved posterolateral margin.

The unpaired (fused) parietal forms a rather rectangular and flat skull table characterized by extensive dermal ornamentation (Fig. 3A). The parietal skull roof carries four distinct tubercular protuberances. Posterolateral processes of the parietal define the posteromedial margins of the upper temporal fenestrae as well as the deeply concave occiput and meet the squamosal in an interdigitating suture that runs across an osteodermal encrustation located at the posteromedial margin of the upper temporal fossa (left side of skull in Fig. 3A). The lateral margin of the skull table narrowly projects laterally beyond the descending
flange of the parietal, which participates in the formation of a secondary lateral wall of the braincase in a manner described in more detail below.

The presence and position of the pineal foramen in Placochelys remain uncertain. Jaekel (1907, Pl. I) figured a relatively small pineal foramen located between the parietals at the level of the anterior margin of the upper temporal fossa but clearly behind the frontoparietal suture. Jaekel's (1907, Pl. I) drawing includes an element of reconstruction, however, because a massive break passes through the skull at precisely this level.
Huene (1931, Pl. I) nevertheless followed Jaekel's (1907) lead but increased the size of the pineal foramen located in the same position (i.e., behind the frontoparietal suture). Other cyamodontoids (Cyamodus, Protenodontosaurus, Psephoderma: see below) all have an equally large and anteriorly placed pineal foramen, but the frontal reaches farther back and narrowly approaches, or even enters, its anterior margin. Although Huene's (1931) reconstruction appears plausible by comparison with other cyamodontoids, the cast of the skull of the holotype before its preparation by Strunz shows a distinct splint of bone embedded in the break in exactly the location where Jaekel (1907) and Huene (1931) placed the pineal foramen. The two possible conclusions are that this splint of
bone is in a natural position, in which case Placochelys would lack a pineal foramen, or alternatively, the splint of bone is in a displaced position, in which case Jaekel's (1907) and Huene's (1931) reconstructions might be correct. The skull roof of MB.R. 1765 is severely damaged, with its anterior part missing. The break through the skull table lies at a level of the anterior margin of the upper temporal fossa. This again might indicate an area of relative weakness, perhaps caused by a large and anteriorly placed pineal foramen.

The postorbital broadly enters the posteroverentral margin of the orbit, from where it extends posteriorly to define the anterior and the greater part of the lateral margin of the upper temporal fossa. Huene (1931) believed the postorbital to extend far back along the medial margin of the upper temporal fossa, exposed in dorsal view lat-
eral to the parietal. This configuration of the postorbital could not be confirmed for the holotype, where the postorbital meets the parietal at the anteromedial margin of the upper temporal fossa, or for MB.R.1765. In lateral view, however, the postorbital can be observed to form a posterior vertical flange that extends backward for a considerable distance below the overhanging rim of the parietal skull table (Fig. 4A), overlapping the ventral flange of the parietal and completing the anterodorsal part of the secondary lateral wall of the braincase dorsal to the epipterygoid. At the postdorsal corner of the orbit, the postorbital forms a stout ventromedial process that abuts the lateral surface of the anterodorsal corner of the epipterygoid. The postrolateral process of the postorbital extends along the lateral margin of the upper temporal fossa to a level behind the midpoint of the longitudinal diameter of the latter. This postorbital process does not narrow significantly at its posterior extremity, and meets the squamosal in an interdigitating suture (but see discussion below).

The jugal carries a narrow anterior process that forms most of the ventral margin of the orbit dorsal and medial to the maxilla (Figs. 3A, 4A). At the anterolateral margin of the subtemporal fossa, the jugal forms a distinct posteroventral lappet, ornamented with a pattern of radiating grooves and ridges. Behind the orbit, up to a level of about the midpoint of the postorbital arch, the jugal is sutured to the postorbital. More posteriorly, however, the jugal separates from the postorbital and narrows to a pointed tip located somewhat in front of the posterior end of the postorbital, at about the level of the midpoint of the longitudinal diameter of the upper temporal fossa and about the lower third of the height of the temporal arch. Together, the dorsal margin of the jugal and the ventral margin of the postrolateral process of the postorbital define a distinct V-shaped sutured pattern (the tip of the V pointing forward), thus embracing the anterior process of a bone whose identity remains to be discussed (see discussion below and Fig. 4A).

The squamosal of cyamodontoid placodonts is a very complex bone. Its body defines the postrolateral margin of the upper temporal fossa as well as the dorsal, lateral, and ventral margins of the posttemporal fossa. A dorsomedial process of the squamosal meets the postrolateral process of the parietal at the postrolateral margin of the upper temporal fossa anteriorly and at the dorsal margin of the posttemporal fossa ventrally. These sutural relations are very distinct, both in the holotype of Placochelys and in MB.R. 1765 (Fig. 5A). In dorsal view, the contact of the squamosal with the parietal is bridged by an elongated dermal encrustation located at the posterior margin of the upper temporal fossa (left side of the skull in Fig. 3A). This dermal encrustation tends to obscure the squamosal–parietal suture in the holotype, particularly on the right side of the skull, whereas MB.R. 1765 clearly shows this interdigitating suture traversing the postrolateral part of the dermal encrustation (Fig. 5A). In lateral view and inside the temporal fossa, a narrow process of the squamosal can be followed along the dorsal margin of the posttemporal fossa, meeting the postrolateral process of the epipterygoid in the anterodorsal corner of the posttemporal fossa. A similar contact of the epipterygoid with the squamosal at the anterodorsal corner of the posttemporal fossa is also observed in Cyamodus rostratus (Kuhn-Schnyder, 1965a), but this character remains unknown for Cyamodus kuhnschnyderi (Nosotti & Pinna, 1996), Protenodontosaurus, and Psephoderma.

A ventromedial process of the squamosal curves around the lateral margin of the posttemporal fossa, thereby establishing a broad ventrolateral contact with the quadrate. Specimen MB.R. 1765 shows particularly well how this process of the squamosal extends anteromedially along the anterior aspect of the paroccipital process (Fig. 5B). Sutured to the opisthotic, this process of the squamosal forms the postrolateral margin of the pteroccipital foramen (sensu Nosotti & Pinna, 1993b, to be discussed in detail below), which is bordered anteromedially by the opisthotic.

A neomorphic process of the squamosal, the otic process sensu Nosotti and Pinna (1993b), extends anterolaterally from the lower margin of the posttemporal fossa along the dorsal margin to the dorsomedial flange of the quadrate ramus of the pterygoid and meets the prootic at the anterolateral corner of the pteroccipital foramen. As a result, the otic process of the squamosal forms the lateral margin of the pteroccipital foramen, which is bordered anterolaterally by the prootic (Figs. 3A, 6A, 6B).

It is the anterior and lateral relations of the squamosal that remain the most controversial aspect of the dermatocranium in placodonts (Pinna, 1989; Zanon, 1989). The debate largely results from the difficulty of separating the squamosal from the quadratojugal within the temporal arch of placodonts. Pinna (1989; see also Pinna & No-
Fig. 5. Skull of *Placochelys placodonta* Jaekel (paratype, MB.R. 1765): A, dorsal view; B, ventral view. Scale bar = 20 mm. For abbreviations, see p. 3.

sotti, 1989; Nosotti & Pinna, 1993b) reconstructed a very narrow squamosal that is barely exposed in the lateral view of the temporal arch both in *Placodus* and cyamodontoids. This leaves room for an expansive quadratojugal that broadly enters the lateral margin of the upper temporal fossa between the postorbital and squamosal. Examination of all *Placodus* skulls in public repositories (Rieppel, 1995a) did not yield conclusive evidence to support Pinna’s (1989) reconstruction of the squamosal and quadratojugal in that taxon. In fact, none of the specimens shows a distinct and unequivocal suture line separating the squamosal from the quadratojugal within the temporal arch (Rieppel, 1995a). The delineation of quadratojugal and squamosal in cyamodontoids is further
complicated because the lateral surface of the posterior part of the temporal arch is subject to the encrustation of dermal tubercles that obscure sutural patterns. The only specimen apparently supporting Pinna's (1989) reconstruction of a small squamosal in cyamodontoids is *Cyamodus cf. rostratus* SMNS 17403 (Nosotti & Pinna, 1993b, Fig. 3), which shows what looks like a V-shaped contact of the squamosal with the quadratojugal at the posterolateral corner of the upper temporal fossa (but see the detailed description of the specimen below).

A quadratojugal is unquestionably present in Placochelys, and it covers the lateral surface of the quadrate as in all other cyamodontoids. The suture separating the quadratojugal from the shaft of the quadrate is distinct in the occipital view of the skull (Fig. 4B). Equally distinct is the suture between quadratojugal and squamosal on the posterolateral aspect of the skull, at the level of the...
dorsal head of the quadrate. More anteriorly and laterally, this suture disappears under a dermal tubercle. Squamosal and quadratojugal therefore remain indistinct from one another in the posterior part of the lateral surface of the temporal arch of the holotype (Fig. 4A). The medial surface of the temporal arch likewise offers no further clues.

In M.B.R. 1765, the same sutural relations between postorbital and jugal can be observed as were described for the holotype. The two bones again embrace a V-shaped anterior process of a posterior element (Fig. 5A). The pointed posterior tip of the jugal again lies somewhat in front of the posterior end of the postorbital and above the

FIG. 6. Placochelys placodonta Jaekel (holotype, FAFI Ob/2323/Vt.3); right lateral braincase wall, partially reconstructed. Scale bar = 20 mm. For abbreviations, see p. 3.
ventral margin of the temporal arch. In this specimen, however, a suture line can be observed to extend backward from the posterior tip of the jugal in a more or less horizontal direction until it disappears under dermal encrustation on the postero-lateral aspect of the temporal bar. In addition, the right side of the skull of MB.R.1765 rather clearly shows the anterior tip of the quadratojugal tapering off along the ventral margin of the lower temporal arch below the jugal, reaching far forward to a level in front of the anterior margin of the upper temporal fossa (Fig. 5A). A similar anterior extension of the quadratojugal can be reconstructed for the left temporal arch of the holotype (Fig. 4A). A horizontal suture extending backward from the posterior tip of the left jugal can also be identified in "Macroplacus" raeticus (Schubert-Klempauer, 1975; Rieppel, 1995a, Fig. 22), and, as in Placochelys, it appears to horizontally subdivide the posterior part of the temporal arch into a dorsal squamosal, broadly entering the upper temporal fossa, and a ventral quadratojugal. This, in any case, is the most plausible reconstruction of the relationship of these two bones when observations on the holotype of Placochelys placodonta and MB.R. 1765 are combined. All that is required is to link the suture that runs backward from the posterior tip of the jugal with the suture that separates the quadratojugal from the squamosal at the postero-dorsal corner of the skull, a connection that is obscured by dermal encrustation of the temporal region of the skull. The anterior extent of the quadratojugal may be autapomorphic for Placochelys, but this character remains insufficiently known in other cyamodontoids for meaningful comparison.

If the quadratojugal is reconstructed, as argued above, to form most of the ventral margin of the temporal arch and to be separated horizontally from the squamosal, the jugal and postorbital are left to embrace between themselves the anterior tip of the squamosal. In Placochelys, the anterior tip of the squamosal also reaches to a level in front of the anterior margin of the temporal fossa, an autapomorphy of the genus in comparison to other cyamodontoids.

In ventral view the skull shows the paired internal nares to be separated by paired vomers (Fig. 3B). The sutural contact of the vomer with the maxilla is distinct at the anterior margin of the internal nares on both sides. The ventral surface of the rostrum is painted with resin, obscuring further details of the relationships of the vomer with the maxilla and premaxilla. However, there is no indication of large anterior processes of the vomers, entering deeply between the premaxillaries, as is indicated in the figure published by Huene (1931). Posteriorly, the vomer contacts the palatine at the posteromedial corner of the internal naris.

As in all placodonts, the palatine is enlarged at the expense of the pterygoid. In Placochelys, it carries a smaller anterior and a much enlarged posterior tooth plate (Table 1). The palatine forms most of the posterior and lateral margin of the internal naris. Anteriorly and laterally, the palatine contacts the maxilla. At the anterior margin of the subtemporal fossa, the palatine carries a distinct lateral process that embraces the posterior end of the maxilla and contacts the jugal laterally (Fig. 3B). This lateral process cannot represent the ectopterygoid, as indicated in the figure published by Huene (1931), because it carries on its dorsal surface the anterior tip of a groove that housed the palatoquadrate cartilage in the living animal. Posteriorly, the palatine meets the pterygoid in an interdigitating suture that curves around the posterior margin of the posterior palatine tooth plate. Within a distinct depression on the palatine–pterygoid suture lies the large, transversely oriented dental lamina foramen, located postero-medially to the posterior palatine tooth plate (Fig. 3B). A small dental lamina foramen is located postero-medially to the anterior palatine tooth plate in MB.R. 1765 (Fig. 5B), but a similar foramen is not distinct in the holotype. In both specimens, irregular sutural lines are observed at the palatine–pterygoid contact, delineating a triangular area in the midline of the palate between the two bones (Figs. 3B, 5B). It appears possible that the dermal palate includes a small heterotopic ossification between palatines and pterygoids. In lateral view, the palatine can be seen to extend backward medial to the pterygoid to meet the quadrate along the lateral margin of the palatoquadrate cartilage recess (described in more detail below); more anteriorly, the dorsal surface of the palatine carries a groove that housed the palatine process of a cartilaginous palatoquadrate, which persisted in the adult.

The pterygoids complete the posterior part of the dermal palate. They meet one another in an interdigitating suture, which in the holotype shows an irregularly curved course (Fig. 3B). Laterally, the pterygoid forms a prominent, longitudinally oriented ventral flange and extends anteriorly to the level of the posterior third of the longitudinal diameter of the posterior palatine tooth plate. The ventral pterygoid flange forms a single
ventral projection. Compared to other cyamodontoids (see below), the palatal exposure of the pterygoid is relatively long in Placochelys: dividing the distance from the posterior margin of the pterygoid to the posterior dental lamina foramen by the distance from the posterior dental lamina foramen to the posterior margin of the internal naris yields a quotient of 0.45. Posterolaterally, the pterygoid forms a short quadratojugal view. The overlap of these two bones is well exposed in lateral view, as will be discussed in more detail below.

The presence or absence of an ectopterygoid in cyamodontoid placodonts again remains a matter of debate. Although generally assumed to be present (Huene, 1931; Pinna & Nosotti, 1989; Nosotti & Pinna, 1996), its delineation from the palatine and pterygoid has been notoriously difficult. The presence of an ectopterygoid in Psephoderma could not be ascertained (personal observation), and an ectopterygoid is positively absent in Protenodontosaurus (Nosotti & Pinna, 1998; personal observation). The lateral view of the skull (holotype) of Placochelys shows the pterygoid to be sutured to the quadratojugal opening and to the palatine anterodorsally (Figs. 6A, 6B). As is also seen in ventral view, the anterolateral tip of the pterygoid reaches to about the posterior third of the longitudinal diameter of the posterior palatine tooth plate. Exposed in lateral view in front of the pterygoid, a suture line appears to separate from the palatine a small, splintlike element that might represent an ectopterygoid. If so, the ectopterygoid would only line the anteromedial margin of the subtemporal fossa with hardly any ventral exposure at all. However, the supposed palatine-ectopterygoid suture seen in lateral view could also represent a crack, since no clear separation of an ectopterygoid from the palatine can be seen in ventral view.

Two elements ossify in the palatoquadrate of reptiles, the quadrate and the epitypoid. The quadrate of Placochelys can be described as being composed of a shaft and a broad anteromedial wing. The posterior aspect of the quadrate shaft is distinctly concave. The lateral surface of the shaft is covered by the quadratojugal (Fig. 3A). The mandibular condyle of the quadrate is bipartite, a central concavity matching the saddle-shaped articular surface of the lower jaw. A shallow stapedial recess is located on the anteromedial aspect of the quadrate shaft, located narrowly above the mandibular condyle (Figs. 3B, 5B); it must have received the (cartilaginous?) distal end of the stapes. In the holotype, a relatively large foramen can be identified, located lateral to the dorsal head of the quadrate, between the latter and the squamosal (Fig. 4B). The quadratojugal is excluded from this foramen on the left side but narrowly enters its ventral margin on the right side. The foramen may have served the passage of a lateral branch of the internal carotid or stapedial artery respectively to the temporal musculature. A comparable foramen is not distinct in MB.R.1765 (observed by deformation of the skull?) and is absent in all other cyamodontoids (but see the discussion of Macrophadus, below). The broad anteromedial wing of the quadrate forms the sloping posterior wall of the temporal fossa from which the posterior part of the external jaw adductor must have originated. It is well exposed in lateral view, as it demarcates the posterolateral margin of a deep palatoquadrate cartilage recess (Fig. 6).

The broad and complex epitypoid is the dominant element in the secondary lateral wall of the braincase. The bone can be described as consisting of two parts, an anterior portion with a deeply concave lateral surface and a posterior portion with a distinctly convex lateral surface (Fig. 6). These two parts of the epitypoid may correspond to the anterior “palatal ramus” and posterior “quadrate ramus” of the epitypoid of Cyamodus kuhnschodyeri (Nosotti & Pinna, 1996), although the opening that separates these two parts of the epitypoid in the latter is absent in Placochelys (the lateral opening within the epitypoid of Cyamodus kuhnschodyeri appears to be the result of incomplete ossification; Nosotti & Pinna, 1996: 27). The posterior part of the epitypoid of Placochelys shows a deeply concave posterior margin that defines the anterior margin of the trigeminal incisure, enclosed between the epitypoid and the prootic. Posterodorsally, the epitypoid is extended into a long, slender process that runs across the dorsal margin of the prootic and meets the squamosal in the anterodorsal corner of the posttemporal fossa (Fig. 6). Posteroventrally, the epitypoid narrowly contacts the prootic on the left side of the skull (of the holotype), thus closing the trigeminal incisure ventrally; a similar contact is absent on the right side of the skull. The ventral margin of the posterior part of the epitypoid shows a surface
of unfinished bone, which overhangs the medial margin of the palatoquadrate cartilage recess. The anterior part of the epipterygoid is sutured to the dorsal surface of the palatine and reaches far forward to a level dorsal to the posterior palatine tooth plate (Figs. 5A, 5B). The anteroventral tips of the epipterygoids of both sides converge toward the midline of the skull.

The prootic is exposed in lateral view (Fig. 6) as it emerges from below the narrow posterodorsal process of the epipterygoid. Its lateral surface is distinctly convex. The anterior margin of the prootic defines the posterior margin of the trigeminal incisure. The ventral margin of the prootic broadly meets the neomorphic otic process of the squamosal in an oblique suture. These two elements together form the ventral margin of the posttemporal fossa, which also represents the anterior margin of the pterocipital foramen (Figs. 3A, 6A). Laterally, the otic process of the squamosal together with the ventral margin of the prootic define the postero-medial margin of the palatoquadrate cartilage recess.

The palatoquadrate cartilage recess is a character of all cyamodontoid placodonts included in this study whose skulls are adequately preserved and prepared to reveal the morphology of the lateral braincase wall (Figs. 3A, 4A, 6). It is represented by a characteristic cleft with a triangular outline of its posterior part, bordered laterally by the medial wing of the quadrate and by the palatine, bordered medially by the squamosal, prootic, and epipterygoid, and floored by the pterygoid posteriorly and by the palatine anteriorly. This recess continues anteriorly as a distinct groove on the dorsal surface of the palatine, which in its anterior part turns laterally toward the anterior corner of the subtemporal fossa. In the living animal, this recess and groove must have housed cartilage of the palatoquadrate, which persisted in the adult in its classic position dorsal to the dermal palate (pterygoid and palatine) and which connected the two ossifications within the palatoquadrate (i.e., the quadrate and epipterygoid).

The pterocipital foramen (Nosotti & Pinna, 1993b) is another synapomorphy shared by all cyamodontoids included in this study with adequately preserved and prepared skulls. Whereas Placodus retains a complete cranioquadrate passage (Rieppel, 1995a), the latter is obliterated in cyamodontoids in its anterior part by fusion of the dermal palate to the basicranium and by the broad overlap of the dorsal wing of the pterygoid with the antero-medial wing of the quadrate. This overlap also closes a gap which in the skull of Placodus persists between the quadrate and pterygoid laterally and the lateral braincase wall medially, and through which the stapedial (temporal) artery reached the jaw adductor musculature. In cyamodontoid placodonts, the stapedial (temporal) artery reaches the jaw adductor musculature through the pterocipital foramen, located at the ventral margin of the posttemporal fossa (Figs. 3, 5, 6). It is bordered anteriorly by the otic process of the squamosal and the prootic, and posteriorly by the squamosal and the opisthotic, the latter extended into the paroccipital process. As the stapedial (temporal) artery branches off the internal carotid within the posterior part of the cranioquadrate passage, it turns dorsally to pass through the pterocipital foramen in front of the paroccipital process; it reemerges from the same foramen at the ventral margin of the posttemporal fossa, through which it gains access to the temporal musculature.

The occipital view of the skull features the relatively large posttemporal fossae, bordered dorsally by the occipital flange of the parietal and squamosal and ventrally by the slender paroccipital process (Fig. 4B). The supraoccipital is a trapzoidal element carrying a low median crest. It is obliquely inclined, contacts the parietal in an interdigitating suture anteriorly, and defines the dorsal margin of the foramen magnum posteriorly. The lateral margin of the foramen magnum is formed by the exoccipital. The exoccipitals of either side do not meet dorsal to the occipital condyle, which is formed by the basioccipital only. The occipital condyle of MB.R. 1765 shows a distinct notochordal pit on its posterior surface (Fig. 5B). The metotic (jugular or vagus) foramen (Rieppel, 1985) is enclosed between the exoccipital and the opisthotic. Neither the holotype nor MB.R. 1765 shows an internal subdivision of the metotic foramen that would have separated the exit of the roots of the glossopharyngeal, vagus, accessory, and hypoglossal nerves. Below the metotic foramen and lateral to the occipital condyle, the braincase forms two ventral processes on either side of the skull. The medial one, close to the occipital condyle, is the ventrally directed basioccipital tuber. A ventral process of the opisthotic is located lateral to the basioccipital tuber. The two ventral processes together enclose an opening or foramen, which may have trapped the internal carotid at the entry into the cranioquadrate passage. In the holotype, the basioccipital tuber and the opisthotic process do not extend ven-
trally to meet the basisphenoid or the posterior margin of the pterygoid, and the two structures also fail to make a ventral contact with each other, such that the passage of the internal carotid between the opisthotic and basioccipital is open ventrally (Fig. 4B). In MB.R. 1765, the opisthotic process and the basioccipital tuber are more strongly developed and meet each other ventral to the passage of the internal carotid, which is thereby captured in a closed foramen (Fig. 5B). Whether the close approximation of these two processes to the basisphenoid and pterygoid reflects natural relations or results from dorsoventral compression of the skull is difficult to determine. But given the relatively larger size of both structures in the specimen MB.R. 1765, it appears possible that the area was damaged during preparation of the holotype. In both skulls of Placochelys, the opisthotic is pierced by a small foramen located just above the ventral flange. The function of this foramen remains unknown; separate exit(s) for the root(s) of the hypoglossal nerve would be expected to be located within the exoccipital medial to the passage of the internal carotid.

Laterally, the opisthotic extends into a slender paroccipital process. The distal end of the paroccipital process abuts a distinct buttress, located on the lower surface of the squamosal medial to the dorsal head of the quadratojugal (Figs. 3B, 5B, 7). In MB.R. 1765, but not in the holotype, the squamosal buttress can be seen to extend into a medially directed ridge on the lower surface of the squamosal, which follows the anterodorsal aspect of the paroccipital process and meets the opisthotic in an oblique suture at the posterior margin of the paroccipital foramen (see above for a detailed description of the squamosal). Medial to this contact, MB.R. 1765 also displays the vestibular (oval) fenestra of the otic capsule, enclosed by the prootic anteriorly and the opisthotic posteriorly (Fig. 5B). Opisthotic and prootic remain separate, as is indicated by a distinct suture at the dorsal margin of the vestibular fenestra. The vestibular fenestra lies deep inside the posterior part of the cranioquadrate passage. In front of it, the cranioquadrate passage is obliterated by the fusion of the dermal palate to the basioccipitum and by the broad overlap of a dorsal flange of the pterygoid with the anteromedial flange of the quadrate. No stapes is preserved in MB.R. 1765, but an imaginary straight line that extends from the vestibular fenestra in a posterolateral direction connects the latter with the stapedial recess on the quadrate. The location of the paroccipital foramen behind this imaginary line would seem to indicate that the stapedial artery, which branches off from the internal carotid after the latter has entered the cranioquadrate passage through the gap between the basioccipital tuber and the ventral opisthotic process, would have passed behind the stapes on its way to the temporal region of the skull. However, the location of the paroccipital foramen with respect to the paroccipital process in the three-dimensionally preserved holotype of Placochelys suggests that the stapedial artery passed in front of the stapes instead.

The left side of the occiput of the holotype shows what looks like a distally bifurcated paroccipital process, or a sturdy process emerging from behind and below the paroccipital process (Figs. 4B, 8). This element was tentatively identified as the distal end of a massive stapes by Nosotti and Pinna (1996: 33). Following this interpretation, cyamodontoid placodonts would have lost an impedance matching middle ear and increased the volume of the stapes in a system that relied on sound transmission through bone only. Close inspection of the holotype shows, however, that the supposed stapes is not distinctly separated from the paroccipital process. Indeed, the two structures appear to be separated by breaks only, and where breaks are absent, the two structures appear to be confluent. In search of alternative explanations for the supposed stapes, reference may be made to the "lateral tubercler" on the paroccipital process of Cyamodus kuhnschmidtii: "By its posteroventral margin, close to the squamosal, the paroccipital process bears a small, downward and posteriorly projecting tubercle” (Nosotti & Pinna, 1996: 19). This structure, how-
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ever, is much smaller than the supposed stapes in the holotype of Placochelys, and a comparable "lateral tubercle" is absent on the perfectly preserved paroccipital processes of MB.R.1765. Instead, the latter specimen shows a slight expansion of the ventral surface of the paroccipital process into a weakly protruding flange with a rugose surface indicating muscle attachment, probably of the longissimus capitis muscle. Even if broken, this flange would not be large enough to match the supposed stapes in the holotype. However, MB.R. 1765 also shows a distinct ridge on the ventral surface of the squamosal, originating at the squamosal buttress for the paroccipital process and extending medially along the anterodorsal aspect of the latter (Fig. 5B). A comparable ridge is not easily identified in the holotype, and perhaps the supposed stapes could represent a broken segment of this ridge. In the end, however, the identity of the bone fragment tentatively identified as stapes in the holotype of Placochelys remains debatable, as was also noted by Nosotti and Pinna (1996). Should it indeed represent the stapes, it would add further weight to the argument that the stapedial (temporal) artery passed in front of the latter on its way through the pteroccipital foramen.

Breakage of the skull roof in MB.R. 1765 exposes details of the basicranium in dorsal view (Fig. 5A). Easily identified is the sella turcica on the basisphenoid–parasphenoid complex, located in front of a distinct dorsum sellae and pierced by two foramina through which the cerebral carotids must have gained access to the cranial cavity. The basisphenoid–parasphenoid complex is broken shortly in front of the sella turcica. The passage of the cerebral carotids through foramina in the sella turcica indicates that the internal carotid must have pursued an intracranial course after having traversed the posterior part of the cranoquadratus passage and after having given rise to the stapedial (temporal) artery. Unfortunately, none of the available skulls of caymodontoid placodonts allows detailed reconstruction of the course of the internal carotid canal through the basicranium. Only in Cyamodus kuhnschneideri is there some indication that the internal carotid entered the basi-sphenium between the basisphenoid and the otic capsule at the depth of the cranoquadrate passage. The internal carotid likewise passes between the basisphenoid and the otic capsule in the eosauropterygian genera Nothisaurus and Simosaurus (Rieppel, 1994a). Continuing anteriorly within this basicranial canal, the internal carotid must have bifurcated, the dorsal branch emerging through the sella turcica as cerebral carotid and the anterior branch continuing within the basicranial canal as palatine artery. This reconstruction of the course of the internal carotid raises the question as to how the palatine artery gained access to the soft palate, which it supplies with arterial blood. The only foramina in the dermal palate located at a level in front of the sella turcica are those identified above as dental lamina foramina. The large foramina located posteromedial to the posterior palatine tooth plates lie in close proximity to the foramina for the cerebral carotids through the sella turcica, which indicate the level of bifurcation of the internal carotid. It is conceivable that the palatine artery could have gained access to the soft palate by passing through these posterior dental lamina foramina.

Similar questions relate to the passage of the lateral head vein and the profundus branch of the trigeminal nerve through the cavum epipericum, which, in a generalized reptile skull, constitutes the anterior continuation of the cranoquadratus
passage, obliterated in cyamodontoids. MB.R. 1765 shows the basisphenoid–parasphenoid complex to lie dorsal to the dental palatines (Fig. 5A). No ossified base of the pila antotica (clinooid process) can be seen ascending dorsally from the lateral margin of the basisphenoid at the level of the sella turcica or dorsum sellae. There appears to be no ossification in the primary lateral wall of the braincase in *Placochelys*, in contrast to *Placodus*, where such an ossification was described as an “alisphenoid bridge” by Broili (1912).

The epipterygoid is located well lateral to the outer margin of the basisphenoid–parasphenoid complex, the latter representing the level of the primary lateral wall of the braincase. The body of the epipterygoid is obliquely inclined with respect to the dorsal surface of the palatine, meeting the latter at an acute angle. Through this relation of the bones, a narrow space becomes enclosed between the medial surface of the epipterygoid and the dorsal surface of the palatine, as can also be seen in a horizontally split skull fragment of a cyamodontoid from the Muschelkalk of Makhtesh Ramon, Negev (HUF-Pal. 220; Rieppel, Mazin & Thernov, 1999, Fig. 7). MB.R. 1765 is unusual, however, in that a vertical lamina of bone appears to descend from the margins of the broken skull roof to the dorsal surface of the palatine medial to the epipterygoid but lateral to the lateral margin of the basisphenoid–parasphenoid complex (Fig. 5A). This vertical lamina of bone appears to be separated from the epipterygoid by a gap that opens in a minute “foramen” or cleft close by the anterior tip of the epipterygoid on its medial side. Because it has no relationship to the lateral margin of the basisphenoid–parasphenoid complex, this vertical lamina of bone cannot represent an ossification of the primary lateral wall of the braincase. Also, the anterior “foramen” located between the vertical lamina and the epipterygoid appears to be too small to represent the anterior opening of a cavum epipetricum enclosed between the vertical lamina and the epipterygoid. It therefore appears that the epipterygoid has been longitudinally split because of dorsoventral compression of the skull, resulting in a vertical lamina that appears to be separated from the laterally placed part of the epipterygoid. Alternatively, it might be assumed that the epipterygoid broke along a horizontal line and that the dorsal part of the bone, which is very thin at its anterior margin in the holotype, was pushed ventrally medial to the base of the epipterygoid because of dorsoventral compression. This interpretation is supported by the observation that neither the holotype of *Placochelys* nor the horizontally split skull of the cyamodontoid from Makhtesh Ramon (HUF-Pal. 220) show a vertical lamina of bone separated from, and located medial to, the basal part of the epipterygoid that, because it cannot be an ossification of the primary lateral wall of the braincase, would have to represent a vertical downgrowth from the parietal, frontal, postorbital, or a combination thereof.

Whereas the maxillary and mandibular branches of the trigeminal nerve would have emerged from the trigeminal incisure behind the epipterygoid, the profundus branch would have emerged anteriorly from the cavum epipetricum (i.e., from the gap between the epipterygoid and the lateral margin of the basisphenoid–parasphenoid complex). The course of the lateral head vein, which in reptiles passes through the cranioquadrate passage and the cavum epipetricum, is less easily reconstructed for cyamodontoids because of the obliteration of the anterior part of the cranioquadrate passage (Nosotti & Pinna, 1996). Kuhn-Schnyder (1960) suggested that the lateral head vein would have escaped the posterior part of the cranioquadrate passage through the pteroccipital foramen, rather than passing through the cavum epipetricum. This certainly remains a possibility, but it must be remembered that there is a certain plasticity in the differentiation of the cranial venous system. During embryonic development, the primary head vein (vena capitis medialis) forms loops and sinuses surrounding the roots of the cranial nerves and the auditory sac as it becomes replaced, at least in part, by the lateral head vein (vena capitis lateralis), and as differences in the differentiation of these veins persists among reptiles in general, and in squamates in particular (van Gelderen 1924; Goodrich, 1930), the cranial veins of cyamodontoids may have been differentiated in a pattern that may not be easily compared with that seen in extant reptiles.

Another unsolved problem of the cranial anatomy of cyamodontoid placodonts is the course of the palatine and hyomandibular branches of the facial nerve. In reptiles, the facial nerve usually exits through a foramen located between the commissura basicaulapar and the commissura prae-facialis of the endocranium, which link the otic capsule with the basal plate and which both ossify as part of the prootic. However, the prootic of *Placochelys* lacks a foramen for the exit of the facial nerve (Fig. 6), as is also the case in *Cyamodus kuhnschnyderi* (Nosotti & Pinna, 1996).
Table 2. Measurements of the dentary tooth plates of *Placochelys placodonta* (holotype, MAFT Ob/2323/Vt.3). All measurements in mm; approximate values in parentheses.

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One specimen (MSNS 1923GP) of *Protenodonto- saurus* was observed to show an internal subdivision of the trigeminal incisure by a vertical strut of bone (Nosotti & Pinna, 1996). Should the posterior division of the incisure have served the exit of the hyomandibular branch of the facial nerve, the latter would have to have reached the middle ear region through the pteroccipital foramen (Nosotti & Pinna, 1996). Similarly, the paratype of *Cyamodus kuhnschnyderi* (SMNS 16270) shows, on the right side of the skull, a foramen at the ventral margin of the prootic closely behind the trigeminal incisure. Should this foramen have served as the exit of the hyomandibular branch of the facial nerve, it would again have to be assumed that the latter reached the middle ear cavity through the pteroccipital foramen. Alternatively, the hyomandibular branch might have exited the prootic in close proximity to the vestibular (oval) fenestra deep in the craniocaudal passage, a region not well exposed in any of the cyamontoid skulls available for study. The palatine branch of the facial nerve, on the other side, appears to have pursued an intracraniial course, joining the internal carotid and palatine artery respectively on their way through the basicranium (Nosotti & Pinna, 1996).

**Morphological Description of the Lower Jaw**

The lower jaw (Fig. 9) was separated from the skull by Strunz after the description of the holotype by Jaekel (1907). As is true for the rostrum, the tip of the mandibular symphysis is incomplete. The retroarticular processes also appear to be incomplete, probably because of damage inflicted on them through Strunz’s removal of dermal tubercles that were fused to the articular. The tip of the right coronoid process is incomplete, whereas the tip of the left coronoid process, although subject to some damage, appears to retain its original height at least at its anterodorsal corner. The total length of the (better preserved) left mandible is 122 mm; its total height at the anterodorsal margin of the coronoid process is 56.5 mm. Each dentary carries on its posterior part two tooth plates, of which the posterior one is distinctly larger than the anterior one (Table 2).

The dentaries form the deep, massive, and elongated mandibular symphysis, with some participation of the splenials at the ventral margin of the latter. Posteriorly, the dentary extends to a level well behind the anterior margin of the large coronoid process, thus carrying the large posterior tooth plate to a position partially medial to the anterior part of the coronoid process. The dentary is broadly exposed in lateral view, whereas the splenial gains only a limited lateral exposure along the ventral margin of the anterior part of the mandible. These relations are reversed on the medial aspect of the lower jaw, with a relatively narrow exposure of the dentary and a broad exposure of the splenial. The two bones are separated from one another by the prearticular.

The coronoid process is formed exclusively by the large coronoid, the dominant element on the lateral surface of the lower jaw. As is typical for most cyamodontoids, the coronoid reaches far down, closely approaching the ventral margin of the lower jaw (Fig. 9A). An anteroventral process of the coronoid, which overlaps the posterior part of the dentary, tapers to a pointed tip at a level below the anterior dentary tooth plate. The posteroverentral margin of the coronoid is rounded instead (distinct on the right mandible only). The lateral surface of the coronoid is turned outward along its ventral margin, forming a distinct shelf that overhangs the contact of the splenial with the angular along the ventral margin of the lower jaw. This shelf delineates the ventral extent of the area of insertion for superficial jaw adductor muscle fibers on the lateral surface of the coronoid.

The posterior part of the lower jaw includes the large angular, which extends anteriorly to a level in front of the apex of the coronoid process, where it tapers off in an overlapping sutural contact with the splenial. Behind the coronoid process, the lateral exposure of the angular is larger (deeper) than that of the surangular. The suture between the surangular and angular is not very distinct, however, but seems to correspond to a distinct and curved ridge on the lateral surface of the lower jaw. Concave ventrally, this ridge delineates the insertional facet for the superficial portion of the pterygoideus muscle. Along the dorsolateral edge of the
mandible and behind the coronoid process, the surangular forms a distinct, dorsally protruding rim lateral to the articular surface of the lower jaw, but does not appear to participate in the formation of this articular surface itself. The articular surface of the mandibular joint is saddle-shaped, matching the surface of the mandibular condyle of the quadrate. The articular extends posteriorly into a short retroarticular process. The retroarticular process is very distinct in the placodontoid genera Placodus and Paraplacodus (Rieppel, 1995a). In the better known genus Placodus, the retroarticular process is long, slender, and turned slightly upward. In contrast, the retroarticular process of cyamodontoid placodonts is generally short, stout, and has a posterovertrally sloping surface, as is seen in a perfectly preserved left mandible (Fig. 10) of Cyamodus hildegardis (Pimuz T2796; Kuhn-Schnyder, 1959, Pl. 1, Fig. b; Pinna, 1992, Pl. 10, Fig. 8). In Placochelys the chorda tympani foramen is located on the dorsal surface of the retroarticular process closely behind the articular facet within the articular.

The prearticular is a large element that, together with the angular, closes the large Meckelian canal medially (Fig. 9B). The latter opens posteriorly on the medial aspect of the lower jaw, where it forms a deep adductor fossa. The adductor fossa has a considerable longitudinal extension medial to the coronoid process and extends downward to

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**Fig. 9.** Lower jaw of *Placochelys placodonta* Jaekel (holotype, FAFI Ob/2323/Vt.3): A, lateral view; B, medial view. Scale bar = 20 mm. For abbreviations, see p. 3.
the ventral margin of the lower jaw. Two parallel, longitudinally oriented ridges are located on the dorsal surface of the angular at the bottom of the adductor fossa. These may have secured the attachment of tendinous plates of the bodenaponeurosis, into which inserted the fibers of the medial and deep portions of the external jaw adductor muscle. Similar ridges are seen at the bottom of the adductor fossa in Placodus (Rieppel, 1995a).

Dermal Ornamentation of the Skull

Cyamodontoid placodonts generally show a tubercular dermal ornamentation of the temporal bones of the skull. A closer look at Placochelys reveals two different components in the dermal ornamentation of the skull. The postfrontal, postorbital, and the parietal in particular show a pattern of ornamentation that might be called dermal encrustation, resulting in the formation of projections or bosses (Figs. 3A, 4A). The ossification center of the postfrontal and postorbital is elevated into a low and blunt apex, from which grooves and ridges radiate toward the margins of the bone. Reflecting the growth pattern of the underlying bone, this dermal encrustation appears to have developed simultaneously with the ossification of the underlying bone itself. The same appears to apply to the four relatively low and ill-defined tubercular encrustations observed on the parietal skull table and to the encrustations across the parietal–squamosal suture at the posteromedial margin of the upper temporal fossa. Whether these projections or bosses reflect areas of epidermal scales remains unknown, although it is likely. A much more pronounced pattern of dermal ornamentation is found on the surface of the posterior part of the squamosal and quadratojugal in the form of distinct dermal tubercles that are particularly well-developed at the posterolateral margins of the temporal region of the skull (Figs. 3, 4). These tubercles have a sharply defined base, which appears to have secondarily fused to the underlying bone. Their position correlates in no way with the growth pattern of the underlying bone. In specimens of Cyamodus hildegardis (PIMUZ T4763, T4771; Peyer, 1931a), it can be seen that the large temporal tubercles located on the posterior margin of the squamosal (PIMUZ T4771; Pinna, 1992, Fig. 7, right side of skull) match those aligned along the lateral margins of the carapace (PIMUZ, T4763; Peyer, 1931a, Pl. 15, right posterolateral margin of dorsal shield) both in size and shape. To judge from the mode of their attachment to the surface of the underlying temporal bones of the skull, it appears that these large tubercles initially developed independently from the underlying bone and only later fused to the surface of the latter.

The inference that these large and distinct dermal tubercles are secondarily fused to the underlying bone is supported by Jaekel’s (1907) figure of the holotype of Placochelys, which shows on both sides of the skull two such tubercles fused to the dorsal surface of the retroarticular process closely behind the mandibular joint, formed by the articular. As the latter represents an endoskeletal element, dermal tubercles must have fused to it after its ossification. The dermal tubercles on the retroarticular process were removed through preparation by Strunz.

Comparison of the Cranial Anatomy of Placochelys placodonta with That of Other Cyamodontoid Placodonts

A number of well-preserved and well-prepared skulls of cyamodontoid placodonts are available that allow a detailed comparison with the skull of Placochelys placodonta. These include Cyamodus rostratus (Münster, 1839) (UMO BT 748; original of Drevermann, 1928, and Kuhn-Schnyder, 1965a; SMNS 17403, referred specimen); Cyamodus kuhnschnyderi Nosotti and Pinna, 1993a (SMNS 15855, SMNS 16270; see also Nosotti & Pinna, 1996); Henodus chelyops v. Huene, 1936 (GPIT “specimens I and II,” syntypes of Huene, 1936; “specimens IV and VI,” collected in 1959); Macroplacus raeticus Schubert-Klempnauer, 1975 (BSP 1967 I 324); Protenodontosaurus italicus
Fig. 11. Skull of *Cyamodus rostratus* Münster (holotype, umo BT 748): A, dorsal view; B, ventral view; C, left lateral view. Scale bar = 20 mm.

Pinna, 1990b (MFSN 1819GP, MFSN 1923GP; see also Nosotti & Pinna, 1998), and *Psephoderma alpinum* Meyer, 1858a, b (MSNM V471, see also Pinna & Nosotti, 1989). All of the taxa mentioned above have been subject to personal observation and form the basis of the following comparative analysis.

The Cranial Anatomy of *Cyamodus rostratus* (Münster, 1839)

*Cyamodus rostratus* is the type species of the genus *Cyamodus* (H. v. Meyer, 1863). It is represented by an incomplete skull (umo BT 748, holotype) from the lower upper Muschelkalk (mo1) of Bayreuth (Bindlach, Lainecker Höhenzug), Bavaria, Germany (Fig. 11). umo BT 2172 and SMF R-4040 are two isolated lower jaws from the same locality. SMNS 17403 is an incomplete skull from the lower upper Muschelkalk (Trochitennkalk, mo1) from the Burre Quarly, Gaismühle near Crailsheim, southern Germany.

*Cyamodus rostratus* may represent the most generalized cyamodontoid with respect to many features of its cranial anatomy (Figs. 12, 13). The skull of *Cyamodus rostratus* (umo BT 748) is incompletely preserved and was redescribed by Kuhn-Schnyder (1965a). Both temporal arches are missing, as is the right suspensorium. The basi-
cranial length (tip of rostrum to basioccipital condyle) measures 106 mm. The longitudinal diameter of the left orbit measures 27.0 mm; the transverse (vertical) diameter of the same orbit measures 25.0 mm. The longitudinal diameter of the left upper temporal fossa approximates 60 mm; its transverse diameter can be estimated to measure 43 mm. By comparison with other cyamodontoids, the skull of *Cyamodus rostratus* shows a relatively high and narrow temporal region and deep orbits facing laterally.

The premaxillaries form a broad, short rostrum. Each premaxilla bears two teeth, which are bulbous and rounded but still form an anterior transverse crest reminiscent of chisel-shaped anterior premaxillary teeth seen in the sister-taxon of cyamodontoids, *Placodus* (Rieppel, 1995a). Short posterior (nasal) processes of the premaxillae enter between the external nares and meet the nasals in a V-shaped suture at about the level of the mid-point of the longitudinal diameter of the external nares (Fig. 12A). In ventral view, distinct yet slender posterior (vomerine) processes of the premaxillae meet the equally slender vomers at a level in front of the midpoint of the longitudinal diameter of the internal naris (Fig. 12B). The margin of the internal naris is fairly complete on the right side of the skull and shows that the premaxilla remains excluded from the anterior margin of the external naris by the vomer and maxilla (the suture between the latter two elements is indistinct). In lateral view, the transverse process of the premaxilla reaches backward to a level slightly in front of the posterior margin of the external naris. It forms the anteroventral margin of the external nares and meets the maxilla in a V-shaped suture (the apex pointing backward).

The nasals are broad, leaf-shaped structures (Fig. 12A). They define the posteromedial margin of the external nares and meet each other along the midline, thereby broadly separating the premaxilla from the frontal. Each nasal forms a short and tapering posterior process; together these embrace an anteromedial process formed by the frontals. Posterolaterally, the nasal meets the prefrontal, thus separating the frontal from the maxilla.

The frontals are paired and elongated elements that posteriorly reach to a level behind the anterior margin of the upper temporal fossa (Fig. 12A). Anterolaterally, each frontal forms a distinct yet slender anterolateral process that enters between the prefrontal and the nasal. Between the prefrontal and the postfrontal, the frontal broadly enters the dorsal margin of the orbit. The orbital margin of the frontal is distinctly concave. Although closely approaching the pineal foramen, the frontals remain excluded from it by the parietal. The posterior end of the frontal is rather broad and meets the parietal in a more or less transversely oriented, weakly interdigitating suture. Each frontal carries three distinct grooves on its posterior (postorbital) part that converge toward the pineal foramen.

The parietal forms a flat skull table with concave lateral margins, owing to a posterior constriction of the skull table. Distinct yet short anterolateral processes of the parietal are embraced by the posterior ends of the frontal and of the postfrontal. The relatively large pineal foramen is located close to the anterior margin of the parietal (Fig. 12A). The medial suture, separating the originally paired parietals, is still visible at the anterior margin of the pineal foramen. The laterally descending flange of the parietal is distinct. It contributes to the formation of a secondary lateral wall of the braincase as it meets the epipterygoid ventrally and the squamosal posteroventrally. The dermal encrustations on the parietal skull table resemble those of *Placochelys*: an unpaired postero- medial one, and two protuberances along each side of the skull table.

The prefrontal is small but relatively broadly exposed in dorsal view by comparison with *Placochelys*. Located at the anterodorsal margin of the orbit, it contacts the frontal dorsally, the nasal anteriorly, and the maxilla ventrally. It closely approaches but remains excluded from the lacrimal foramen, which is enclosed entirely by the maxilla.

The postfrontal is a broad, plate-like and roughly triangular element broadly entering the posterodorsal margin of the orbit (Fig. 12A). The posterolateral margin is deeply concave and angled. The posterior process tapers to a slender tip that lies alongside the parietal, extending backward to the same level as the frontal and separated from the anteromedial margin of the upper temporal fossa by a broad posteroventral process of the postorbital.

The postorbital again is a relatively large element that broadly enters the posteroventral margin of the orbit (Fig. 12A). A relatively broad posterodorsal process meets the parietal at the anteromedial margin of the upper temporal fossa at a level shortly in front of the posterior tip of the postfrontal, but well behind the level of the anterior margin of the upper temporal fossa. In contrast to *Placochelys*, the postorbital only margin-
ally overlaps the laterally descending flange of the parietal and does not extend further backward on the descending process of the parietal than does its dorsally exposed part.

Each maxilla carries two small, bulbous teeth, located at the level of the internal naris (Fig. 12B). Only the left internal naris is preserved, and its posterior margin appears smooth and natural. This indicates that the posterior maxillary tooth is located in front of the posterior margin of the internal naris. The maxilla enters the anterolateral margin of the internal naris, but the precise location of its contact with the vomer along the anterior margin of the internal naris cannot be assessed. The palatine meets the maxilla along the posterolateral margin of the internal naris at a level of about the midpoint of the longitudinal diameter of the latter. Behind the internal naris, the maxilla can be followed in ventral view as a tapering shelf of bone that meets the jugal well in front of the anterior margin of the subtemporal fossa (Fig. 12B).

In lateral view, the maxilla is seen to broadly enter the posteroventral margin of the external naris (Fig. 13A). Between the external naris and the orbit, the maxilla forms a distinct yet small
and slender ascending process, wedged in between the nasal and prefrontal. Further back, the maxilla broadly enters the ventral margin of the orbit, enclosing the lacrimal foramen at the anteroventral corner of the orbit (Figs. 12A, 13A). Posteriorly the maxilla meets the jugal in an essentially vertically oriented, sigmoidally curved, and interdigitating suture at a level somewhat behind the posterior margin of the orbit. Unlike in other cyamodontoids, the maxilla contacts the postorbital at the posteroventral margin of the orbit (Fig. 13A).

The jugal is incompletely preserved because of breakage of the temporal arch. In lateral view, the jugal is seen to form a short, small, anterior process that enters between the postorbital and maxilla but remains excluded from the orbital margin by the contact of the latter two bones (Fig. 13A). In ventral view, the jugal is seen to define the anterior margin of the subtemporal fossa. The right side of the skull shows an anterior palatal process of the jugal that enters deeply between the maxilla and the palatine, reaching anteriorly to a level slightly in front of the anterior palatine tooth plate (Fig. 12B). This corresponds to the level of anterior extension of the postorbital along the posteroventral margin of the orbit. Preservation is not good enough to ascertain whether the jugal be-
Table 3. Measurements of the palatine tooth plates of *Cyamodus rostratus* (holotype, UMO BT 748). All measurements in mm; approximate values in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>right palatine</th>
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<tr>
<td></td>
<td>longi-</td>
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<td></td>
<td>nal Φ</td>
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<tr>
<td>first toothplate</td>
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</tr>
<tr>
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<td>9.5</td>
</tr>
<tr>
<td>third toothplate</td>
<td>27.5</td>
</tr>
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</table>

comes exposed in dorsal view in the floor of the orbit between the maxilla and the postorbital laterally and the palate medially, or whether the palate meets the maxilla and postorbital dorsal to this anterior process of the jugal. In lateral view, the jugal can be observed to form a distinct, tapering postero medial process that extends along the anteromedial margin of the subtemporal fossa, where it enters between the palate dorsally and the pterygoid ventrally (Fig. 13A). A similar postero medial process of the jugal has not been re corded for other cyamodontoids. The ectoptery goid would be expected to be located at the anteromedial margin of the subtemporal fossa, but it is absent in *Cyamodus rostratus*.

The palatal view of the skull is somewhat difficult to interpret because of damage due to preservation and preparation (Fig. 12B). The vomers are paired elements that separate the internal nares from one another, but other than that little can be said about the precise nature of their contacts to neighboring bones. The palatines are the dominant elements in the dermal palate, each carrying three tooth plates, of which the posterior most plate is much larger than the two anterior ones (Table 3). The nature of the dentition in *Cyamodus rostratus* has generated considerable controversy because some of the teeth are obviously glued to the underlying bone surface at places where they may not have been originally located. This is particularly true of the anteriormost left palatine tooth. Kuhn-Schnyder (1965a) recapitulated the controversy and concluded that *Cyamodus rostratus* has two premaxillary, two maxillary, and three palatine teeth, the same tooth count proposed by H. v. Meyer (1863). I concur with this conclusion. The palatine bones themselves are badly broken, and the medial suture between them can be only partially identified. The left posterior palatine tooth plate is incompletely erupted. The posterior dental lamina foramina are distinct, located posterior to the palatine tooth plates on the palate–pterygoid suture.

The right pterygoid is incompletely preserved, but the left pterygoid indicates that the length of its palatal exposure is short relative to the length of the palate. The distance from the posterior margin of the dermal palate to the posterior dental lamina foramen is slightly larger or equal to 10 mm; the distance from the (left) posterior dental lamina foramen to the posterior margin of the left internal naris approximates 58 mm. The ratio of pterygoid length to palatine length thus is approximately 0.17.

The (left) pterygoid forms a distinct, longitudinally oriented ventral flange that unfortunately is broken along its ventral edge. It is therefore impossible to unequivocally ascertain whether there was a single or a double ventral projection on the pterygoid flange. However, the bipartition of the broken bone surface by a small intermediate stretch of finished bone with a slightly concave surface strongly suggests a double ventral projection, as is also observed in specimen SMNS 17403 (see below). The left lateral view of the skull shows rather distinctly the anterior extent of the pterygoid along the medial margin of the subtemporal fossa (Fig. 13A). The pterygoid extends to a level slightly behind the anterior margin of the posterior palatine tooth plate and approaches the anterior margin of the subtemporal fossa more closely than in other cyamodontoids.

The quadrate has a weakly concave posterior margin and is covered laterally by the quadrato jugal. The suture separating the quadrato jugal from the quadrate and the squamosal is distinct in occipital view; in lateral view, cracks and dermal encrustations obscure the dorsal delineation of the quadrato jugal from the squamosal.

The dominant element in the lateral wall of the braincase is the epipterygoid (Fig. 13A). As in other cyamodontoids, the epipterygoid can be described as consisting of two parts, a posterior part

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Fig. 13. A, Skull of *Cyamodus rostratus* Münster (holotype, UMO BT 748) in left lateral view. B, Left side of the occiput of *Cyamodus rostratus* Münster (holotype, UMO BT 748). C, Right side of the occiput of *Cyamodus rostratus* Münster (referred specimen, SMNS 17403). Scale bar = 20 mm. For abbreviations, see p. 3.

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with a convex lateral surface and an anterior part with a concave lateral surface, trending toward the midline of the skull. The ventral margin of the posterior part of the epipterygoid is formed by unfinished bone and overhangs the palatoquadrate cartilage recess. The ventral margin of the anterior part is sutured to the dorsal surface of the palatine. The dorsal margin of the epipterygoid meets the laterally descending flange of the parietal. Unlike *Plaechoelys*, *Cyamodus rostratus* shows no distinct ventromedial process of the postorbital abutting the lateral surface of the anterior dorsal part of the epipterygoid. Instead, the ventral process of the parietal is exposed as a narrow strip of bone between the posteromedial process of the postorbital (lining the anteromedial margin of the upper temporal fossa) and the dorsal margin of the epipterygoid. Between these two bones, the descending process of the parietal can be followed anteriorly up to the posterior margin of the foramen interorbitale (paired openings between the orbits filled, in life, by the cartilaginous interorbital septum; Gaffney, 1972), such that the epipterygoid contacts the parietal rather than the postorbital at the posterodorsal corner of the foramen interorbitale.

The posterior margin of the epipterygoid is deeply concave and forms the anterior margin of the trigeminal incisure. The posterior margin of the trigeminal incisure is formed by the prootic. Behind and dorsal to the trigeminal incisure and above the prootic, the epipterygoid forms a distinct, slender posterior process that meets the squamosal at about the midpoint of the dorsal margin of the posttemporal fossa (Fig. 13A).

The posterodorsal, posterior, and posteroventral margin of the posttemporal fossa is formed by the squamosal (Fig. 13B). The otic process of the squamosal is shorter in *Cyamodus rostratus* than in *Plaechoelys*; it meets the prootic at about the midpoint of the ventral margin of the posttemporal fossa, corresponding to the midpoint of the anterior margin of the paroccipital foramen (Fig. 12A; not exposed in lateral view in *Cyamodus rostratus*). At the same time, the prootic and the otic process of the squamosal form the dorsal margin of the posterior part of the palatoquadrate cartilage recess.

The ventral margin of the palatoquadrate cartilage recess is formed by the palatine anteriorly and by the quadrate posteriorly. Other than in *Plaechoelys*, the palatine does not contact the quadrate lateral to the recess in *Cyamodus rostratus* (Fig. 13A). This results in a greater width of the palatoquadrate cartilage recess, with the pterygoid forming its lateral margin between palatine and quadrate.

The right side of the occiput is very poorly preserved in the holotype of *Cyamodus rostratus*. On the left side (Fig. 13B), the posttemporal fossa is larger than in SMNS 17403 or in *Cyamodus kuhn-schnyderi* (see descriptions below). It is possible, however, that the lateroventral margin of the posttemporal fossa is incomplete (broken); parts of the squamosal may be missing, such that the pteroccipital foramen forms a deep cleft located in the lateroventral corner of the posttemporal fossa. On the other hand, breakage of the squamosal cannot be unequivocally ascertained, such that the configuration of the pteroccipital foramen in *Cyamodus rostratus* may represent the plesiomorphic condition relative to other cyamodontoids (see discussion of the derivation of the cyamodontoid braincase from that of *Placodus*, below). Other than at the lateroventral corner, the margins of the posttemporal fossa are complete, indicating a relatively large size.

The holotype of *Cyamodus rostratus* shows the distal tip of the posterior dorsal process of the epipterygoid to become exposed at the dorsomedial corner of the posttemporal fossa in occipital view (as in SMNS 17403, see below). In addition, the specimen shows the bilaterally symmetrical presence of an additional separate ossification in the occiput, a narrow strip of bone that extends from the medial corner of the posttemporal fossa toward the juncture of supraoccipital and exoccipital (Fig. 13B). The ventral suture, separating this element from the opisthotic, is distinct on both sides of the skull; the dorsal suture, separating this element from the supraoccipital, is distinct on the left side of the skull but appears partially fused on the right side. No comparable epiotic ossifications are known in other cyamodontid skulls.

Kuhn-Schnyder (1965a) described the presence of postparietals and tabulars in the occiput of the holotype of *Cyamodus rostratus*; however, the supposed suture separating the (dorsal) parietal from the (ventral) postparietal corresponds to the margin of a dermal encrustation situated on the posterior margin of the parietal skull table. The sutures indicated by Kuhn-Schnyder (1965a) to be located between the postparietals and tabulars remain enigmatic.

The supraoccipital is a relatively broad plate carrying a low median crest and defining the dorsal margin of the foramen magnum. The lateral margins of the foramen magnum are formed by
the exoccipitals. The basioccipital, forming the occipital condyle, is badly eroded and difficult to separate from the exoccipitals. However, a distinctly thickened rim runs along the ventral margin of the foramen magnum that seems to be bipartitioned at the midline of the skull. If indeed composed of the exoccipitals, this rim would indicate that the latter bones meet dorsal to the basioccipital, as they do in Cyamodus kuhnschnyderi.

The opisthotic forms the paroccipital process, which is severely damaged by a horizontal crack passing through it (Fig. 13B). This crack also obscures the vagus foramen. In ventral view, a medioventral extension of the squamosal appears sutured to the anterior aspect of the paroccipital process (as in SMNS 17403, see below). The distal end of the paroccipital process expands into a distinct, posteroventrally directed tubercle, as is also observed in SMNS 17403, as well as in Cyamodus kuhnschnyderi (Nosotti & Pinna, 1996). There is, in Cyamodus rostratus, no distinct buttress on the squamosal to receive the distal end of the paroccipital process.

Specimen SMNS 17403 is an incomplete skull that was used by Nosotti and Pinna (1993b) in support of their interpretation of the relations of the squamosal to the quadratojugal in the temporal arch. The specimen is supposed to show a distinctive suture separating the squamosal from the quadratojugal in the posterolateral corner of the upper temporal fossa. This suture starts laterally as a crack, below which the suture cannot be pursued on the lateral surface of the temporal arch. On the narrow dorsal surface of the temporal arch, the suture forms a “V” with the apex pointing backward. The lateral shank of that “V” crosses a dermal tubercle, but because these dermal tubercles secondarily fuse to the posterolateral aspect of the temporal arch, one would expect the suture to be concealed by this tubercle rather than passing through it. The medial shank of the suture meets the margin of the temporal fossa, but from there the suture cannot be followed onto the medial surface of the temporal arch. It is for these reasons that I consider this supposed suture between squamosal and quadratojugal not to be unequivocally distinct from a break or an artifact of preparation. By contrast, there is on the lateral surface of the temporal arch, at about the level of the dorsal head of the quadratojugal and below a posterolaterally placed dermal tubercle, a horizontal groove that might likewise be interpreted as a suture between the (dorsal) squamosal and the (ventral) quadratojugal in a position comparable to that seen in Placochelys.

Fig. 14. Cyamodus rostratus Münster (referred specimen, SMNS 17403); double ventral projection of the pterygoid flange. Scale bar = 10 mm.

The right lateral wall of the braincase again shows rather distinctly the posterior dorsal process of the epipterygoid, which meets the squamosal at the anterodorsal margin of the posttemporal fossa, and from below which emerges the prootic. The ventral view of the skull shows the large posterior palatine tooth plates with the dental lamina foramina located posterior and posteromedial to the latter. The longitudinally oriented ventral flanges of the pterygoid are well preserved on both sides of the skull, and both show a distinctly concave ventral margin. This results in a double ventral projection of the pterygoid flange, the anterior one located at the level of the posterior dental lamina foramina, the posterior one located at the posterolateral corners of the dermal palate (Fig. 14).

The most important information that can be obtained from specimen SMNS 17403 relates to the well-preserved right side of the occiput (Fig. 13C). Because of an increased occipital exposure of the parietal, squamosal, and opisthotic, the posttemporal fossa appears reduced by comparison with the holotype of Cyamodus rostratus and more closely resembles the occiput of Cyamodus kuhnschnyderi, which again shows reduced posttemporal fossae. Because the pteroccipital foramen is also of conventional size and position (at the lower margin of the posttemporal fossa) in SMNS 17403, the question arises again whether the lateroventral corner of the posttemporal fossa of the holotype of Cyamodus rostratus was subject to damage. As in the holotype of Cyamodus rostratus, however, SMNS 17403 shows the posterior dorsal process of the epipterygoid gaining an oc-
cipital exposure at the dorsomedial corner of the posttemporal fossa (Fig. 13C).

The right paroccipital process of specimen SMNS 17403 is intact. Its distal end is expanded into a distinct posterolateral tubercle, a character shared by the holotype of *Cyamodus rostratus* and by *Cyamodus kuhnschnyderi* (Nosotti & Pinna, 1996). Again, there is no buttress on the squamosal to receive the distal end of the paroccipital process. Instead, the distal end of the paroccipital process (opisthotic) meets the squamosal in a broad, interdigitating suture that trends ventrolaterally from the lateroventral corner of the posttemporal fossa (Fig. 13C). A similar sutural relation of the distal end of the paroccipital process to the squamosal appears to be present in the holotype of *Cyamodus rostratus* and in *Cyamodus kuhnschnyderi* (Nosotti & Pinna, 1996).

Specimen UMO BT 2172 (Drevermann, 1928, Pl. 23, Fig. 2) is a lower jaw with both rami in articulation (Fig. 15) that may be referred to *Cyamodus rostratus*. The bone surface is badly eroded, and the tips of the retroarticular processes as well as the apex of both coronoid processes are incomplete. Each mandible carries an anterior tooth of a generally bulbous shape but retaining a transversely oriented anterior crest. This anterior tooth is followed, after a short diastema, by two dentary tooth plates, of which the posterior one is distinctly larger (Table 4). The only unusual feature of the specimen is that the elongated lower jaw symphysis is deeply excavated (hollow) if looked at in posterior view.

Specimen SMF R-4040 is a much better preserved but smaller (? juvenile; Drevermann, 1928) left mandible referable to *Cyamodus rostratus*, which was described by Drevermann (1928, Pl. 23, Figs. 3a–d) and Rieppel (1995a, Fig. 31). It shows all the cyamodontoid characteristics, such as the large coronoid process formed by the coronoid bone, which closely approaches the ventral margin of the lower jaw, and the posterior dentary tooth plate, which is partially located medial to the coronoid process. The suture between the surangular and angular is distinctive in this specimen, perhaps because of its possible juvenile status (Rieppel, 1995a, Fig. 31). It shows that in the area behind the coronoid process, the lateral exposure of the surangular is larger (deeper) than that of the angular, in contrast to *Placochelys* (but note the difficulty in delineating the angular–surangular suture in the latter specimen). In SMF R-4040, part of the angular–surangular suture is ob-

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<tbody>
<tr>
<td></td>
<td>longi-tudinal Ø</td>
<td>trans-verse Ø</td>
</tr>
<tr>
<td>anterior dentary tooth</td>
<td>14.7</td>
<td>12.2</td>
</tr>
<tr>
<td>posterior dentary tooth</td>
<td>34.2</td>
<td>27.3</td>
</tr>
</tbody>
</table>
Table 5. Dentitional characters for the species of the genus *Cyamodus.*

<table>
<thead>
<tr>
<th>Species</th>
<th>Maxilla</th>
<th>Palatine</th>
<th>Posterior palatine tooth-plug long.</th>
<th>Trans. Ø</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. rostrinus</em></td>
<td>2</td>
<td>3</td>
<td>1.19</td>
<td></td>
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<tr>
<td><em>C. muensteri</em></td>
<td>3</td>
<td>2</td>
<td>1.32</td>
<td></td>
</tr>
<tr>
<td><em>C. laticeps</em></td>
<td>3</td>
<td>2</td>
<td>1.38</td>
<td></td>
</tr>
<tr>
<td><em>C. tarnowitensis</em></td>
<td>3</td>
<td>2</td>
<td>1.41</td>
<td></td>
</tr>
<tr>
<td><em>C. kuhnenschneideri</em></td>
<td>2</td>
<td>2</td>
<td>1.16 - 1.29</td>
<td></td>
</tr>
</tbody>
</table>

secured by a laterally protruding boss, which may represent a dermal encrustation on the lower jaw (less distinct and perhaps abraded in UMO BT 2172). SMF R-4040 shows four dentary teeth increasing in size from front to back, of which the posteriormost one is again much larger than the three anterior ones. This may represent ontogenetic tooth variation. Kuhn-Schnyder (1959) described the ontogenetic reduction of tooth positions in *Cyamodus hildegardis,* which also affects dentary teeth. The diastema observed between the anterior and the two posterior dentary teeth in UMO BT 2172 may thus have formed by reduction of one dentary tooth, the second from the front end of the mandible in SMF R-4040.

The Cranial Anatomy of *Cyamodus muensteri* (Agassiz, 1839)

Agassiz figured and named (*Placodus muensteri*) the holotype on plate 71, published as part of volume II of his *Recherches sur les Poissons fossiles* in 1839; the accompanying text was published in chapter VI, 2nd part, volume II in 1844 (Brown, 1890). The holotype of *Cyamodus muensteri* is a small cymodontoid skull (bsp AS VII 1210) that is badly preserved and poorly prepared (Fig. 16). The maximum length of the skull is 106.5 mm; the maximum width is 115 mm. Large parts of the skull are reconstructed and heavily painted. Agassiz (1833–1845) diagnosed the specimen mainly on the basis of its dentition, yet noted the unusually short rostrum and the wide temporal arches (both reconstructed in plaster, however).

Indeed, the entire rostrum was missing in the original skull. Attempting a reconstruction of the skull, Münster rounded off its anterior end with
plaster (as indicated by a dotted line in the figure published by Münster 1830) and arranged a series of small teeth (three on either side; the first right "maxillary" tooth is now broken) along its margin, as figured by Agassiz (1833–1845). The reconstruction of the skull by Münster is certainly unnatural, as was already noted by Meyer (1863), and the only indication of what the specimen may originally have looked like is Münster's (1830) first illustration. This shows the two enlarged, posterior palatine tooth plates in situ. Dividing the longitudinal diameter of the better preserved right posterior palatine tooth (25.9 mm) by its transverse diameter (19.6 mm) yields a ratio of 1.32, which is larger than the equivalent ratio for Cyamodus rostratus but very close to the values obtained for Cyamodus "laticeps" (see below). In front of the left posterior palatine tooth plate is the smaller, anterior palatine tooth plate, aligned with the left posteriormost maxillary tooth, which is located lateral to it. The right side of the skull shows three marginally positioned teeth increasing in size from front to back, as is also the case for the three maxillary teeth of Cyamodus "laticeps" (Owen, 1858). As noted by Meyer (1863, Pl. 31, Fig. 2), the anteriormost one of these three marginal teeth (now broken) is located slightly more medially than the posterior ones, as is again the case for the anteriormost maxillary tooth of Cyamodus "laticeps." Cyamodus muensteri can therefore be reconstructed to share three maxillary teeth with Cyamodus "laticeps" (and Cyamodus tarnowitizensis Gürich, 1884). Dentitional characters (Table 5) therefore suggest synonymy of Cyamodus muensteri and Cyamodus "laticeps" (the first name takes priority; the holotype of Cyamo-
Fig. 17. Continued.

dus tarnowitzensis Gürich, 1884, can no longer be located today, and the schematic illustration of the poorly preserved specimen is not diagnostic at the species level.

The Cranial Anatomy of Cyamodus "laticeps" (Owen, 1858)

The holotype of Cyamodus "laticeps" (BMNH R 1644) is an incomplete skull from the Upper Muschelkalk (mol) of Bayreuth (Fig. 17). The right posterior lateral part, comprising the skull table and the temporal region, is missing. Owen’s (1858, Pls. IX and X) illustrations represent a mirror image of the specimen. The skull is completely prepared, especially the left side of the braincase and the preserved left side of the occiput. It also appears that parts of these regions have been reconstructed and smoothed over using a mixture of glue and ground bone substance, as was commonly done with fossils for sale from Bayreuth, but without X-ray analysis, the extent of reconstruction is impossible to discern. The maximal length of the skull, as preserved, is 186 mm; the maximal width is 154 mm.

In size and general appearance, the skull closely resembles that of Cyamodus kuhnschnyderi (see below). The basicranial length can be reconstructed to approximate 150 mm in Cyamodus "laticeps," whereas the transverse diameter of the (left) upper temporal fossa may have approximat-
ed 65 mm. Dividing the basicranial length by the transverse diameter of the upper temporal fossa yields a ratio of approximately 2.3 (i.e., very close to *Cyamodus kuhnshnyderi*) and distinctly smaller than the ratio in cyamodontoids outside the genus *Cyamodus*, which all have a relatively narrower upper temporal fossa. *Cyamodus* “laticeps” differs from *Cyamodus kuhnshnyderi* in its dentition, however, as well as in the relation of the nasal and premaxillary. Because of damage done to the bone surface during early preparation, suture lines can be only partially identified on the skull of *Cyamodus* “laticeps,” primarily in the preorbital region of the skull. In the snout, the maxilla appears to meet the premaxilla in a suture that enters the anterolateral corner of the external naris. If correctly identified, this suture forms an anteriorly wide-open V as it trends toward the lateral margin of the upper jaw. The maxillary–premaxillary suture lies in a distinctly more anterior position in *Cyamodus* “laticeps” by comparison with *Cyamodus rostratus* and *Cyamodus kuhnshnyderi* (Nosotti & Pinna, 1996). The possibility remains, however, that what appears to be the premaxilla–maxilla suture may, in fact, be a break.

The external nares of *Cyamodus* “laticeps” are elongate and kidney-shaped. Their lateral (ventral) margin is formed almost exclusively by the maxilla. The nasal broadly enters the posterior and posteromedial (posterodorsal) margin of the external nares, whereas the premaxilla forms its anterior and anteromedial (anterodorsal) margin. Other than in *Cyamodus kuhnshnyderi*, the nasals are paired in *Cyamodus* “laticeps,” and they are separated from one another by elongate posterior (nasal) processes of the premaxillae, which meet the frontal at a level shortly in front of the anterior margin of the orbit (Fig. 17A). The frontal forms distinct anterolateral lappets, which remain separated from the maxilla by a broad contact of the nasal with the prefrontal. In *Cyamodus kuhnshnyderi*, the nasals are fused and meet the frontal in an almost straight transverse suture at a level shortly behind the level of the posterior margin of the external nares.

The prefrontal of *Cyamodus* “laticeps” is distinct on the right side of the skull, located at the anteromedial (anterodorsal) margin of the orbit and excluded from the lacrimal foramen, which is enclosed by the maxilla only. Closely comparable to *Cyamodus kuhnshnyderi*, a distinct “basiorbital furrow” (Nosotti & Pinna, 1996) lines the lateral (ventral) margin of the orbit, but within it only two foramina can be identified in *Cyamodus* “laticeps” (Fig. 17A). The larger anterior foramen represents the lacrimal foramen, whereas the smaller posterior one must represent the infraorbital foramen (*sensu* Oelrich, 1956), transmitting the infraorbital nerve. Subsequent to preparation and preservation, the elements bordering the basi orbital furrow cannot be identified.

Other than these, few sutural details can be gleaned from the dorsal view of the skull. The anterior tip of the left postfrontal can be identified at the postero medial (posterodorsal) margin of the orbit, which by comparison with the right prefrontal indicates that these two elements were separated from one another by the frontal along the dorsal margin of the orbit. The frontal is unpaired (fused). The lateral part of the suture separating the maxilla from the jugal is distinct on the left side of the skull, but this suture cannot be traced to the lateral (ventral) margin of the orbit. The posterior tip of the maxilla can be seen to extend to a level somewhat behind the midpoint of the longitudinal diameter of the orbit but in front of the posterior margin of the latter. Extrapolating from the identifiable part of the maxillary–jugal suture, the latter must have lined at least the posterior part of the basi orbital furrow. There is a weak indication of the suture separating the postorbital from the jugal at the postero lateral (posteroventral) corner of the orbit, but this could also represent a crack. The left temporal arch is damaged, as the dorsoventral compression of the skull resulted in the formation of a deep trough, but the unaltered dorsal (medial) part of the surface preserves the interdigitating suture separating the postorbital from the squamosal. Large tubercles have secondarily fused to the surface of the squamosal along the posterior and postero lateral margin of the upper temporal fossa.

The lateral braincase wall reveals very little structural detail. The most conspicuous feature is the trigeminal incisure, located between the epi pterygoid (anteriorly) and the prootic (posteriorly). The contours of these two elements, as well as the palatoquadrate cartilage recess and the pter ooccipital foramen, remain indistinct, which raises the suspicion that at least part of the lateral braincase wall has been reconstructed. The same is true for the preserved (left) part of the occiput.

The ventral view of the skull reveals even fewer sutural details (Fig. 17B). Identifiable are the ventromedial suture line between palatines, vomers, and premaxillae, and the suture between the quadrate ramus of the (left) pterygoid and the
Table 6. Measurements of the tooth plates of *Cyamodus muensteri* (holotype of *C. "laticeps," BMNH R 1644. All measurements in mm.

<table>
<thead>
<tr>
<th></th>
<th>longitudinal Ø</th>
<th>transverse Ø</th>
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<tbody>
<tr>
<td>1st premaxillary</td>
<td>10.6</td>
<td>9</td>
</tr>
<tr>
<td>2nd premaxillary</td>
<td>8</td>
<td>8.2</td>
</tr>
<tr>
<td>1st maxillary</td>
<td>11.3</td>
<td>10.4</td>
</tr>
<tr>
<td>2nd maxillary</td>
<td>13.2</td>
<td>11.5</td>
</tr>
<tr>
<td>3rd maxillary</td>
<td>17.2</td>
<td>17</td>
</tr>
<tr>
<td>1st palateine</td>
<td>21.5</td>
<td>17.8</td>
</tr>
<tr>
<td>2nd palateine</td>
<td>44.3</td>
<td>33</td>
</tr>
</tbody>
</table>

The Cranial Anatomy of *Cyamodus kuhnschnyderi* Nosotti and Pinna, 1993a

*Cyamodus kuhnschnyderi* (SMNS 15855, 16270) has been the subject of a recent monographic description (Nosotti & Pinna, 1996). The species shares with *Cyamodus rostratus* the relatively wide upper temporal fossae. Dividing the basicranial length (tip of snout to occipital condyle) by the transverse diameter of the upper temporal fossa yields a ratio of 2.3 in *Cyamodus kuhnschnyderi* (SMNS 15855, with parts of the left temporal arch preserved) and a ratio of approximately 2.45 for *Cyamodus rostratus*. All other cyamodontoids have relatively narrower upper temporal fenestrae, with a corresponding ratio ranging from 3.4 to 4.95.

The posterior (nasal) processes of the premaxillae meet the nasal at the level of about the midpoint of the longitudinal diameter of the external naris. Unlike all other cyamodontoids included in this study, the nasals are fused in *Cyamodus kuhnschnyderi*. In SMNS 16270, a partially fused suture is still apparent at the posterior margin of the nasal, but the nasals are clearly fused in their anterior part. The nasal broadly contacts the prefrontal, thus separating the frontal from the maxilla. The frontals are paired but may be partly fused at their posterior margin. They meet the (fused) parietal in a deeply interdigiting suture but remain narrowly excluded from the pineal foramen, which lies in an anterior position within the skull table. As in *Cyamodus rostratus*, the parietal forms short anterolateral processes, which are embraced by the frontal and the postfrontal. In addition to these anterolateral processes, each parietal forms a more medially located anterior process, which is embraced by the frontal only. Sim-
ilar processes are absent in *Cyamodus rostratus*. The posterolateral margin of the large postfrontal of *Cyamodus kuhnschnyderi* is deeply concave and angulated. The postfrontal closely approaches the anteromedial margin of the upper temporal fossa, separated from the latter by a narrow contact of the parietal with the postorbital.

The lateral view of the skull is very incomplete in both specimens, and the identification of sutures is rendered difficult by the extensive restoration of the specimens. The short jugal indicated in the reconstruction of the skull by Nosotti and Pinna (1996) is almost certainly incorrect and reflects the incompleteness of the temporal arches in both specimens. The postorbital of *Cyamodus kuhnschnyderi* does not form a posteromedial process that overlaps the laterally descending flange of the parietal, as seen in *Cyamodus rostratus*. The epitypargyroid contacts the parietal at the posterodorsal margin of the foramen interorbitale. Neither of the specimens is well enough preserved to allow the assessment of whether or not the epitypargyroid forms a posterior dorsal process meeting the squamosal at the dorsal margin of the posttemporal fossa. As in *Cyamodus rostratus*, the palatine fails to meet the quadrate lateral to the palatoquadrate cartilage recess (SMNS 15855). Other aspects of the lateral wall of the braincase of *Cyamodus kuhnschnyderi* have been discussed in comparison with Placochelys in the descriptive section above, such as the incomplete ossification of the epitypargyroid in both specimens and the possible course of the facial nerve through a foramen at the ventral margin of the prootic, close behind the trigeminal incisure (SMNS 16270).

In ventral view, the premaxillaries can be seen to remain excluded from the internal nares by a contact of the maxilla and vomer. There is no evidence for the presence of an ectopterygoid in *Cyamodus kuhnschnyderi*. The palatal exposure of the pterygoid is short relative to the length of the palatine. Dividing the length of the pterygoid (from its posterior margin to the dental lamina foramen on the palatine–pterygoid suture) by the distance from the pterygoid–palatine suture to the posterior margin of the internal nares yields values ranging from 0.2 to 0.3 for *Cyamodus kuhnschnyderi*. The longitudinally oriented ventral flange of the pterygoid is prominent and bears two distinct ventral projections: the anterior at the level of the posterior dental lamina foramen, the posterior at the posterolateral corners of the dermal palate (SMNS 15855, right side of skull).

*Cyamodus kuhnschnyderi* also differs from all other cyamodontoids with the exception of *Macroplacus raetius* (Schubert-Klemmnaer, 1975) and the specimen SMNS 17403 (referred to *Cyamodus rostratus* above) by a significant reduction in the size of the posttemporal fossa. This results from an expansion of the occipital exposure of the parietal, squamosal, and opisthotic. The exoccipitals meet dorsal to the occipital condyle in *Cyamodus kuhnschnyderi*. The right metotic (jugular, vagus) foramen of SMNS 16270 preserves an internal subdivision by a vertical strut of bone that separates a smaller anterior passage (transmitting the glossopharyngeal nerve?) from a larger posterior division (transmitting the vagus complex?). The paroccipital processes are relatively well preserved in specimen SMNS 15855, which shows the anterior aspect of the distal end of the right paroccipital process to be broadly sutured to the squamosal. The posteroventral aspect of the distal end of the paroccipital process is expanded into a distinct tubercle that projects into the space representing the posterior opening of the cranioquadrate passage.

*Cyamodus kuhnschnyderi* shows a distinct "basiorbital furrow" (Nosotti & Pinna, 1996). This is a groove running along the ventrolateral margin of the orbit on the inside of the anterior process of the jugal and of the maxilla, bordered medially by the palatine. Along the ventrolateral margin of the orbit, three foramina can be identified. The posteriormost one lies within the basiorbital furrow, between the jugal and the palatine; the intermediate one lies at the anterior end of the basiorbital furrow, between the maxilla and the jugal; and the anterior one lies at the anteroventral corner of the orbit in front of the basiorbital furrow, entirely within the maxilla. Nosotti and Pinna (1996) identified the anterior foramen as the lacrimal foramen and the intermediate one as the infraorbital foramen (*sensu* Oelrich, 1956), transmitting the infraorbital nerve. The interpretation of these foramina proposed by Nosotti and Pinna (1996; see above) leaves the posteriormost foramen unexplained. I concur with Nosotti and Pinna (1996) that the infraorbital nerve would have come to lie in the basiorbital furrow, but instead of passing across the posteriormost foramen located in that furrow, it most probably passed through it on its way to the superior alveolar canal. Following this interpretation, the anterior two foramina in the anteroventral corner of the orbit would have transmitted the branches of an anteriorly bifurcating lacrimal duct. Rather than the three foramina in *Cyamodus kuhnschnyderi*, there
are only two foramina in the equally distinctly differentiated basi orbital furrow of *Cyamodus "laticeps." This indicates some variation in the soft anatomy structures relating to the basi orbital furrow in *Cyamodus*, which renders the unequivocal identification of the function of these foramina difficult if not impossible.

The Cranial Anatomy of *Cyamodus hildegardis* Peyer, 1931a

Although several skulls of *Cyamodus hildegardis* are available, its cranial anatomy remains very poorly known because of the severe dorsoventral compression of the material (Peyer, 1931a, 1935; Pinna, 1992). The dentition, and its ontogenetic variation, was analyzed by Kuhn-Schnyder (1959). Personal inspection of the available material of *Cyamodus hildegardis* did not result in the collection of new data. One of the better preserved skulls (PIMUZ T4771) shows large dermal tubercles fused to the posterolateral side of the squamosal, similar to those observed in *Cyamodus kuhnschnyderi*. Doubts have been expressed that the three species of the genus *Cyamodus* could be treated as congeneric (Kuhn-Schnyder, 1960), and Nosotti and Pinna (1996) have treated the genus *Cyamodus* as paraphyletic. This problem cannot be solved easily, because the cyamodontoid material from the Germanic Muschelkalk consists almost exclusively of skulls, whereas *Cyamodus hildegardis* is best known from its postcranial skeleton. If the three carapace fragments from the Muschelkalk have been correctly assigned to *Cyamodus kuhnschnyderi* by Nosotti and Pinna (1996, Fig. 14), they would indicate that the dermal armor of the latter taxon is distinct from that of *Cyamodus hildegardis*. The enlarged posterior tooth plates of *Cyamodus hildegardis* are more distinctly elongated than those of the *Cyamodus* from the Germanic Muschelkalk and approach proportions otherwise typical for the Alpine genus *Psephoderma* (Table 7; see also comments below).

As incomplete as our current knowledge is of the cranial anatomy of *Cyamodus hildegardis*, the taxon can be coded for 35.2% of the 54 characters used in the cladistic analysis discussed below. The addition of *Cyamodus hildegardis* to the analysis did not result in a loss of resolution and corroborated, on the basis of cranial characters, the monophyly of the genus *Cyamodus*, including *C. hildegardis*.

### Table 7. Proportions of the posterior palatine tooth plate throughout the Cyamodontoidea.

<table>
<thead>
<tr>
<th>Species</th>
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<tr>
<td><em>Cyamodus rostratus</em></td>
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</tr>
<tr>
<td><em>Cyamodus kuhnschnyderi</em></td>
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<td></td>
</tr>
<tr>
<td><em>Cyamodus laticeps</em></td>
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<td></td>
</tr>
<tr>
<td><em>Cyamodus muensteri</em></td>
<td>1.32</td>
<td></td>
</tr>
<tr>
<td><em>Cyamodus hildegardis</em></td>
<td>1.33 - approx. 1.4</td>
<td></td>
</tr>
<tr>
<td><em>Protenodontosaurus laticeps</em></td>
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<td></td>
</tr>
<tr>
<td><em>Placochelys placodonta</em></td>
<td>approx. 1.23 - 1.3</td>
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<td><em>Psephoderma alpinum</em> (juvenile)</td>
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</tr>
<tr>
<td><em>Psephoderma alpinum</em> (adult)</td>
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<td></td>
</tr>
<tr>
<td><em>Placochelys alpis sordidae</em></td>
<td>1.44</td>
<td></td>
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<tr>
<td><em>Placochelys stoppanii</em></td>
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The Cranial Anatomy of *Henodus chelyops* v. Huene, 1936

*Henodus chelyops* is known from a total of eight specimens (comprising seven skulls), all of which come from the same deposit and locality, the upper Gipskeuper (Carnian) of Lustnau near Tübingen, southwestern Germany. Not all the skulls are currently accessible for investigation, because some are mounted on permanent exhibit, and preservation is not equal in all available skulls. The present description is based on the skulls of specimens I and II (syntypes, Huene, 1936), and the skulls of specimens IV and VI, which were collected in 1959 (Fischer, 1959) and have never been the subject of a detailed description before (Stein, 1993). Specimen I (Fig. 18) is a skull from which the left mandible has been removed and the right mandible has been left in articulation. This is one of the best specimens for study of the preorbital region of the skull in dorsal view. Although the skull roof is poorly preserved, this specimen shows good detail in the dermal palate and is the best skull for study of the quadrato suspension and the occiput. Specimen II (Fig. 19A) is the best skull for study of the skull roof and the temporal region behind the orbits. It also provides good detail on the structure of the dermal palate and some information on the occiput. Both
lower jaws have been removed from the skull and preserve most information on the structure of the mandible. The skull of specimen IV (Fig. 19B) shows good detail of the structure of the dermal skull in the pre- and postorbital region. The occiput and palate are rather poorly preserved, as are the mandibles. The skull of specimen VI is generally poorly preserved but provides excellent detail on the nature of the contact between frontal, postfrontal, and parietal.

Henodus is a highly autapomorphic cyamodontoid in every aspect of its anatomy (Fig. 20). Unlike in all other cyamodontoids, the rostrum of Henodus is extremely short yet broad, and the postorbital segment of the dermacranium forms a broad, flat covering of the braincase. Both the structure of the dermal palate and its dentition differ markedly from what is seen in other cyamodontoids. The skull of Henodus initially creates the false impression of being extremely depressed, but closer inspection shows that it is distinctly curved relative to the long axis of the lower jaw. The preorbital region is steeply inclined relative to the skull table, such that the external nostrils and the orbits face more or less anteriorly relative to the long axis of the lower jaw.

The premaxillae and maxillae form a short yet broad, spatulate rostrum. Immediately behind the premaxillae the skull is strongly constricted, a trait that corresponds to the rostral constriction observed in other sauropterygians. The skull reaches its narrowest dimension just behind the orbits. As the elements of the skull roof and cheek region together form an essentially horizontal dermal cover of the skull, the ancestral cheek emargination results in a weakly expressed concavity of the lateral margins of the skull table. The skull table reaches its greatest lateral extension just above the quadrate suspension. The posterior margin of the skull table is deeply concave, the squamosals projecting backward far beyond the level of the occiput, as is also the case in other cyamodontoids.

The paired premaxillae are the principal elements forming the rostrum, and have a complex morphology (Fig. 21A). Anteriorly the premaxillae form a transversely oriented, vertically descending flange that terminates in a ventral cutting

Fig. 18. Skull of Henodus chelyops v. Huene (syntype, GPF uncatalogued, specimen I of Huene, 1936): A, dorsal view; B, ventral view. Scale bar = 20 mm.
Fig. 19. Skull of *Henodus chelyops* v. Huene. A, Syntype, GPIT uncatalogued, specimen II of Huene (1936), dorsal view. B, GPIT uncatalogued, specimen IV, skull with lower jaw, left lateral view. Scale bar = 20 mm.
This cutting edge is reinforced on its anterior surface by a series of incompletely individualized denticles (Fig. 22), a strip of enamel lining the anterior surface of the cutting edge and mimicking the presence of a row of minute teeth in the more or less regularly spaced indentations and the development of pulp cavities (Stein, 1993, 1995; Reif & Stein, 1999). In dorsal view the premaxilla is exposed as a rather narrow strip of bone that defines the entire anterior margin of the external nares and meets the maxilla in the anterolateral (anteroventral) margin of the external nares, as is also the case in other sauropthygians. Posteriorly the premaxillae carry ascending nasal processes that define the medial margins of the external nares and project posteriorly up to the level of the anterior margin of the orbits, entering between the anterior parts of the frontals (Figs. 21A, B).

The nasal is a small, triangular element located at the posteromedial margin of the external naris, its apex pointing posteriorly. Together with the posterior (nasal) process of the premaxilla, the nasal embraces a well-developed anterolateral process of the frontal. Posterolaterally, the nasal contacts the medial (ascending) process of the maxilla (Figs. 21A, B).

In dorsal view, the maxilla caps the premaxilla laterally as it forms the lateral margin of the broad, spatulate rostrum. Behind the premaxilla,
Fig. 21. Skull of Henodus chelyops v. Huene. A, Dorsal view (specimen IV, GPF uncatalogued). B, Dorsal view (specimen I of Huene, 1936). Scale bar = 20 mm. For abbreviations, see p. 3.

Fig. 22. Premaxillary denticles in Henodus chelyops v. Huene (specimen II of Huene, 1936).

at a level between the external naris and the orbit, the maxilla shows a distinct lateral constriction (Figs. 20, 21). The ascending process of the maxilla is medially directed and forms the posterolateral (posteroventral) margin of the external naris before entering between the nasal and prefrontal. The nasal and prefrontal generally remain separated from one another by a contact of the ascending process of the maxilla with the anterolateral process of the frontal, although this contact may be very narrow (specimen II, Fig. 20B). Posteriorly the maxilla is separated from the jugal by a suture that in dorsal view appears V-shaped (the apex pointing backward) and is located at about the level of the midpoint of the longitudinal diameter of the orbit (Fig. 20A). The maxilla therefore defines the anterolateral (anteroventral) margin of the orbit, where it forms a pronounced basiorbital furrow (Figs. 20A, 21A, B), otherwise recorded for Cyamodus kuhnschnyderi and C. “laticeps” only among cyamodontoids (Nosotti & Pinna, 1996). In Henodus, two distinct foramina are located in the anteiror half of the basiorbital furrow, of which the anteiror one may correspond to the lacrimal foramen, whereas the posterior one may have served the passage of the maxillary
branch of the trigeminal nerve. In this character, *Henodus* resembles *Cyamodus “laticeps”* more closely than *Cyamodus kuhnschnyderi*. A lacrimal is absent in *Henodus*.

The prefrontal is a curved and rather slender element that forms most of the anterior margin of the orbit. It contacts the maxilla anteriorly and laterally (ventrally) and the frontal medially (dorsally). It always remains separate from the postfrontal along the dorsal margin of the orbit, which is formed by the concave lateral margin of the frontal (Figs. 20B, 21A).

The frontals are paired elongate and rather slender elements. They reach their maximal width at the level of the anterior margin of the orbit. Posteriorly, each frontal forms a narrow and elongate posterolateral process, each of which is embraced by equally narrow and elongate anterior processes of the parietal. The details of the contact between frontals and parietal are well preserved in specimens II (Fig. 20B), IV (Fig. 21A), and VI (Fig. 21B). The parietal is unpaired (fused). It forms an anteromedial process that enters between the postolateral processes of the frontal. More laterally, the parietal forms a more elongate and equally slender anterior process that enters between the postolateral process of the frontal and the postfrontal and may extend anteriorly up to a level close to the posterior margin of the orbit.

The postfrontal broadly enters the postomedial (postorodorsal) margin of the orbit. Shortly behind the orbit the postfrontal is distinctly constricted, which results in an angulation of its lateral margin (Fig. 21A). The posterior process of the postfrontal, which extends between the anterolateral process of the parietal and the postorbital, appears broad at its posterior end as it meets the parietal in a deeply interdigitating suture in specimen IV. By contrast, the postfrontal tapers to a blunt tip posteriorly in specimens I and II.

The postorbital is a large, broad, platelike element that defines the postolateral (postorobial) margin of the orbit and partially invades the space of the upper temporal fenestra (Fig. 20B). The element covers most of the postorbital area of the skull in front of the parietal and is bifurcated posteriorly as it embraces the tapering anterior end of the squamosal. The postomedial process of the postorbital extends along the postfrontal and meets the parietal in a deeply interdigitating suture. This postomedial process may (specimen II, Fig. 20B) or may not (specimen IV, Fig. 21A) exceed the postfrontal in length; it corresponds to that part of the postorbital that in the plesiomorphic condition lines the anteromedial margin of the upper temporal fossa. The postolateral process of the postorbital may (specimen IV) or may not (specimen II) exceed the postomedial process in length, and in the plesiomorphic condition contributes to the formation of the temporal arch as it lines the anterolateral margin of the upper temporal fossa.

The jugal enters the lateral (ventral) margin of the orbit between the maxilla anteriorly and the postorbital posteriorly. It forms the anterior part of the lateral margin of the (horizontally exposed) cheek before it starts to taper off posteriorly. This posterior process of the jugal may (specimen II, Fig. 20B) or may not (specimen IV, Fig. 21A, left side of skull) reach as far back as the posterior tip of the postorbital. Specimen IV, however, shows that this character is subject to variation between the left and the right side of the skull.

None of the specimens shows a clear demarcation of the squamosal from the quadratojugal. In front of the dorsal head of the quadratojugal, three anterior prongs can be identified within the (horizontally exposed) cheek region of the skull. The two medial prongs are here interpreted as representing the squamosal, embracing the postolateral process of the postorbital. The squamosal always remains shorter than the third, lateral prong, which forms the posterior part of the lateral margin of the (horizontally exposed) cheek and which is interpreted as the quadratojugal (by analogy to other cyamodontoids, Fig. 20B). The quadratojugal reaches anteriorly to a level close to the posterior margin of the orbit (specimen IV, Fig. 21A).

Large osteoderms have secondarily fused to the surface of the squamosal and quadratojugal along the postolateral and lateral margins of the skull table.

The upper temporal fossa is obliterated in *Henodus* (at least in the adult). Closure of the upper temporal fossa is mainly due to lateral spreading of the parietal ossification in a fan-shaped manner, best seen in specimens II (Fig. 20B) and IV (Fig. 21A). The only specimen that retains a vestigial upper temporal opening with a smooth, natural margin is specimen II (left side of the skull). The hole in the left side of the skull roof of specimen I (Fig. 18) is certainly an artifact of preservation. At this juncture, a brief comment on the skull of specimen III appears to be in order, because it was claimed by Huene (1938) to show well-developed temporal fossae on both sides of the skull. Although difficult to access because it is mounted on permanent exhibit, the skull of specimen III
allows some observations. The skull is not smaller than that of any of the other specimens. The so-called temporal fenestrae have irregular contours, and these differ on the two sides of the skull, suggesting that these temporal openings are the result of breakage, as is unquestionably the case with the opening in the left side of the skull roof in specimen I. In fact, the corresponding area of the skull roof appears relatively weak and prone to breakage in all Henodus skulls. The area of the conjectural temporal fossa is strongly depressed on the right side of the skull in specimen II, and it has been severely damaged in specimens IV and VI. Weakness of this area of the skull roof may result from a lateral thinning of the spreading of the parietal ossification responsible for the obliteration of the plesiomorphic temporal fenestra.

Most of the skulls have sustained a longitudinal break, obscuring the pineal foramen and making it difficult to assess whether the parietal is paired or fused. Specimen IV indicates, however, that the parietal is fused at least behind the pineal foramen. Specimen II shows the elongate and narrow pineal foramen to be located at the anterior end of the parietal (Fig. 20B). The frontal remains excluded from the pineal foramen. It remains unclear, however, whether the parietal is fused or whether it shows a midline suture in front of the pineal foramen.

The structure of the dermal palate of Henodus is again highly autapomorphic (Fig. 20C). The premaxilla is the dominant element in the broad rostrum in ventral view. The cutting edge of the premaxilla overbites the anterior cutting edge of the dentary. In the lateral part of its ventral surface, the premaxilla shows a distinct, transversely oriented trough which receives the lateral part of the cutting edge of the dentary. The broad premaxilla appears to enter the anterior margin of the internal naris. None of the specimens shows complete sutural contact between the premaxilla and the vomer. A short stretch of an obliquely oriented suture is seen on the left side of the palate of specimen II, located between the internal nares and indicating that the vomer enters the medial margin of the latter.

The maxilla reaches its maximum width in its anterior part, where it forms a lateral projection of the rostrum and enters the lateral margin of the internal naris. The ventral surface of the maxilla carries the highly characteristic, sigmoidally curved groove (Figs. 20C, 23), which was believed by Huene (1936) to have carried keratinous structures similar to baleen. Huene (1936) even claimed to have prepared such structures from the maxilla of one specimen, but this piece can no longer be located today.

None of the specimens shows in ventral view the sutural separation between the jugal and the maxilla, which in dorsal view is located at the level of the midpoint of the longitudinal diameter of the orbit. The suture between the maxilla and the palatine is distinct, however, running from the posterolateral corner of the internal naris posteri-orly and slightly laterally and terminating at about the posterior two-thirds of the maxillary groove (Fig. 20C). In none of the specimens is it possible to assess whether the posterior third of this groove is still formed by the slender maxilla extending backward between the jugal and palatine or whether this groove continues behind the maxilla either on the jugal or on the palatine.

There is no evidence for the presence of an ectopterygoid in Henodus.

The palatine is an elongate and rather slender element that is broadest in its anterior part, where it forms the posterior margin of the internal naris. A single small palatine tooth plate is located on
the posterior part of the palatine, at the back end of the maxillary groove (Fig. 20C). The dental lamina foramen is located posterior and postero-medial to the palatine tooth plate.

The paired vomers are broad elements that form the medial margins of the internal nares, from where they extend backward to meet the elongated pterygoids. The vomers separate the anterior parts of the palatines from one another. Unlike in any other cyamodontoid, the posterior parts of the palatines are separated by the paired pterygoids (Figs. 20C).

At the level behind the palatine tooth plate and its dental lamina foramen, the pterygoid extends laterally to cover the entire width of the dermal palate. The pterygoid also forms a weakly expressed, longitudinally oriented flange posterior to the palatine tooth plate with a single ventral projection. The short quadrate ramus of the pterygoid emerges from above this ventral flange and extends posterolaterally to contact the quadrate. In contrast to other cyamodontoids, the pterygoids broadly extend anteriorly between the palatines and meet the vomers at approximately the midpoint of the length of the palatines (Fig. 20C).

The quadrate and its suspension are again of a peculiar structure in Henodus, best observed in specimen I (Figs. 20A, 24). The mandibular condyle is transversely expanded and bipartite, to match the saddle-shaped surface of the mandibular articulation. The medial articular facet on the mandibular condyle is distinctly larger than the lateral facet. The lateral surface of the shaft of the quadrate is covered by a descending process of dermal bone, presumably part of the quadratojugal. Below the skull table, the quadrate expands into a large, elongated, posterior (suprastapedial) process, accentuating the concavity of its posterior margin. The posterior tip of that dorsal expansion of the quadrate abuts a distinct flange descending from the ventral surface of the squamosal. Between the dorsal expansion of the quadrate, the skull roof, and the descending flange of the squamosal there persists, in all specimens of Henodus, a gap that leads into the temporal vacuity of the skull.

None of the specimens of Henodus shows a well-preserved occiput, but some information can be obtained from specimens I and II. The post-temporal fossae are large (i.e., not reduced as in Cyamodus kuhnschnyderi or Macroplacus). The exoccipitals meet dorsal to the basioccipital in the occipital condyle. The sutureal contact of the exoccipital to the supraoccipital, to the basioccipital lateral to the occipital condyle, and to the opisthotic remains indistinct. As in other cyamodontoids, the opisthotic forms a distinct ventral flange, which together with the basioccipital tuber enclosed the passage of the internal carotid. The ventral opisthotic flange remains separate from the basioccipital tuber as well as from the basi-craniun. There is evidence for the expansion of the distal end of the paroccipital process into a ventrally directed tuber (now broken), comparable to the same character observed in Cyamodus kuhnschnyderi.

The distal end of the paroccipital process abuts the medial surface of the flange descending from the lower surface of the squamosal. On the left side of the skull of specimen II, this ventral process of the squamosal expands into a ventral flange that meets a dorsal flange originating from the quadrate ramus of the pterygoid. The squamosal and pterygoid thus define the closed lateral margin of the posterior opening of the cranioquadrate passage, but at the same time conceal the point of articulation of the stapes with the quadrate in the posterior or ventral view of the skull.

The lateral braincase wall is rather poorly preserved in all specimens available. As in other cyamodontoids, the most prominent element is the broad epipterygoid. Details of its relation to neighboring elements cannot be ascertained. A pteroccipital foramen can be identified in specimen I, but the sutures between the surrounding elements again remain indistinct. A palatoquadrate cartilage recess is present but still filled with matrix on the left side of the skull of specimen I. It is bordered ventrally by the palatine and pterygoid and posteriorly by the quadrate. It remains
unclear whether the palatine contacts the quadrate lateral to the palatoquadrate recess. The ventral margin of the palatoquadrate cartilage recess is complete, however, and does not show the gap that exists in these cyamodontoids where the palatine remains separate from the quadrate.

Specimens II and III show well-developed and well-ossified hyoid elements overlying the posterior part of the dural palate.

The lower jaw of Henodus is unusually deep and massive (Fig. 25). The anterior end of the dentary is sharply turned inward to form a transversely oriented cutting edge. No toothlike structures have ever been identified on the dentary. The mandibular symphysis is narrow and delicate, presumably a secondary development correlated with the development of a spatulate snout.

Behind the anterior, transversely oriented cutting edge the dentary carries a sigmoidally curved groove, the counterpart of the maxillary groove (Fig. 25C). At the posterior end of the dentary, behind that groove, is located the single and relatively small dentary tooth plate, opposing the palatine tooth plate with an occlusal surface that tilts somewhat medially.

The coronoid process is less well developed in Henodus compared with other cyamodontoids, which reflects a lesser degree of durophy in this genus. As in other cyamodontoids, the coronoid process is formed by the coronoid only, which also defines the anterior margin of the adductor fossa. Ventrally, the coronoid expands across the lateral surface of the mandible in a fan-shaped manner, but not to the same degree as is observed in other cyamodontoids, so that it remains rather broadly separated from the ventral edge of the lower jaw (Fig. 25A). The right mandible of specimen II shows a relatively broad contact between the dentary and the coronoid dorsally and between the splenial and angular ventrally. Both these latter elements gain a broad exposure on the lateral surface of the lower jaw. The lateral surface of the mandible furthermore shows a characteristic relief in that the surangular and angular form a distinct vertical step at the level of the anterior end of the adductor fossa. Superficial jaw adductor muscle fibers must have glided across the dorsal margin of that step (formed by the surangular) as they expanded to insert into the lateral surface of the coronoid, surangular, and dentary. The ventral margin of the mandible, composed of

Fig. 25. Lower jaw of *Henodus chelyops* v. Huene (partially reconstructed, based mainly on specimens I and II of Huene, 1936). A, Lateral view; B, medial view; C, dorsal view. Scale bar = 20 mm. For abbreviations, see p. 3.
splenial and angular, is distinctly sculpted and uneven in all specimens of *Henodus*.

The adductor fossa is a deep yet anteroposteriorly relatively short trough located medial to and behind the coronoid process. Anteriorly, the adductor fossa extends to a level well in front of the posterior margin of the dentary tooth plate.

The articular facet of the mandibular joint closes the adductor fossa posteriorly. The articular surface itself is strongly saddle-shaped and biconcave to accommodate the mandibular condyle of the quadrate. The chorda tympani foramen is distinct and located on the dorsal surface of the retroarticular process just behind the articular facet (Fig. 25C).

The retroarticular process is very prominent. It is deep, its dorsal surface slants posterovertrally, and it is distinctly sculpted to facilitate the attachment of muscle fibers or tendons.

The medial surface of the lower jaw (Fig. 25B) is covered by the prearticular, angular, splenial, and dentary. The prearticular and angular meet the dentary and splenial in an almost vertically oriented suture at the level of the coronoid process. The dentary and splenial close Meckel's canal in medial view. The canal opens anteriorly just behind the medial bent of the anterior end of the dentary.

The Cranial Anatomy of *Macroplacus raeticus* Schubert-Klempnauer, 1975

*M. raeticus* is based on an incomplete skull (asp 1967 I 324; Fig. 26) from the Bavarian Alps (Rhaetian Koessen-Formation, Hinterstein bei Hindelang im Allgäu: Schubert-Klempnauer, 1975). The skull is relatively large (maximal length as preserved: 181 mm; maximal width: 180.6), with a broad and relatively high temporal region. The rostrum is missing, with an oblique anterior break passing through the left external naris and just in front of the right external naris. The skull was subject to considerable erosion. It was prepared with acid and subsequently heavily coated with varnish. This, together with a tendency toward fusion of the bones, renders the unequivocal identification of sutures difficult if not impossible in some areas of the skull. The most prominent feature of the skull is the enormous posterior palatine tooth plates. Their distinctly elongate shape may have been the reason why Pinna (1978) considered *Macroplacus* a junior synonym of *Psephoderma* (*Psephoderma raeticus*).

Unfortunately, the most diagnostic feature of the skull, the rostrum, is incomplete in *Macroplacus*. In *Psephoderma*, the rostrum carries paired grooves on its lower surface that lead up to the internal nares, and the maxilla carries a distinct anterior process entering the rostrum in ventral view along the lateral margin of this ventral groove. In *Macroplacus*, the ventral surface of the preserved proximal part of the rostrum is deeply concave, forming a single longitudinal groove or trough (Fig. 26C). Likewise, the maxilla does not extend as far anteriorly along the lateroventral margin of the rostrum as it does in *Psephoderma*. Finally, the proportions and shape of the upper temporal fossae of *Macroplacus* are distinctly different from those of *Psephoderma alpinum*, which shows elongated but relatively narrow temporal fossae (see Table 8).

The dorsal view of the skull of *Macroplacus* (Fig. 26B) shows greatly enlarged posterior (nasal) processes of the premaxillae, that define the entire dorsal (medial) margin of the external nares and extend backward to the level of the anterior margin of the orbits, where they meet the frontals in an interdigitating suture. The nasals are relatively small, triangular elements that define the posterior margin of the external nares, and remain separated from one another by the broad posterior (nasal) processes of the premaxillae. The nasals narrow toward their posterior ends as they meet the prefrontals, thus separating the frontal from the maxilla. The posterior tip of the nasal lies at the same level as the posterior tip of the nasal process of the premaxilla. The two bones embrace a relatively small yet distinct anterolateral process of the frontal.

The maxilla forms most of the ventral and posterovertral margin of the external naris (Fig. 26A). Unlike in *Placochelys* and *Cyamodus*, the maxilla of *Macroplacus* does not expand medially to floor the external nares. Between the external nares and the orbit, the maxilla forms a distinct and pointed ascending process that is embraced by the nasal (anteriorly) and the prefrontal (posteriorly). Further back, the maxilla enters the anterovertral margin of the orbit. The lacrimal foramen is located in the anterovertral corner of the orbit and is fully enclosed by the maxilla (Fig. 26B). Posteriorly, the maxilla meets the jugal at the level of the midpoint of the longitudinal diameter of the orbit. Immediately below the ventral margin of the orbit, the suture separating the max-
Fig. 26. Skull of *Macroplacus raeticus* Schubert-Klemplauer (holotype, BSP 1967 I 324): A, left lateral view, B, dorsal view; C, ventral view. Scale bar = 20 mm. For abbreviations, see p. 3.
Table 8. Skull proportions of cyamodontoid placodonts. Measurements based on the holotype except ***, which is MSNM V471. Abbreviations: basicranial, distance from tip of snout to occipital condyle; long., longitudinal; temp.f., upper temporal fossa; trans., transverse; *) approximate values as reconstruction of the skull or severe preservational distortion of the skull is involved; **), measurements based on the right side of the skull.

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<tr>
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<td>4</td>
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<td><em>Macroplacus</em></td>
<td>-</td>
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<td>1.72</td>
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<td><em>Placochelys placodonta</em></td>
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<td>3.62</td>
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<td>3.38</td>
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<tr>
<td><em>Psephodera alpinum</em>**</td>
<td>2.46</td>
<td>4.95</td>
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illa from the jugal is V-shaped, the apex pointing backward. More ventrally, the maxillary–jugal suture becomes vertically oriented and interdigitating. It curves around the ventral margin of the skull shortly behind the posterior maxillary tooth (Fig. 26A).

As in all other cyamodontoids, the prefrontal is located at the anterodorsal margin of the orbit and displays limited dorsal exposure. It descends far down along the anterior margin of the orbit, closely approaching but not quite reaching the lacrimal foramen.

The delineation of the postfrontal and postorbital is difficult. The figures of the specimen (Figs. 26A, B) therefore entail an element of reconstruction. On the right side of the skull, a distinct, slightly interdigitating suture can be followed from the postero dental (posteromedial) margin of the orbit in a posterolateral direction at first, before the suture abruptly turns in a postero-medial direction, continuing its course up to the level of the anterior margin of the upper temporal fossa, where the suture turns laterally and becomes more deeply interdigitating. By comparison with other cyamodontoids, this suture must demarcate the medial and posterior margin of the right postfrontal, the latter establishing a medial contact with the frontal and a posterior contact with the parietal.

A distinct and interdigitating suture running into the posterolateral corner of the left orbit must delineate the anteroventral tip of the left postorbital. From the orbit this suture trends in a posterodorsal direction as it extends into the temporal arch. As it approaches the upper margin of the temporal arch, it forms a distinct vertical step, but then continues horizontally below the dorsal margin of the temporal arch before entering the margin of the temporal fossa at a level well behind the midpoint of the longitudinal diameter of the upper temporal fossa. This suture delineates the posterior lateral process of the postorbital, which in Macroplacus reaches far back within the temporal arch, as it also does in Placochelys and Psephoderma.

What remains unclear on both sides of the skull is the suture separating the postorbital from the postfrontal within the postorbital arch. Along the posterior margin of the left orbit there is a rather distinct step that might indicate the anteroventral tip of the postfrontal. Beyond that, however, it remains unclear whether the posterolateral margin of the postfrontal was smoothly curved or deeply convex and angulated, and whether the postfrontal was broadly or narrowly separated from the anteromedial margin of the upper temporal fossa by a contact of the postorbital with the parietal (the suture in the drawing represents a reconstruction without observational basis).

The jugal meets the maxilla at the level of the midpoint of the longitudinal diameter of the orbit. It therefore defines the posterior half of the ventral margin of the orbit. In Macroplacus, the jugal does not extend anteriorly beyond the level of the midpoint of the longitudinal diameter of the orbit as it does in Placochelys, where the jugal closely approaches the lacrimal foramen. Whether the jugal forms a distinct ventral expansion behind the maxilla as in other cyamodontoids cannot be established because of breakage. The jugal extends into the temporal arch to a level in front of the midpoint of the longitudinal diameter of the orbit, distinctly less far posteriorly than the postorbital. The posterior end of the jugal tapers to a blunt tip; this tip and the postorbital together embrace the anterior end of the squamosal (Fig. 26A). Along the ventral margin of the temporal arch, the jugal meets the quadratojugal at a level well behind the anterior margin of the upper temporal fossa, that is, further back than in Placochelys.

Macroplacus is an important specimen for reconstructing the relations of the quadratojugal and squamosal within the temporal arch. The V-shaped suture (apex pointing anteromedially) that separates the squamosal from the parietal along the posteromedial margin of the upper temporal fossa is distinct on the left side of the skull. No suture can be observed on either side of the skull that would separate the squamosal from the quadratojugal at the posterolateral margin of the temporal fossa, as would be required on the basis of Nosotti and Pinna’s (1993b) reconstruction of the temporal region of cyamodontoids (see also Pinna, 1989). Instead, the left side of the skull shows a horizontal line or groove that extends backward from the posterior end of the jugal and appears to represent the suture separating the dorsal squamosal from the ventral quadratojugal within the temporal arch (Fig. 26A). More posteriorly, this suture disappears below dermal encrustations on the posterolateral aspect of the temporal arch.

The frontals are paired, although the suture between the two elements may be partially obscured. Between prefrontal and postfrontal, the frontal forms the concave dorsal margin of the orbit. Unlike in any other cyamodontoids, the frontal widens conspicuously behind the orbit because of the concave median margin of the post-
frontal (Fig. 26B). The frontoparietal suture remains obscure, which makes it impossible to establish whether or not the frontal enters the pineal foramen.

The large pineal foramen is located at the level of the anterior margin of the temporal fossa. A longitudinal crack runs through the parietal skull table close to its midline, but fusion of the parietals is indicated by the absence of any trace of a suture either at the anterior or at the posterior margin of the pineal foramen. The parietal skull table is slightly constricted at its posterior end. Dermal encrustations are present, but ill-defined and weakly expressed on the skull table.

The ventral view of the skull (Fig. 26C) displays the dentition of *Macroplacus*, which comprises two maxillary teeth and two palatine tooth plates. The right maxilla is well delineated in ventral view. Although shorter than in *Plaichoelys*, *Protenodontosaurus*, and, especially *Psophoderma*, the maxilla carries an anterolateral process that tapers off along the lateral margin of the rostrum—unlike in *Cyamodus*, where the maxillary—premaxillary suture is transversely oriented (*C. kuhnschnyderi*) or even trends in a posterolateral direction (*C. rostratus*). Unfortunately, the anterior delineation of the vomers is difficult, which makes it impossible to unequivocally assess whether the premaxilla enters the internal naris in *Macroplacus*. The suture separating the maxilla from the palatine enters the lateral margin of the internal naris at about the level of the midpoint of its longitudinal diameter. From there the suture curves around the anterior palatine tooth plate and then trends posterolaterally toward the pointed posterior tip of the maxilla, which remains excluded from the anterior margin of the subtemporal fossa by a contact of the palatine with the jugal. The maxilla carries two tooth plates, the posterior one somewhat larger than the anterior one (Table 9). A nutritive foramen is located medial to the anterior maxillary tooth entirely within the maxilla. The nutritive (dental lamina) foramen of the posterior maxillary tooth plate is located behind the tooth on the maxilla—palatine suture.

At the level of the anterior margin of the subtemporal fossa, the palatine forms a lateral process that meets a medial process of the jugal (Fig. 26C). The jugal reaches to the anteromedial corner of the subtemporal fossa but does not extend backward along the medial margin of the latter as it does in *Cyamodus rostratus*.

The palatines are paired, much enlarged elements, each carrying the hypertrophied posterior palatine tooth plate along with a smaller, anterior palatine tooth (Table 9, Fig. 26C). The available specimens of *Psophoderma* indicate a relative size increase in the posterior palatine tooth plates during ontogeny. Given the relatively large size of the skull of *Macroplacus*, the hypertrophy of the posterior palatine tooth plates may be the result of their positive allometric growth. The right posterior palatine tooth plate is missing. A posterior dental lamina foramen cannot be identified behind or within its wide tooth socket. The left posterior dental lamina foramen is represented by a narrow groove, located on the palatine—pterygoid suture posteromedial to the posterior palatine tooth plate.

Because of the large size of the palatine, the pterygoid gains a narrow palatal exposure only. Dividing the distance from the posterior margin of the (left) pterygoid to the left dental lamina foramen (13 mm) by the distance from the left dental lamina foramen to the posterior margin of the internal nares (76.5 mm) yields a quotient of 1.7. The pterygoid forms a distinct longitudinally oriented ventral flange, but erosion on both sides of the skull renders it impossible to assess whether they formed a single or double ventral projections. Along the medial margin of the subtemporal fossa, the pterygoid extends anteriorly to the level of the posterior third of the longitudinal diameter of the posterior palatine tooth plate. There is no evidence for the presence of an ectopterygoid in *Macroplacus*. The quadrate ramus of the pterygoid is short and stout, and meets the quadrate in an interdigitating suture. The articular surface on the mandibular condyle of the quadrate is biconcave, matching the saddle-shaped surface of the mandibular articulation.

The lateral wall of the braincase is poorly preserved on both sides of the skull. A number of interesting observations can nevertheless be recorded. The palatoquadrate recess is distinct, but

<table>
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<th>Table 9. Measurements of the maxillary and palatine tooth plates of <em>Macroplacus raeticus</em> (holotype, BSP 1967 I 324). All measurements in mm.</th>
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<td>anterior maxillary tooth</td>
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<td>anterior palatine tooth</td>
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<td>posterior palatine tooth</td>
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Fig. 27. Skull of *Protenodontosaurus italicus* Pinna (holotype, MFSN 1819GP): A, right lateral view; B, dorsal view; C, ventral view. Scale bar = 20 mm. For abbreviations, see p. 3.
as in Cyamodus, the palatine fails to contact the quadrate at the lateral margin of the latter (Fig. 26B). This allows the pterygoid to enter the lateral margin of the palatoquadrate cartilage recess between palatine and quadrate. The exact contours and relations of the epityp IG and prootic are difficult to establish, although the trigeminal incisure is distinct on the left side of the skull. The right side of the skull shows a distinct medioventral process of the postorbital that, as in Pla- 
cochelys but unlike Cyamodus, abuts the lateral aspect of the epityp IG at the posterodorsal corner of the foramen interorbitale.

The posttemporal fossa is even more reduced in Macroplacus than in Cyamodus kuhnschnyderi by the expansion of the occipital exposure of the parietal, squamosal, and opisthotic. The relations of the epityp IG and squamosal along the dorsal margin of the posttemporal fossa remain obscure. The ventral margin of the posttemporal fossa, which coincides with the anterior margin of the pteroccipital foramen, is formed by the squamosal in the posterior half and by the prootic in the anterior half. The otic process of the squamosal therefore remains relatively short in Macro-
placus, similar to that of Cyamodus rostratus, but unlike that of Placocheelys, where it forms the entire ventral margin of the posttemporal fossa and extends beyond the anteromedial corner of the latter.

The occiput of the skull of Macroplacus is badly eroded. Only rudiments of the paroccipital processes can be identified, with their distal tips sutured to the squamosal. Basioccipital, exoccip-
tals, and supraoccipital are all missing. A gap between the rudiments of the left opisthotic and squamosal represents the pteroccipital foramen. As preserved, this foramen is located behind and below the squamosal–prootic bridge, which defines the ventral margin of the posttemporal fossa in lateral view. With respect to this character, *Macroplacus* resembles *Cyamodus rostratus*, but as in the specimen of the latter taxon it remains unclear to what degree this character is the result of erosion or breakage.

*Macroplacus* is unique among cyamodontoids in that a foramen pierces the shaft of the quadrate just above the mandibular condyle (exposed in posterior view: Schubert-Klemmnauer, 1975, Pl. 5, Fig. 3). This foramen has smooth edges and is bilaterally symmetrical. Its function remains unknown, as does the function of the foramen that pierces the suspensorium between quadrate, quadratojugal, and squamosal in *Placochelys*.

The Cranial Anatomy of *Protenodontosaurus italicus* Pinna, 1990b

*Protenodontosaurus italicus* is known from two skulls (MFSN 1819GP, 1923GP) from the Carnian of Chiout Zguin east of Dogna, Udine, northeastern Italy (Pinna, 1990b). These skulls were recently the subject of a detailed description by Nosotti and Pinna (1999). The skull of *Protenodontosaurus* (Fig. 27) is distinctly higher than that of other cyamodontoids. The taxon differs from all other cyamodontoids by the presence of a single maxillary tooth (Fig. 27C). The persisting maxillary tooth is located lateral to the anterior palatine tooth, which is the position of the posteriormost maxillary tooth in all other cyamodontoids except *Cyamodus rostratus*. This indicates that *Protenodontosaurus* has reduced the anterior maxillary tooth (teeth) and retained the posteriormost one for biomechanical reasons. Reduction of the maxillary dentition leaves a distinct diastema separating the maxillary from the premaxillary dentition (Nosotti & Pinna, 1996). A similar diastema, but less distinctly developed, is present in those specimens of *Cyamodus kuhnschndyleri* that retain a single pair of premaxillary teeth only (character 8 of Nosotti & Pinna, 1996: 35). In a third specimen of the same species (MHH 1294; Rieppel & Hagdorn, 1999) with two pairs of premaxillary teeth, no diastema is present between premaxillary and maxillary teeth. Given the lack of premaxillary teeth in *Placochelys* and *Pseudochelys*, a diastema separating premaxillary and maxillary teeth is autapomorphic for *Protenodontosaurus* among cyamodontoids and is correlated with the reduction of the maxillary dentition.

The premaxillaries form a short and rounded rostrum. The posterior nasal processes of the premaxillaries are rather short and meet the nasal between the external nares in a V-shaped suture (with the apex pointing backward). The nasals are paired, slender, triangular elements that form the entire dorsal (medial) margin of the external nares. The tapering posterior tips of the nasals extend backward to a level behind the anterior margin of the orbits. A narrow contact of prefrontal and nasal separates the frontal from the maxilla. A distinct anterolateral process of the frontal is embraced by the prefrontal and the nasal (Fig. 27B).

The prefrontal is located rather high on the anterodorsal margin of the orbit and has a relatively narrow dorsal exposure. It descends along the anterior margin of the orbit but does not approach the anterior tip of the jugal as closely as in *Placochelys*.

The maxilla meets the premaxilla at the anteroventral (anterolateral) margin of the external naris. It forms all of the ventral (lateral) and posterior margin of the external naris. Because of the skull proportions of *Protenodontosaurus*, the maxilla is almost as high as it is long (Fig. 27A). The distinct ascending process narrowly enters the anteroventral (anterolateral) corner of the orbit, and its pointed tip is embraced by the prefrontal and maxilla.

In the anteroventral margin of the orbit, two foramina can be identified, both fully enclosed by the maxilla (Fig. 27B). The larger foramen is located medial to the ventral marginal rim of the orbit and represents the lacrimal foramen. The smaller foramen lies on the lateral aspect of the maxilla, that is, lateral to the ventral marginal rim of the orbit. The infraorbital foramen (*sensu* Oelrich, 1956), transmitting the infraorbital nerve would have to lie inside the orbit, but it cannot be located in *Protenodontosaurus* (Nosotti & Pinna, 1996). Nosotti and Pinna (1998) concluded that the infraorbital nerve must have passed medial to the preorbital bridge formed by the prefrontal, maxilla, and palatine. This interpretation leaves the lateral foramen located within the maxilla unexplained, which raises the question of whether *Protenodontosaurus* had an anteriorly bifurcating lacrimal duct, the branches of which...
passed through paired foramina in the maxilla at the anteroventral corner of the orbit. Cyamodus kuhnschnyderi is unique in that it shows three foramina along the lateroventral margin of the orbit, and a bifurcating lacrimal duct may be hypothesized to have been present in this taxon (see above). Although one of the two lacrimal foramina is not in exactly the same topological position with respect to surrounding bones and the orbit in the two taxa, a bifurcating lacrimal duct might have been a character shared by Protenodontosaurus and Cyamodus kuhnschnyderi. Alternatively, Protenodontosaurus might have had a simple lacrimal duct passing through the larger foramen located on the inside of the orbital rim, whereas the smaller foramen located on the maxilla, close to but lateral to the orbital rim, might represent an unusually high placement of the posteriormost superior alveolar foramen.

The vertical portion of the interdigitating suture between maxilla and jugal lies at about the level of the midpoint of the longitudinal diameter of the orbit in Protenodontosaurus (Fig. 27A), comparable to what is seen in Macroplacus but in a somewhat more anterior position than is observed in Placochelys, in which the vertical suture between maxilla and jugal lies behind the level of the midpoint of the longitudinal diameter of the orbit.

The frontals of Protenodontosaurus are paired and meet the parietal in a deeply interdigitating suture at a level between the orbit and the upper temporal fossa (Fig. 27B). The orbital margin of the frontal, between pre- and postfrontal, is straight rather than concave. The frontal closely approaches but does not enter the pineal foramen (Nosotti & Pinna, 1998). The postfrontal is a broad, triangular element with a weakly concave and evenly curved postorbital margin. It remains broadly separated from the upper temporal fossa by the postorbital, which meets the parietal at the anteromedial margin of the upper temporal fossa (Fig. 27B). A broad separation of the postfrontal from the upper temporal fossa is also observed in Psephoderma and, to a lesser extent, in Cyamodus rostratus, but not in Placochelys or Cyamodus kuhnschnyderi, where the contact of postorbital and parietal is narrow. The postorbital broadly enters the posteroventral margin of the orbit. It extends backward into the temporal arch, forming the anterior and anterolateral margin of the upper temporal fossa. The posterior tip of the postorbital remains restricted to a level in front of the longitudinal diameter of the upper temporal fossa.

The jugal broadly enters the ventral margin of the orbit and closely approaches but does not enter the lacrimal foramen (Fig. 27A). Posteriorly it extends along the ventral margin of the temporal arch to about the same level as the postorbital does along the dorsal margin of the temporal arch. Together, these two elements embrace the anterior tip of the squamosal, which remains restricted to a level behind the anterior margin of the upper temporal fossa in Protenodontosaurus and hence does not reach as far anteriorly as in Placochelys.

The parietal skull table, formed by the fused parietals, is broad and shows straight lateral margins. The large pineal foramen is located anteriorly in the skull table (Fig. 27B). Dermal encrustations are present but poorly defined. As far as can be determined, they resemble those of Placochelys, with a pair of encrustations along either side of the parietal skull table and an unpaired postero medial encrustation located at the posterior margin of the skull table. The diverging posterior processes of the parietal meet the squamosals along the postero medial margins of the upper temporal opening in an interdigitating suture, which is distinct in the second specimen (MFSN 1923GP) only. Dermal encrustations create a distinct step at the posterior corner of the upper temporal fossa on both sides of the skull that might be mistaken for a suture separating a small squamosal from the large quadratojugal. Whether the quadratojugal entered the postorbital margin of the upper temporal fossa remains indistinct in Protenodontosaurus because of dermal encrustations on the temporal arch, which obscure the suture relations, and because of the incompleteness of the specimens.

The ventral view of the skull (Fig. 27C) shows the much enlarged vomers, which extend far forward into the rostrum, an autapomorphy of Protenodontosaurus. The enlarged vomers exclude the premaxillaries from the internal nares. Posteriorly the vomers do not extend beyond the level of the posterior margins of the internal nares as they do in Cyamodus kuhnschnyderi and Placochelys (unknown in Cyamodus rostratus and Psephoderma). The maxilla narrowly enters the anterolateral margin of the internal naris, between the anterior vomer and the posterior palatine. A distinct nutritive (dental lamina) foramen is located within the maxilla behind the maxillary tooth plate. In ventral view, the posterior end of the maxilla tapers to a pointed tip that remains ex-
Table 10. Measurements of the maxillary and palatine tooth plates of *Protenodontosaurus italicus* (holotype, MFSN 1819GP). All measurements in mm.

<table>
<thead>
<tr>
<th></th>
<th>left</th>
<th>right</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>longitudinal Ø</td>
<td>transverse Ø</td>
</tr>
<tr>
<td>maxillary tooth</td>
<td>20.2</td>
<td>13.4</td>
</tr>
<tr>
<td>anterior palatine tooth</td>
<td>12.8</td>
<td>13.3</td>
</tr>
<tr>
<td>posterior palatine tooth</td>
<td>36.0</td>
<td>28.5</td>
</tr>
</tbody>
</table>

included from the anterior margin of the subtemporal fossa by a contact of the jugal and palatine. On the left side of the skull of the holotype (MFSN 1819GP), a lateral process of the palatine meets the jugal, as is also the case in *Placochelys*; on the right side of the same specimen, the jugal is seen to extend medially to meet the palatine. In *Protenodontosaurus*, the jugal does not extend backward along the anteromedial margin of the subtemporal fossa, as it does in *Cyamodus rostratus*.

As in other cyamodontoids, the palatine carries two tooth plates, of which the posterior one is much larger than the anterior one (Table 10). The posterior dental lamina foramina are located behind the posterior palatine tooth plates on the palatine–pterygoid suture. Although the posterior palatine tooth plates are not as disproportionately enlarged as in *Macroplacus*, the relative palatal exposure of the pterygoid is very short in *Protenodontosaurus*. The ratio of the length of the pterygoid (from its posterior margin to the dental lamina foramen on the palatine–pterygoid suture) to the distance from the pterygoid–palatine suture to the posterior margin of the internal naris is 0.2 for *Protenodontosaurus*. This indicates that the relative length of the palatal exposure of the pterygoid is not simply a reflection of the relative size of the posterior palatine tooth plates. The pterygoid forms a longitudinally oriented ventral flange with a single ventral projection. The pterygoid extends anteriorly along the medial margin of the subtemporal fossa to the level of about the midpoint of the longitudinal diameter of the posterior palatine tooth plate. An ectopterygoid is absent in *Protenodontosaurus*.

The lateral view of the braincase shows the distinct palatoquadrate cartilage recess with a comparatively broad contact of the palatine with the anteromedial wing of the quadrate along its lateral edge (Fig. 27B). The postero dorsal margin of the palatoquadrate cartilage recess is formed by the otic process of the squamosal, which in *Protenodontosaurus* extends far anteriorly, closely approaching the trigeminal incisure located between the prootic and epipterygoid. As mentioned above, the second specimen (MFSN 1923GP) shows an internal subdivision of the trigeminal incisure by a vertical strut of bone. The epipterygoid is a broad element that in the second specimen (MFSN 1923GP) is incompletely ossified. Unfortunately, the dorsal relations of the epipterygoid remain incompletely known for *Protenodontosaurus*. In particular, it is impossible to ascertain whether the epipterygoid forms a posterior dorsal process that meets the squamosal at the dorsal margin of the posttemporal fossa.

The posttemporal fossa is large in *Protenodontosaurus*, with the pteroscapular foramen located at its ventral margin. As in *Placochelys*, the pteroscapular foramen appears slightly recessed below and behind the ventral margin of the posttemporal fossa (Fig. 27B). The exoccipital forms the lateral margin of the foramen magnum and between itself and the opisthotic encloses the jugular foramen. The jugular foramen is not subdivided internally in *Protenodontosaurus*. The exoccipitals meet each other dorsal to the occipital condyle formed by the basioccipital alone, a character shared with *Cyamodus kuhnshnyderi* (Nosotti & Pinna, 1996) but absent in *Placochelys* (and *Psedoderma*: see below). As in other cyamodontoids, the anterior aspect of the relatively slender paroccipital process is lined by the squamosal, but a distinct squamosal buttress receiving the distal end of the paroccipital process, as seen in *Placochelys* (and *Psedoderma*: see below), is absent in *Protenodontosaurus*. The foramen for the internal carotid is closed ventrally in *Protenodontosaurus* by a ventral contact of the basioccipital tuber and the ventral process of the opisthotic, yet the opisthotic pedicle remains widely separated from the posterior margin of the basiocranium or pterygoid, respectively.

Enlarged temporal tubercles secondarily fused to the underlying bone are absent on the lateral surface of the temporal arch of *Protenodontosaurus*, whereas they do occur in *Cyamodus kuhnshnyderi* and *Placochelys*. Unfortunately, the posterior margin of the upper temporal fenestra is poorly preserved on both sides of the skull of *Protenodontosaurus*, so that it is impossible to ascertain whether such temporal tubercles were restricted to a posterior position as in *Psedoderma* or were altogether absent in *Protenodontosaurus*. 
Psephoderma alpinum was originally based on an isolated carapace (H. v. Meyer, 1858) from the Rhaetian Koessen-Formation of the Bavarian Alps (Winkelmoos Alpe), but today it is known from several articulated specimens, two of which are complete (Pinna & Nosotti, 1989; Renesto & Tinctori, 1995). All of these specimens have sustained severe dorsoventral compression, which has obscured some details of skull anatomy. The specimens yielding the most information on the cranial anatomy of Psephoderma is the isolated skull from Monte Cornizzolo (MSNM V471; Pinna, 1976a; Pinna & Nosotti, 1989). This skull too was subjected to some dorsoventral compression, however, which resulted in extensive breakage in the preorbital region. Also, the specimen is incompletely prepared: both orbits and the left temporal fossa are still filled with matrix, and the lateral wall of the braincase is only incompletely exposed in the right temporal fossa (Fig. 28).

Other than by the morphology of the rostrum (see above), the genus is unique among cyamodontoids in the relative proportions of the upper temporal fossa. The skull is depressed yet narrow, and the temporal fossae in particular are relatively short and distinctly narrower than in other cyamodontoids (Table 8).

The paired premaxillaries form the elongated, narrow, edentulous rostrum (Fig. 29). Posteriorly the premaxillaries extend into distinctly enlarged posterior (nasal) processes that project backward far beyond the level of the posterior margins of the external nares, entering deeply in between the frontals (Pinna & Nosotti, 1989). The premaxillae thus completely separate the nasals from one another, a character that Psephoderma (Fig. 29B) shares with Macroplacus. The nasals are reduced to small, elongate elements located entirely posterior to the external nares, between the premax-
illa and the prefrontal, although their precise outline can no longer be determined because of breakage. A break runs transversely through the posterior (nasal) processes of the premaxillaries at the level of the anterior margin of the external nares, creating a distinct step that might be mistaken for a separation of the premaxillaries from large nasals.

The exact contours of the prefrontal are also difficult to identify because of breakage, but, as in all other cyamodontoids, a lacrimal is absent. The maxilla is an elongated yet very low element that extends anteriorly into the rostrum (see above) and posteriorly to a level slightly behind the midpoint of the longitudinal diameter of the orbit, where it meets the jugal in a V-shaped su-

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Fig. 29. Skull of *Psephoderma alpinum* H. v. Meyer (MSSM V471): **A**, left lateral view; **B**, dorsal view; **C**, ventral view. Scale bar = 20 mm. For a list of abbreviations see p. 3.
ture (with the apex pointing backward; Fig. 29A). An ascending process of the maxilla cannot be identified, but even if this should be attributable to breakage, the process must have been rudimentary, given the low profile of the skull. The posterior end of the maxilla extensively enters the anterior ventral (lateral) margin of the orbit. Because of incomplete preparation, the lacrimal foramen cannot be identified. The right side of the skull would seem to indicate that the jugal did not extend anteriorly along the ventral margin of the orbit beyond the level of the midpoint of the longitudinal diameter of the latter, although if true, the maxilla would extend along the medioventral margin of the orbit much farther back than is indicated by the lateral exposure of the bone. The left side of the skull shows no indication of the anterior tip of the jugal.

The frontals are paired, each forming a distinct anterolateral process that is embraced by the premaxilla and prefrontal (Fig. 29B). A contact of the prefrontal with the nasal separates the frontal from the maxilla. Between prefrontal and postfrontal, the frontal forms the concave dorsal margin of the orbit. The large and elongate pineal foramen lies at the anterior end of the parietal, at a level between the orbit and the upper temporal fossa. On the right side of the skull, a narrow entry of the frontal into the anterior margin of the pineal foramen can be identified. The postfrontal is a comparatively small, triangular element located at the posterodorsal corner of the orbit. Its postrolateral margin is concave but evenly curved rather than angulated. A contact of the postorbital with the parietal broadly separates the postfrontal from the anteromedial margin of the upper temporal fossa.

The postorbital is a large element that forms most of the broad postorbital arch (Figs. 29A, B). It defines the posteroventral (postrolateral) margin of the orbit. Along the lateral margin of the upper temporal fossa, the postorbital extends backward to a level well behind the midpoint of the longitudinal diameter of the upper temporal fossa, a character that *Psephoderma* (Fig. 29B) shares with *Placochelys* and *Macroplacus* but not with *Protenodontosaurus*, in which the postorbital extends only to about the midpoint of the longitudinal diameter of the upper temporal fossa (this character remains unknown for *Cyamodus*).

The parietals of *Psephoderma* are fused and form a broad parietal skull table with distinctly concave lateral margins due to a constriction of its posterior part. Instead of dermal encrustations, the skull table is ornamented with a pattern of ridges and grooves radiating from its center of ossification to the margins of the bone. Behind the pineal foramen, the concave anteromedial margin of the fused parietal forms a distinct step that continues laterally along the anteromedial margin of the postorbital. In this way the pineal foramen comes to lie in a distinct depression, which is a unique character of *Psephoderma*. The right side of the skull shows a distinct yet slender anterior process of the parietal that extends beyond this step medial to the postorbital, postfrontal, and frontal to form the lateral margin of the pineal foramen.

The left temporal arch shows particularly well the sutures delineating the posterior processes of the postorbital and jugal, together embracing the anterior process of the squamosal which, unlike in *Placochelys*, extends anteriorly to a level beyond the anterior margin of the upper temporal fossa (Fig. 29A). The quadratojugal extends anteriorly along the ventral margin of the temporal arch beyond the level of the midpoint of the longitudinal diameter of the upper temporal fossa, but it does not reach beyond the level of the anterior margin of the upper temporal fossa, as is the case in *Placochelys*.

Because of breakage of the bone surface, the relations of the vomers remain obscure in the ventral view of the skull of *Psephoderma* (Fig. 29C), but, especially on the left side of the skull, it appears that the premaxilla enters the anterior margin of the internal naris, whereas it remains excluded therefrom in all other cyamodontoids, with the possible exception of *Macroplacus*. The maxilla enters the anterior lateral margin of the internal naris, between the premaxilla anteriorly and the palatine posteriorly. The left side of the skull shows a distinct medial process of the jugal, which meets the palatine at the anteromedial margin of the subtemporal fossa and thus excludes the maxilla from the latter. There is no indication that the jugal extends backward along the medial margin of the subtemporal fossa, as it does in *Cyamodus rostratus*.

The posterior palatine tooth plates of *Psephoderma* are distinctly elongated (at least in the adult, see Tables 7 and 11), a character also shared by *Macroplacus*. The posterior dental lamina foramina are located on the pterygoid–palatine suture postero medial to the posterior palatine tooth plates. In spite of the elongation of the palatine
tooth plates, the pterygoid retains a relatively long palatal exposure compared with Protenodontosaurus (without elongation of the posterior palatine tooth plates) and Macroplacus (with much enlarged posterior palatine tooth plates). The relative length of the palatal exposure of the pterygoid can therefore be treated as a character that, to some degree at least, is independent from the relative size of the posterior palatine tooth plates (see also the discussion above). Dividing the length of the pterygoid (from its posterior margin to the dental lamina foramen on the palatine–pterygoid suture) by the distance from the pterygoid–palatine suture to the posterior margin of the internal naris yields a ratio of approximately 0.36 for Psephodera (MSNM V471). The pterygoid forms a longitudinally oriented ventral flange with a single ventral projection. The left pterygoid is seen to extend anteriorly along the medial margin of the subtemporal fossa to the level of the posterior third of the longitudinal diameter of the posterior palatine tooth plate. An ectopterygoid is absent (Fig. 29C).

The lateral wall of the braincase is only partially exposed, and little anatomical detail is revealed because of poor preservation and preparation. The palatoquadrate cartilage recess is distinct, however, and the palatine contacts the anteromedial lamina of the quadrate along its lateral edge.

The occiput of Psephodera is deeply excavated. The occipital exposure of the braincase was subject to erosion, which obscured structural detail. The quadratojugal is clearly demarcated from the quadrate in occipital view. There is a distinct buttress on the lower surface of the left squamosal, abutted by the distal tip of the slender paroccipital process (Fig. 29B). A comparable squamosal buttress is present in Placochelys, but not in Cyamodus or in Protenodontosaurus. The ventrally descending flange of the opisthotic is distinct and in Psephodera contacts the posterior margin of the pterygoid. Among the other cyamodontoids included in this study, a comparable contact is observed only in the Berlin specimen of Placochelys (MB.R. 1765).

Compared with Cyamodus and Placochelys, enlarged temporal tubercles secondarily fused to the underlying bone are reduced in Psephodera, where they are restricted to the posterior extremity of the squamosals but do not appear on the lateral surface of the posterior part of the temporal arch (as indicated in the reconstruction of Pinna & Nosotti, 1989).

**Autapomorphies in the Skull of the Cyamodontoidea**

In addition to highly diagnostic characters of the postcranium, such as the development of an extensive dermal armor or dermal encrustations on the skull, the cranial anatomy offers additional evidence of the monophyly of the Cyamodontoidea (Rieppel & Zanon, 1997). The palatal dentition is reduced to two tooth plates on the palatine (one in Henodus: Huene, 1936). The postfrontal remains excluded from the upper temporal fenestra by a contact of the postorbital with the parietal (the postfrontal enters the anteromedial margin of the upper temporal fossa in Placodus [Rieppel, 1995a], a condition that is also plesiomorphic for Eosauropterygia [Rieppel, 1997]). The pineal foramen is large, displaced anteriorly, and may border on the frontoparietal suture. The jugal extends far backward in the temporal arch, contacting the quadratojugal and the squamosal posteriorly (perhaps also in Placodus, but not in Paraplacodus [Rieppel, 1995a]; a short jugal was reconstructed for Cyamodus kuhnschnyderi by Nosotti & Pinna, 1996, but the temporal arch is incomplete in both specimens). The ectopterygoid is missing (but see the discussion of Placochelys above). Most distinctive for cyamodontoids, however, is the structure of the secondary lateral wall of the braincase, which incorporates the palatoquadrate. The epipterygoid is very broad. It extensively overlaps the dorsal surface of the palatine and is connected to the quadrate by palatoquadrate cartilage, which persisted in the adult. The palatine contacts the quadrate lateral to the palatoquadrate cartilage recess in some taxa, and a groove on the dorsal surface of the palatine accommodates the persistent anterior (palatine) process of the palatoquadrate. Posteriorly, the palatoquadrate cartilage recess is floored by the pterygoid, the dorsal wing of which broadly overlaps with an anterior wing of the quadrate. Together with the fusion of the palatobasal articulation, this broad overlap of pterygoid and quadrate obliterates the anterior part of the cranioquadrate passage. As a consequence, the stapedial (temporal) artery reaches the jaw adductor musculature through the pteroccipital foramen. Finally, the internal carotid enters the cranioquadrate passage through a foramen located between the basicranial tuber and a ventral process of the opisthotic and continues anteriorly in a basiincranial canal. This whole character complex is unique among amniotes but is shared by all cyamodontoid placodonts.
Because the clade that includes Placodus and Paraplacodus is the sister group of the Cyamodontoida, it is interesting to compare the derived structure of the cyamodontoid braincase with the more generalized braincase anatomy of Placodus (the braincase of Paraplacodus is not known). The best-preserved and best-prepared skull of Placodus is the specimen UMO BT 13, originally described by Sues (1987) and redescribed by Rieppel (1995a). In contrast to cyamodontoids, Placodus has an epityroid with a broad base but a relatively narrow dorsal process. Broili (1912, Pl. 14, Fig. 6) described a recess located between the posteroventral aspect of the base of the epityroid (covered by unfinished bone) and the anteromedial aspect of the quadrate, above the pterygoid. Huene (1931) correctly assumed that this recess must have housed persistent palato-quadrate cartilage. The specimen UMO BT 13 shows nicely (Fig. 30) the extensive dorsomedial flange of the quadrate ramus of the pterygoid, which anteriorly supports the broad, fan-shaped base of the epityroid. The dorsal head of the epityroid abuts the descending flange of the parietal at the posterodorsal corner of the foramen interorbitale. A bony process rises up along the medial aspect of the anterior margin of the epityroid, which is clearly located lateral to the rostrum basisphenoidale and hence cannot represent an ossification of the primary lateral wall of the braincase. Its base is broken in UMO BT 13, but Broili's (1912) specimen suggests that this dorsal process originates from the pterygoid. Other than in cyamodontoids, the craniocaudal passage persists in Placodus; it extends from the space between the pterygoid and the dorsolateral aspect of the basioccipital tubers into the cavum epityricum medial to the epityroid (Rieppel, 1995a). The cavum epityricum is represented by the space between the epityroid and the rostrum basisphenoidale. The rostrum basisphenoidale carries the sella turcica, which is pierced by two foramina for the passage of the cerebral carotids into the braincase. From the lateral margin of the sella turcica originates, on either side of the skull, a clinoid process that represents an ossification of the primary lateral wall of the braincase (base of the pila antotica). The clinoid process rises up in a dorsolateral direction and contacts the dorsal tip of the dermal process lining the anteromedial edge of the epityroid. The anterior opening of the cavum epityricum thus is well-defined by the clinoid process and the dorsal process of the ?pterygoid lining the anteromedial

Fig. 30. Left lateral braincase wall of Placodus gigas Agassiz (UMO BT 13). Scale bar = 20 mm. For abbreviations, see p. 3.
margin of the epipterygoid. The internal carotid must have entered the cranioproquadrate passage between the pterygoid and the basioccipital tuber. It must have subdivided within the posterior part of the cranioproquadrate passage, giving rise to the stapedial artery, which must have reached the temporal musculature by passing through a gap between the dorsomedial flange of the quadrate ramus of the pterygoid and the descending flange of the parietal, lateral to the otic capsule and anterior to the paroccipital process (Fig. 30).

As in cyamodontoids, the palatine–pterygoid suture can be traced to the ventral tip of the longitudinally oriented ventral flange of the pterygoid. From there it trends in an anterodorsal direction until it disappears under the epipterygoid. In Placodus, the epipterygoid does encroach on the posterior margin of the palatine, but it does not invade the dorsal surface of the palatine to the same extent as the much broader epipterygoid of cyamodontoids. Posteriorly, the base of the epipterygoid expands over the dorsomedial flange of the pterygoid, terminating in a surface of unfinished bone. As in cyamodontoids, the quadrate of Placodus also carries a distinct anteromedial flange that overlaps the dorsomedial flange of the pterygoid and again terminates in an unfinished margin opposing the posteroventral margin of the base of the epipterygoid. In between these two bones, the pterygoid flange must have been covered by persistent palatoquadrate cartilage in the live animal (Fig. 30). In contrast to cyamodontoids, there is no evidence that a cartilaginous anterior palatal process of the palatoquadrate persisted in Placodus.

As mentioned above, the stapedial artery of Placodus passed through a gap between the dorsal flange of the pterygoid and the descending flange of the parietal. The prootic is exposed at the anteromedial corner of this gap as it emerges from behind the epipterygoid and from below the descending flange of the parietal. Postero-lateral to the prootic, the opisthotic extends into the paroccipital process, again exposed in lateral view between the pterygoid and the parietal. The gap for the passage of the stapedial artery is closed posteriorly by the squamosal.

In cyamodontoid placodonts, this gap for the passage of the stapedial artery is reduced to a small paroccipital foramen (Nosotti & Pinna, 1993b). Closure is the consequence of the formation of a neomorphic otic process of the squamosal, which extends anteriorly along the dorsal margin of the pterygoid flange and meets the prootic, which expands backward. These two bones (in Cyamodus rostratus, see above), or the otic process of the squamosal alone (in Placochelys), form the anterior margin of the paroccipital foramen. In a parallel development, there is an expansion of the squamosal anteromedially along the anterior aspect of the paroccipital process; this, together with the opisthotic, forms the posterior margin of the paroccipital foramen.

**Evolution of the Rostrum and of the Dentition Within the Cyamodontoida**

The most distinctive characters that differ among the cyamodontoid taxa relate to the structure of the rostrum and the dentition. The genus *Cyamodus* retains a short, broad rostrum formed by tooth-bearing premaxillae. There are two teeth in each premaxilla of *Cyamodus rostratus* (Fig. 12B), and between one (Nosotti & Pinna, 1996) and two (Rieppel & Hagdorn, 1999) teeth on the premaxilla of *Cyamodus kuhnschnyderi*. Ontogenetic variations of the dental formula of *Cyamodus hildegardis* have been described by Kuhn-Schnyder (1959).

The rostrum of *Macroplacus* is incomplete, but what is preserved shows a deep trough, or concavity, on its ventral surface between the two premaxillaries (Fig. 26C). The maxilla carries an anterolateral, relatively short yet distinct process that tapers off along the lateral margin of the rostrum well in front of the level of the anterior margin of the internal nares. This sutural pattern contrasts with that of *Cyamodus*, where the suture between the premaxilla and maxilla is more transversely oriented (*C. kuhnschnyderi*) or even trends in a posterolateral direction (*C. rostratus*). The anterior tip of the premaxilla does not extend anteriorly beyond the level of the anterior margin of the internal nares in *Cyamodus*.

The rostrum of *Protenodontosaurus* is more elongated than that of *Cyamodus*, and each premaxilla carries an anterior tooth, plus a second posterior alveolus, which may have carried a second premaxillary tooth or which may represent a replacement pit (Nosotti & Pinna, 1999). As in *Macroplacus*, the maxilla of *Protenodontosaurus* forms an anterior process that participates in the formation of the rostrum. However, this anterolateral process of the maxilla is somewhat longer in *Protenodontosaurus*, and its ventral surface shows a low ridge that, together with its counterpart from the other side of the skull, delineates a
TABLE 11. Data matrix for the analysis of placodont interrelationships. For further details, see text.

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
| 1 | Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | Placodus | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | Paraplacodus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | C. rostratus | ? | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | ? | 0 | 1 | 1 | 0 | 1 |
| 5 | C. hildegardi | 2 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | C. kuhnschneideri | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | ? | 1 | 1 | 1 | 1 | 1 | 1 |
| 7 | Henodus | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | Macroplaus | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | Placochelys | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | Protenodontosaurus | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | Psphoderma | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | Israel | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | Iaticeps | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

broad and shallow trough leading to the internal nares (Fig. 27C).

In Placochelys, the rostrum becomes distinctly elongated and narrow (Fig. 3B). The premaxilla is edentulous. The maxilla again carries an anterior process participating in the formation of the rostrum and together with the premaxilla delineates a distinct sulcus on either side of the ventral surface of the rostrum, leading up to the anterior margin of the internal naris.

In Psphoderma, the rostrum is even more elongate and narrow (Fig. 29C). The premaxilla is edentulous. The maxilla carries an anterior process that participates in the formation of the rostrum and that carries a low ridge on its ventral surface located lateral to the deep premaxillary sulcus. Each premaxilla carries a distinct ridge on its ventral surface along its entire length, defining a deep sulcus on the ventral surface of the rostrum that is united anteriorly but becomes paired by medial ventral ridges on the premaxillae posteriorly as these grooves approach the anterior margin of the external nares. Pinna (1979) described two premaxillary teeth in a juvenile specimen of Psphoderma alpinum, an observation that could not be confirmed on personal inspection of the specimen (MNB 4884a-b).

With the exception of Henodus (Huene, 1936), the rostrum of cyamodontid placodonts can thus be described in terms of a morpholine, progressing from a short, rounded and tooth-bearing structure to an elongated, narrow, edentulous rostrum with deep grooves on its lower surface leading up the internal nares. Some authors reconstruct the lateral margins of these grooves to have been covered by a horned sheath comparable to the rhaphotheca of turtles. Henodus, by contrast, shows a broad and flat rostrum, the anterior cutting edge of which is furnished with a series of denticles as described above (Stein, 1995; Reiff & Stein, 1999).

Among the species of the genus Cyamodus, the

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number of maxillary teeth varies between two and three in adult specimens (Kuhn-Schnyder, 1959, 1965a; Nosotti & Pinna, 1996). Placochelys shows three maxillary teeth, Psephoderma shows two maxillary teeth, and Protenodontosaurus shows a single maxillary tooth plate. All adult specimens of Cyamodus, Placochelys, Protenodontosaurus, and Psephoderma carry a small anterior and a much larger posterior tooth plate on each palatine. Henodus is autapomorphic by the loss of maxillary teeth and by the reduction of the palatine teeth to one relatively small posterior tooth plate. The proportions of the posterior palatine tooth plates vary among cyamodontoid taxa. Cyamodus from the Germanic Triassic (i.e., C. rostratus, C. kuhnschnyderi), as well as Placochelys placodonta and Protenodontosaurus italicus have posterior palatine tooth plates that are between 1.2 and 1.3 times as long as they are wide (Table 7). The southern Alpine species Cyamodus hildegardis shows somewhat more elongated palatine tooth plates (1.3 to 1.4 times as long as they are wide), and in this character approaches Psephoderma alpinum, which in adult specimens shows posterior palatine tooth plates that are 1.4 to 1.5 times as long as they are wide. Interestingly, there is an ontogenetic change of proportions in Psephoderma alpinum, with distinctly more elongated palatine tooth plates in the adult than in the juvenile (Table 7). Macroplacus raeticus shares the elongated posterior palatine tooth plates, which may be the reason why Pinna (1978) treated this taxon as a junior synonym of Psephoderma alpinum.

Cladistic Analysis of Cyamodontoid Interrelationships

The cladistic analysis of cyamodontoid relationships initially included as terminal taxa a hypothetical all-0-ancestor (which roots the tree on the presence of characters), Placodus, Paraplacodus, Cyamodus rostratus, Cyamodus kuhnschnyderi, Henodus chelyops, Macroplacus, Placochelys, Protenodontosaurus, and Psephoderma, and was based on 53 cranial (see Appendix I) and one postcranial (absence or presence of carapace) characters (Table 11). Because of the incomplete knowledge of their cranial anatomy, Cyamodus muensteri (coding based on the holotype of C. laticeps Owen), Cyamodus hildegardis and the cyamodontoid skull from the Muschelkalk of Makhtesh Ramon, Negev, Israel (provisionally referred to ?Psephosaurus by Broten, 1957) were added to the analysis in separate steps. All searches employed PAUP version 3.1.1. (Swoford, 1990; Swoford & Begle, 1993), with the branch-and-bound search option implemented. Diagnostic characters listed below are those obtained by DELTRAN character optimization if not otherwise indicated. Unambiguous symapomorphies, optimizing the same way in ACCTRAN or DELTRAN, are indicated by an asterisk (*). Bootstrap analysis is based on 2,000 replications using the branch-and-bound search option.

The reconstruction of an unrooted network (characters 1, 10, 20, 27, and 30 were uninformative and hence ignored) resulted in a single tree with a tree length of 91 steps (Fig. 31). Although it does not indicate phylogenetic relationships, the network does suggest that the Cyamodontoida could potentially include two separate monophyletic subclades, one comprising the taxa from the Germanic Triassic (Henodus, Cyamodus rostratus, Cyamodus kuhnschnyderi), the other comprising Placochelys and the taxa from the Alpine Tri-
assic (Macropodus, Protenodontosaurus, Pheldoderm). At the very least, the network indicates that grouping some but not all taxa from the Germanic Triassic with those of the Alpine Triassic and vice versa will result in a paraphyletic grouping (for the results obtained on including Cyamodus hildegardis, see below). Indeed, the cyamodontoid relationships suggested by the network are exactly those obtained either by rooting the analysis on the sister group of the Cyamodontoida, the Placodontoida, or by rooting all terminal taxa on an all-ancestor.

With the branch-and-bound search option implemented, a single most parsimonious tree was obtained when the analysis was rooted on the sister group of the Cyamodontoida, that is, the Placodontoida (Placodus, Paraplanodus; characters 1, 10, 20, 27, and 30 were uninformative and hence ignored). Tree length (TL) was 91 steps, the consistency index (CI) was 0.769, and the retention index (RI) was 0.677.

Rooting the analysis of placodont interrelationships on the hypothetical all-0-ancestor (all characters informative) yielded one single most parsimonious tree with a TL of 103 steps, a CI of 0.757, and an RI of 0.706 (Fig. 32). Interestingly, the tree suggests paraphyly of the Placodontoida, with Placodus being more closely related to the Cyamodontoida than to Paraplanodus. This result is potentially important, because Paraplanodus had previously been claimed to be the most generalized placodont known (Peyer & Kuhn-Schneider, 1955), a claim that was refuted by an earlier analysis of placodont interrelationships (Rieppel & Zanon, 1997). Characters that Placodus shares with the Cyamodontoida but that are absent in Paraplanodus are: 17* (1) [ci = 0.5], the postorbital extending along the lateral margin of the upper temporal fossa to a level behind the midpoint of the longitudinal diameter of the upper temporal fossa; 33* (1) [ci = 1], chisel-shaped anterior premaxillary teeth. This latter character is somewhat problematic, as the premaxillary teeth of Protenodontosaurus are not as slender and pointed as those of Paraplanodus, but neither are they as broad and chisel-shaped as those of Placodus. On the basis of the current data matrix, the paraphyly of the Placodontoida obtains only if the premaxillary teeth of Protenodontosaurus are coded as chisel-shaped (1). If they are coded as pointed (0), two trees are obtained, with unresolved relationships of Placodus and Paraplanodus relative to the Cyamodontoida. The same result is obtained if the teeth of Protenodontosaurus are coded as intermediate between the chisel-shaped premaxillary teeth of Placodus and the bulbous premaxillary teeth of Cyamodus. The monophyly of the Placodontoida is recovered if two postcranial characters shared by Placodus and Paraplanodus are added to the matrix (i.e., the hypospheno-hypantrum articulation and the strongly bent lateral gastralia rib elements). For these reasons, support for a relationship of Placodus closer to cyamodontoids than to Paraplanodus is weak; the node collapses in a tree one step longer (TL = 104) yields a total of five trees, 80% of which retain Placodus relatively closer to cyamodontoids than Paraplanodus); the percentage of trees retaining the node in the bootstrap analysis is 69%. Obviously, the hypothesis of a paraphyletic Placodontoida will have to be tested by including postcranial characters in the analysis. Conversely, the monophyly of the Placodontoida currently is weakly supported.

By contrast, the monophyly of the Cyamodontoida is highly supported; the node breaks only in a tree eight steps longer (TL = 111), the percentage of trees retaining the node in the bootstrap analysis is 100%. The characters supporting monophyly of the Cyamodontoida are: 1* (2) [ci = 1], carapace present; 10(1) [ci = 1], pineal foramen displaced anteriorly; 16* (2) [ci = 0.667], postfrontal broadly excluded from temporal fossa; 19* (1) [ci = 1], broad dorsal process of epipterygoid; 20* (1) [ci = 1], epipterygoid sutured to palatine; 24* (1) [ci = 1] epipterygoid meets...
squamosal at dorsal margin of posttemporal fossa; 26* (1) [ci = 1], otic process of squamosal present; 27* (1) [ci = 1], palatoquadrate cartilage recess present; 30* (1) [ci = 1], pterociphalic foramen present; 35* (2) [ci = 1], two maxillary teeth; 36* (2) [ci = 0.75], two palatine tooth plates; 37* (0) [ci = 1], anterior palatine tooth plates round; 53* (1) [ci = 1], retroarticular process short, with sloping surface; and 54* (2) [ci = 1], tubercular osteoderms secondarily fused to squamosal. ACCTRAN optimization adds 8 (1) [ci = 0.5]; 42 (0) [ci = 0.5]; 43 (1) [ci = 1]; 49 (1) [ci = 0.5]; and 52 (1) [ci = 0.5].

Within the Cyamodontoida, Henodus groups with Cyamodus rostratus and Cyamodus kuhnschnyderi (Fig. 32). The node is weakly supported: it breaks in a tree one step longer (TL = 104), and the percentage of trees retaining the node in the bootstrap analysis is less than 50%. Weak support for this grouping results from the autapomorphic structure of the Henodus skull, which results in frequent noncomparable character states (coded as [?]), and from the fact, recognized earlier, that Henodus shares a number of similarities with the placochelyids (Rieppel & Zanol, 1997). Nevertheless, the grouping of Henodus with the other cyamodontoids from the Germanic Triassic is supported by the following characters: 8 (1) [ci = 0.5], the jugal does not extend far anteriorly along the ventral margin of the orbit; 12 (1) [ci = 0.5], parietal with distinct anterolateral process; 15* (1) [ci = 0.5], lateral margin of postfrontal deeply concave and angulated; 48* (1) [ci = 1], posteroventral tuberle present on distal end of paroccipital process; and 49 (1) [ci = 0.5], exoccipital meet above the basioccipital condyle. ACCTRAN optimization adds 9 (1) [ci = 1]; 28 (1) [ci = 0.5]; 33 (2) [ci = 1]; 34 (0) [ci = 0.667]; and 43 (2) [ci = 1].

Cyamodus rostratus and Cyamodus kuhnschnyderi group as a well-supported monophyletic taxon. The node breaks in a tree three steps longer (TL = 106), and the percentage of trees retaining the node in the bootstrap analysis is 97%. Characters diagnostic for the genus Cyamodus are: 7* (1) [ci = 0.5], maxilla floors external naris; 9 (1) [ci = 1], jugal extends backward along the anteromedial margin of subtemporal fossa (needs confirmation for Cyamodus kuhnschnyderi); 13* (1) [ci = 1], frontals extend posteriorly beyond the level of the anterior margin of the upper temporal fossa; 22* (1) [ci = 1], relatively broad upper temporal fossa; 23* (1) [ci = 1], upper temporal fossa at least twice as long as orbit; 33 (2) [ci = 1], premaxillary teeth bulbous, with transverse ridge; 43 (2) [ci = 1], jugal extends medi ally to meet palatine at anterior margin of subtemporal fossa; 45* 7(1) [ci = 1], pterygoid flange with double ventral projection; and 52 (1) [ci = 0.5], coronoid closely approaches the lower margin of the mandible. ACCTRAN optimization adds 46 (1) [ci = 0.667].

These characters diagnose the genus Cyamodus without inclusion of Cyamodus hildegardis. Kuhn-Schnyder (1960: 96) expressed some doubt as to whether hildegardis should be included in the genus Cyamodus, and Nosotti and Pinna (1996, Fig. 24) show the genus to be paraphyletic, with Cyamodus hildegardis more closely related to the Protoendoontosaurus-placochelyid clade than to the Germanic representatives of the genus. At least one character of this analysis would support this conclusion—the relatively narrow upper temporal fossa in Cyamodus hildegardis (see Table 8). However, inclusion of Cyamodus hildegardis (coded for 35.2% of the characters) in a separate analysis yielded one single most parsimonious tree with a TL of 109 steps, a CI of 0.752, and an RI of 0.693 (Fig. 33). Cyamodus hildegardis came out as the sister-taxon of Cyamodus rostratus plus Cyamodus kuhnschnyderi on the basis of the following characters: 23* (1) [ci = 1], upper temporal fossa at least twice as long as orbit; 33 (2) [ci = 1], bulbous premaxillary teeth; and 52 (1) [ci = 0.5], coronoid closely approaching the ventral margin of the mandible.

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**Fig. 33.** Most parsimonious reconstruction of placodont interrelationships, with Cyamodus hildegardis included (single most parsimonious tree with a TL of 109 steps, a CI of 0.752, and an RI of 0.693). For further discussion, see text.
ACCTRAN optimization added 7 (1) [ci = 0.5]; 13 (1) [ci = 1]; 45 (1) [ci = 1]; and 46 (1) [ci = 0.667].

*Cyamodus muensteri* (coding based on the holotype of *C. laticeps* Owen) could be coded for 46.3% of the characters used in this analysis. If this taxon was included but *Cyamodus hildegardis* deleted from the analysis, a total of six equally parsimonious trees would be obtained with a TL of 106 steps, a CI of 0.736, and an RI of 0.699. The strict consensus tree shows unresolved relationships of *Placodus* and *Paraplacodus* relative to the Cyamodontoidea and unresolved relationships among the three species of *Cyamodus* included (*C. rostratus*, *C. kuhnschnyderi*, and *C. muensteri*). If both *Cyamodus muensteri* and *Cyamodus hildegardis* are included in the analysis, a total of 30 equally parsimonious trees are obtained with a TL of 112 steps, a CI of 0.732, and an RI of 0.688. The strict consensus tree retains only two nodes, that is, the monophyly of the Cyamodontoidea, and the sister-group relationship of *Placochelys* and *Psephoderma* within the latter. All other cyamodonoids fall into an unresolved polytomy.

In a tree only one step longer than the most parsimonious reconstruction (TL = 104; Fig. 32, incomplete taxa not included), the node that relates *Macroplacus* to the *Protenodontosaurus*–*Placochelys*–*Psephoderma* clade collapses (the percentage of trees retaining the node in the bootstrap analysis is 57%). The lability of the relationships of *Macroplacus* within the cyamodontoids is due to the fact that the skull, although rather incompletely preserved, shares important characters with *Cyamodus*, as indicated in the morphological description above. These are the short anterior extent of the jugal along the ventral margin of the orbit (8 [1]), the relative shortness of the otic process of the squamosal (26 [1]), and the reduced posttemporal fossa (46 [1]). However, the most parsimonious reconstruction places *Macroplacus* as sister-taxon to *Protenodontosaurus* and the *Placochelys*–*Psephoderma* clade on the basis of the following characters: 18* (2) [ci = 0.5], the suture between the maxilla and the jugal below the midpoint of the orbit; 21* (1) [ci = 1], postorbital forms medioventral process that abuts the epipterygoid; 39* (1) [ci = 1], maxilla with anterolateral process tapering off along lateral margin of the rostrum; 40* (1) [ci = 1], ventral surface of rostrum concave; and 43 (1) [ci = 1], palatine extends laterally to meet jugal. ACCTRAN optimization adds 4 (1) [ci = 0.5]; 5 (1) [ci = 0.5]; 12 (0) [ci = 0.5]; 14 (1) [ci = 0.667]; and 50 (1) [ci = 0.5].

*Protenodontosaurus* is the sister-taxon of the *Placochelys*–*Psephoderma* clade (“placochelyids”) in the most parsimonious reconstruction, although the node is weakly supported. The node collapses in a tree one step longer (TL = 104) yields five trees, of which 80% retain *Protenodontosaurus* as sister-taxon of *Placochelys* and *Psephoderma*, and the percentage of trees retaining the node in the bootstrap analysis is a mere 52%. The sister-group relationship of *Placochelys* and *Psephoderma* is retained in 80% of the trees of the bootstrap analysis; but in a tree only three steps longer (TL = 106), *Protenodontosaurus*, *Placochelys*, and *Psephoderma* all fall into an unresolved polytomy with *Macroplacus* and *Henodus*. The sister-group relationship of *Protenodontosaurus* with the placochelyids is supported by the following characters: 26* (2) [ci = 1], otic process of squamosal extends beyond the medial margin of the posttemporal fossa; 29* (1) [ci = 1], palatine contacts the quadrate lateral to palaquadrate cartilage recess; 31* (1) [ci = 1], prototic exposed in posterior view of skull. ACCTRAN optimization adds 8 (0) [ci = 0.5].

Finally, *Placochelys* is found to be the sister-taxon of *Psephoderma*, a dichotomy that breaks in a tree three steps longer (TL = 106) but is supported by 80% of the trees of the bootstrap analysis. Several synapomorphies support a sister-group relationship of *Placochelys* and *Psephoderma*: 2* (1) [ci = 1], skull depressed; 3* (1) [ci = 1], rostrum narrow and distinctly elongated; 18* (1) [ci = 0.5], suture between maxilla and jugal located below posterior half of the orbit; 32* (1) [ci = 1], premaxillary teeth absent; 41* (1) [ci = 1], ventral surface of rostrum with distinct grooves; 44* (1) [ci = 0.5], palatal exposure of pterygoid relatively long; 47* (1) [ci = 1], squamosal buttress receives distal tip of paroccipital process; 51* (1) [ci = 0.5], anterior tip of dentary edentulous; 52 (1) [ci = 0.5], coronoid closely approaching ventral margin of mandible. ACCTRAN optimization adds 5 (0) [ci = 0.5]; 7 (1) [ci = 0.5]; 49 (0) [ci = 0.5]. Jaekel (1907: 78; Placochelidae), Nopcsa (1923: 12; Placochelynae), Nopcsa (1923: 172; Placochelyinae), and Peyer and Kuhn-Schnyder (1955: 475; Placochelyidae) all introduced a higher yet monotypic category to include *Placochelys* only. Romer (1956: 670) was the first to propose a family Placochelyidae to include *Placochelys* and *Psephoderma*, along with *Psephosaurus* (no cranial material known) and the
enigmatic *Saurophargis* (see Rieppel, 1995b, for comments on the latter genus).

An incomplete cyamodontoid skull known from the lower Muschelkalk of Makhtesh Ramon, Negev, Israel, was provisionally referred to *Psephosaurus* by Brotzen (1957). This specimen could be coded for 29.6% of the characters only. If it is entered into the analysis without inclusion of *Cyamodus hildegardis*, four equally parsimonious trees result with a TL of 104 steps, a CI of 0.75, and an RI of 0.701. The strict consensus tree shows the Negev cyamodontoid to fall into an unresolved polytomy with *Macroplacus*, *Protenodontosaurus*, and the placocheleys (Fig. 34). Three of those four trees retain *Protenodontosaurus* as sister-taxon of the placocheleys. If both the Negev specimen and *Cyamodus hildegardis* are entered into the analysis, a further drop in resolution is observed, with six equally parsimonious trees of TL = 110 steps (CI = 0.745; RI = 0.689). The strict consensus tree shows the Israeli specimen to fall into a polytomy with *Macroplacus*, *Protenodontosaurus*, the placocheleys, and the clade from the Germanic Triassic. Four of those six trees show the Israeli specimen in a trichotomy with *Macroplacus* and the *Protenodontosaurus*—placocheyleid clade. Inclusion of the Negev taxon and *Cyamodus muensteri*, but excluding *Cyamodus hildegardis*, resulted in 24 equally parsimonious trees (TL = 107; CI = 0.729; RI = 0.695), with the three species of *Cyamodus* in an unresolved trichotomy, while the Israeli speci-

men falls into a polytomy with *Macroplacus*, *Protenodontosaurus*, and the placocheleys. However, *Henodus* is retained as sister-group of *Cyamodus*, and the two are retained as sister-taxon of all other cyamodontoids. If the Negev specimen is included in the analysis along with *Cyamodus hildegardis* and *Cyamodus muensteri*, a total of 166 equally parsimonious trees are obtained (TL = 113; CI = 0.726; RI = 0.648), the strict consensus tree of which retains only two nodes, the monophyly of the Cyamodontoidea and the sister-group relationship of *Placochelys* and *Psphoderma*. What little evidence there is suggests that the cyamodontoid from the Muschelkalk of Makhtesh Ramon is relatively more closely related to the taxa from the Alpine Triassic than to the clade from the Germanic Triassic.

**Systematic Paleontology**

**Sauropterygia Owen, 1860**

**Placodontia Zittel, 1887–1890**

**Cyamodontoidea Nopcsa, 1923**

**Definition**—A monophyletic taxon including the Cyamodontida and the Placochelyida.

**Diagnosis**—Dermal armor forming a carapace; palatoquadrate cartilage persisting in adult in a recess between epipterygoid and quadrate; broad dorsal process of epipterygoid; epipterygoid situated primarily to palatine; epipterygoid meets squamosal at dorsal margin of posttemporal fossa; squamosal with otic process enclosing the pteroccipital foramen anteriorly; pineal foramen displaced anteriorly; postfrontal broadly excluded from temporal fossa; two maxillary tooth plates; two palatine tooth plates; anterior palatine tooth plates round; retroarticular process short, with sloping surface; tubercular osteoderms secondarily fused to squamosal.

**Distribution**—Middle to Upper Triassic, western Tethyan faunal province (Europe and northern Gondwanan shelf).

**Comments**—The lower (lower Anisian) and upper (upper Anisian, lower Ladinian) Muschelkalk of the Germanic Triassic has yielded a number of *Cyamodus* skulls, skull fragments, or lower jaws (Gürich, 1884; Meyer, 1863), but only three carapace fragments have been recorded from the upper Muschelkalk (mo2, referred to *Cyamodus kuhnschnyderi* by Nosotti & Pinna, 1996), and

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none has ever been collected in the lower (mu) or lower upper Muschelkalk (mo1). As carapace fragments show a high probability of fossilization at other localities where cyamodontoid placodonts occur, it remains uncertain whether all representatives of the genus Cyamodus (C. rostratus, C. muensteri, C. tarnowitzensis) in fact developed a carapace.

This systematic section provides diagnoses of monophyletic taxa based primarily on cranial anatomy. Species diagnoses will be based on autapomorphies. Not included in this systematic section is Psephosaurus suevicus. Fraas, 1896, because this taxon is known from its carapace only and therefore cannot be diagnosed on the basis of skull anatomy. A proper diagnosis for this taxon, along with the description of a new genus of cyamodontoid placodont, will be presented in the context of a comprehensive review of the cyamodontoid dermal armor.

The palatoquadrate cartilage recess is here coded and treated as an autapomorphy of Cyamodontidae. This accounts for its complex structure, defined by the prootic, epipterygoid, quadrate, pterygoid, and palatine and including an anterior groove holding a persistent palatine process of the palatoquadrate. Palatoquadrate cartilage also persists in Placodus and cryptodire turtles, and its simple presence in the adult could also be treated as synapomorph at a more inclusive level.

Cyamodontida, new taxon

DEFINITION—A monophyletic taxon including the Cyamodontidae and the genus Henodus Huene, 1936.

DIAGNOSIS—Jugal not extending far anteriorly along the ventral margin of the orbit; parietal with distinct anterolateral process entering between frontal and postfrontal; lateral margin of postfrontal deeply concave and angulated; paroccipital process with posteroventral tubercle at its distal end; exoccipitals in contact above the basioccipital condyle.

DISTRIBUTION—Middle and Upper Triassic (lower Anisian through Carnian), Germanic Basin and southern Alps.

Henodus Huene, 1936

TYPE SPECIES—Henodus chelyops Huene, 1936, from the upper Gipskeuper (Carnian) of Lustnau near Tübingen, southern Germany.

DEFINITION—A monotypic taxon including the species chelyops.

DIAGNOSIS—Skull broad and flat; rostrum short and broad; anterior cutting edge of rostrum (pre-maxillaries) lined by a series of incompletely individualized denticles; maxillary without tooth plates but with deep grooves (possibly supporting baleens); palatine with single posterior tooth plate; upper temporal fenestra vestigial or absent; parietal broad and fan-shaped; cephalic condyle of quadrate posteriorly expanded and abutting a ventral flange of the squamosal; palatines separated from one another by broad vomers and pterygoids; dentary with deep groove and single posterior tooth plate; coronoid small, forming small coronoid process and remaining widely separated from lower margin of lower jaw.

DISTRIBUTION—Upper Gipskeuper (lower Carnian, Upper Triassic), southern Germany.

Henodus chelyops Huene, 1936

1936 Henodus chelyops, Huene, pp. 99, 125 ff., Figs. 1–23, Pls. 9–12.
1937 Henodus chelyops, Reiff, pp. 534, 536 ff.
1938 Henodus chelyops, Huene, p. 105 ff., Figs. 1–3, Pl. 17.
1938 Henodus chelyops, Schmidt, p. 62 f., Fig. 1152b.
1939 Henodus chelyops, Kuhn, p. 277.
1942 Henodus chelyops, Kuhn-Schnyder, p. 175.
1942 Henodus chelyops, Reiff, p. 31 ff., Figs. 1–5.
1946 Henodus chelyops, Gregory, p. 315, Fig. 31.
1947 Henodus chelyops, Vialli, p. 112.
1949 Henodus, E.v. Huene, p. 78, Fig. 3b.
1958 Henodus chelyops, Huene, p. 165 ff., Figs. 1–6, Pls. 3–4.
1961 Henodus chelyops, Kuhn, p. 20.
1963 Henodus, Kuhn-Schnyder, p. 74.
1965a Henodus, Kuhn-Schnyder, p. 278.
1968 Henodus chelyops, Müller, p. 205 ff., Figs. 239–242.
1969 *Henodus chelyops*, Kuhn, p. 17 ff., Fig. 6.6–6.12.


1989 *Henodus chelyops*, Mazin, p. 729, Fig. 5B.

1990a *Henodus chelyops*, Pinna, p. 146, Fig. 1.

1990b *Henodus chelyops*, Pinna, p. 11.


1993 *Henodus chelyops*, Pinna and Mazin, p. 126, Fig. 1.


1996 *Henodus chelyops*, Nosotti and Pinna, pp. 22, 36, 38, Fig. 24.

1997 *Henodus chelyops*, Rieppel and Zanon, pp. 202–213, Figs. 2E, 3E.


**LECTOTYPE**—“Specimen II” of Huene, 1936.

**PARATYPE**—“Specimen I” of Huene, 1936.

**STRATUM TYPICUM**—Estherienschichten, uppermost Gipskeuper, lower Carnian, Upper Triassic.

**LOCUS TYPICUS**—Lustnau near Tübingen, southern Germany.

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

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

**REFERRED SPECIMENS**—Specimens III through VIII (GPIT, uncatalogued; Huene, 1938; Fischer, 1959).

**Cyamodontidae Nopessa, 1923**

**DEFINITION**—A monophyletic taxon including the genus *Cyamodus* Meyer, 1863.

**DIAGNOSIS**—Anterior end of maxilla extended medially to floor the external nares; jugal extending backward along anteromedial margin of subtemporal fossa; frontals extending posteriorly beyond the level of the anterior margin of the upper temporal fossa; upper temporal fenestra relatively broad; upper temporal fenestra at least twice as long as orbit; premaxillary teeth bulbous, with transverse ridge; jugal extends medially to meet palatine at anterior margin of subtemporal fossa; pterygoid flange with double ventral projection; coronoid closely approaches the lower margin of mandible.

**DISTRIBUTION**—Middle Triassic (Anisian, Ladinian), Germanic Basin and southern Alps.

**COMMENTS**—The species *Cyamodus tarnowitzensis* Gürich, 1884, is based on an incompletely preserved and poorly illustrated skull from the Karchowice Beds (uppermost lower Muschelkalk (lower Illyrian, lower Anisan) of Tarnowitz in Upper Silesia (now Tarnowskie Gory, Poland), but this skull is now lost. Fragmentary cranial material of a cyamodontoid placodont from the lower Muschelkalk (lower Anisan) of Makhtesh Ramon, Negev, Israel, is not diagnostic at the genus level but has been thought to perhaps belong to the genus *Cyamodus* (Brotzen, 1957; Rieppel, Mazin, & Tchernov, 1999). If so, this occurrence would greatly increase the area of distribution of the genus *Cyamodus*. However, the cladistic analysis reported above does not support inclusion of the Negev cyamodontoid in the genus *Cyamodus*.

**Cyamodus Meyer, 1863**

1839 *Placodus* (partim), Münster, p. 119.

1839 *Placodus* (partim), Agassiz, Pl. 71, Figs. 1–5.

1844 *Placodus* (partim), Agassiz, p. 220.

1858 *Placodus* (partim), Owen, p. 169.

1862 *Placodus* (partim), Braun p. 8.

**TYPE SPECIES**—*Cyamodus rostratus* (Münster, 1839), from the lower upper Muschelkalk (mol) of Bayreuth, southern Germany.

**DEFINITION**—A monophyletic taxon including the species *hildegaridis*, *kuhnschnyderi*, *muensteri*, and *rostratus*.

**DIAGNOSIS**—As for family, of which this is the only known genus.

**DISTRIBUTION**—As for family, of which this is the only known genus.

**Cyamodus hildegaridis Peyer, 1931a**

1931a *Cyamodus hildegaridis*, Peyer, p. 6, Textfig. 5, Pls. 15, 16, 17, Fig. 1.

1933 *Cyamodus hildegaridis*, Kuhn, p. 11 f.

1935 *Cyamodus hildegaridis*, Peyer, p. 20, Pl. 46.

1936 *Cyamodus münsteri*, Huene, pp. 129, 147.
1942 *Cyamodus hildegardis*, Kuhn-Schnyder, p. 175.
1944 *Cyamodus hildegardis*, Peyer, pp. 60–63, Figs. 61, 63.
1947 *Cyamodus hildegardis*, Vialli, p. 111, Table 1.
1956 *Cyamodus hildegardis*, Huene, p. 371.
1959 *Cyamodus hildegardis*, Kuhn-Schnyder, p. 174 ff., Fig. 1, Pl. 1.
1960 *Cyamodus hildegardis*, Kuhn-Schnyder, p. 91 ff., Fig. 1.
1961 *"Cyamodus" hildegardis*, Kuhn, p. 19.
1965a *Cyamodus hildegardis*, Kuhn-Schnyder, pp. 260, 275.
1968 *Cyamodus hildegardis*, Müller, p. 199, Fig. 234.
1968 *Cyamodus hildegardis*, Peyer, p. 153, Fig. 98.
1969 *"Cyamodus" hildegardis*, Kuhn, p. 15.
1974 *Cyamodus hildegardis*, Kuhn-Schnyder, p. 69 ff., Fig. 47.
1975 *Cyamodus hildegardis*, Westphal, p. 111 f., 121, Fig. 10.
1979 *Cyamodus hildegardis*, Kuhn-Schnyder, p. 29, Fig. 23.
1979 *"Cyamodus" hildegardis*, Pinna and Zucchi Stolfa, p. 311.
1980a *Cyamodus hildegardis*, Pinna, p. 275 ff., Figs. 1–6, Pls. 4–6.
1980b *Cyamodus hildegardis*, Pinna, p. 313.
1988 *Cyamodus hildegardis*, Westphal, p. 162, Fig. 11.
1989 *Cyamodus hildegardis*, Mazin, p. 727, Figs. 2C–E.
1989 *Cyamodus hildegardis*, Pinna, p. 150, 154 f.
1989 *Cyamodus hildegardis*, Tschanz, p. 168, Fig. 8.
1990a *Cyamodus hildegardis*, Pinna, pp. 146, 149, 153, Fig. 1.
1990b *Cyamodus hildegardis*, Pinna, p. 11.
1992 *Cyamodus hildegardis*, Alafont, pp. 77, 81.
1993 *Cyamodus hildegardis*, Dalla Vecchia, pp. 53, 55, Fig. 4A–B.
1993 *Cyamodus hildegardis*, Mazin and Pinna, p. 83 ff., Figs. 3, 4, 6a.
1993 *Cyamodus hildegardis*, Pinna and Mazin, p. 126, Fig. 1.
1996 *Cyamodus hildegardis*, Nosotti and Pinna, p. 3 ff., Fig. 24.
1997 *Cyamodus hildegardis*, Rieppel and Zanoni, p. 212.

**HOLOTYPE**—PIMUZ T4763; articulated skeleton.

**STRATUM TYPICUM**—Grenzbitumen-horizon, Anisian–Ladinian boundary, Middle Triassic.

**LOCUS TYPICUS**—Val Porina, Monte San Giorgio, southern Switzerland.

**DIAGNOSIS**—Two premaxillary teeth; three or four maxillary teeth; two or three palatine tooth plates; posterior palatine tooth plates elongate; body heavily armored with bipartite carapace (dorsal shield and tail shield).

**DISTRIBUTION**—Middle Triassic (Anisian-Ladinian boundary), southern Alps.

**REFERRED SPECIMENS**—PIMUZ T58, articulated skeleton; T1285, postcraniol fragment; T2796, subadult skull; T2797, juvenile skull; T2804, tooth-bearing elements as stomach content of *Lariosaurus buzzii* (Tschanz, 1989); T4764, postcranial remains; T4765, fragmentary mandible; T4766, mandibular teeth; T4767, palatine and dentary teeth; T4768, skull; T4770, partial skull; T4771, skull; T4772, isolated teeth. MSNM V458, juvenile skeleton; V478, skull.

**COMMENTS**—The diagnosis of this taxon is incomplete. Pinna (1999) considered *Cyamodus hildegardis* a probable synonym of *Cyamodus laticeps*, but because the latter name was recognized as a junior synonym of *Cyamodus muensteri* above, all three species would have to be synonymized. The dentition of *Cyamodus muensteri* falls into the range of variation of that of *Cyamodus hildegardis*. The latter taxon is known to have developed extensive dermal armor, which remains largely unknown for the other species of this genus. Although this may be a diagnostic feature, the apparent lack of body armor in the species of *Cyamodus* from the Upper Muschelkalk of Bayreuth (*Cyamodus muensteri* and *Cyamodus rostratus*) may also be due to the incompleteness of the fossil record.

*Cyamodus kuhnschnyderi* Nosotti and Pinna, 1993

1928 *Cyamodus* sp., Berckheimer, p. xix, Fig. 1956 *Cyamodus*, Huene, p. 371, Fig. 415.
1959 **Cyamodus** sp., Kuhn-Schnyder, p. 184, Figs. 2c, 3b.

1960 **Cyamodus** sp., Kuhn-Schnyder, p. 96, Figs. 2, 4, 7b, Pl. 7.

1969 **Cyamodus**, Kuhn, p. 16.

1974 **Cyamodus** sp. (Crailsheim), Kuhn-Schnyder, p. 70, Fig. 49.

1979 "**Cyamodus**" sp. (Crailsheim), Pinna and Zucchi Stolfa, p. 312.

1989 **Cyamodus** sp. (Crailsheim), Mazin, p. 728, Fig. 2B.

1990a "**Cyamodus**" sp., Pinna, p. 149, Fig. 1.

1990b **Cyamodus** sp. (Crailsheim), Pinna, p. 11.

1993 **Cyamodus** sp., Mazin and Pinna, p. 84.

1993a **Cyamodus** kuhn-schnyderi, Nosotti and Pinna, p. 847 ff., Figs. 1–2.

1993b **Cyamodus** sp., Nosotti and Pinna, pp. 109, 112, Fig. 3.

1993 **Cyamodus** Khuntschynyderi, Pinna and Mazin, Fig. 1.

1994b **Cyamodus** kuhnscnhyderi, Rieppel, p. 42.


1997 **Cyamodus** kuhn-schnyderi, Rieppel and Zanon, p. 212, Figs. 1C, 2B, 3B.

1999 **Cyamodus** kuhnscnhyderi, Pinna, p. 26 f.

**Holotype**—SMNS 15855; skull.

**Paratypes**—SMNS 16270, skull; 18380, partial lower jaw.

**Stratum Typicum**—Hohenlohe Subformation of the Meissner Formation, **Discoceratitenschichten**, upper Muschelkalk (mo2), lower Ladinian, Middle Triassic.

**Locus Typicus**—Crailsheim, southern Germany.

**Diagnosis**—Nasals fused; anterolateral process of frontal absent; anteromedial process of the parietal embraced by the frontal; a basi orbital furrow present (also in **Cyamodus** "laticeps" and **Henodus**), with three foramina (two in **Cyamodus** "laticeps" and **Henodus**); the epityreogid is incompletely ossified in the adult (may occur convergently in **Protenodontosaurus**).

**Distribution**—Upper Muschelkalk (mo2, lower Ladinian), southern Germany.

**Referred Specimens**—SMNS 15891c, 16725, 81600; carapace fragments.

**Cyamodus muensteri** (Agassiz, 1839)

1830 no name, Münster, p. 3, Fig. 2.

1839 **Placodus Müensteri**, Münster, p. 120.

1840 **Placodus münsteri**, Braun, p. 120 (fide Pinna, 1999).


1858 **Placodus laticeps**, Owen, p. 169, Pl. 9, Figs. 1–2, Pl. 10, Fig. 1.


1984 **Placodus laticeps**, Kuhn, p. 7.


1984 **Placodus laticeps**, Gürich, p. 140.

1984 **Placodus Müensteri**, Gürich, p. 139.

1989 **Placodus laticeps**, Lydekker, p. 7 f., Fig. 1.


1928 **Cyamodus laticeps**, Drevermann, p. 100.

1928 **Cyamodus Müensteri**, Corroy, p. 125.

1928 **Cyamodus laticeps**, Drevermann, p. 292 ff.

1928 **Cyamodus Müensteri**, Drevermann, p. 292 ff.

1928 **Cyamodus Müensteri**, M. Schmidt, p. 410 ff., Fig. 1151.

1931a **Cyamodus laticeps**, Peyer, p. 5.

1931a **Cyamodus münsteri**, Peyer, p. 5.

1931b **Cyamodus laticeps**, Peyer, p. 274.

1931b **Cyamodus münsteri**, Peyer, p. 274.

1933 **Cyamodus münsteri**, Kuhn, p. 11.

1936 **Cyamodus münsteri**, Huene, pp. 129, 147.

1947 **Cyamodus münsteri**, Vialli, Table 1.

1956 **Cyamodus laticeps**, Huene, p. 371.

1956 **Cyamodus münsteri**, Huene, p. 371.

1959 **Cyamodus laticeps**, Kuhn-Schnyder, p. 184 ff., Fig. 2b.

1959 **Cyamodus münsteri**, Kuhn-Schnyder, p. 184 f.

1960 **Cyamodus laticeps**, Kuhn-Schnyder, p. 92.

1960 **Cyamodus münsteri**, Kuhn-Schnyder, p. 92.

1961 **Cyamodus münsteri**, Kuhn, p. 19.

1965a **Cyamodus Müensteri**, Kuhn-Schnyder, p. 259.

1969 "**Cyamodus**" laticeps, Kuhn, p. 15.

1969 "**Cyamodus**" münsteri, Kuhn, p. 15.

1979 "**Cyamodus**" laticeps, Pinna and Zucchi Stolfa, p. 312.

1979 "**Cyamodus**" münsteri, Pinna and Zucchi Stolfa, p. 312.

1980a **Cyamodus laticeps**, Pinna, p. 278.
1980a *Cyamodus muensteri*, Pinna, p. 278.
1988 *Cyamodus laticeps*, Westphal, p. 159.
1988 *Cyamodus muensteri*, Westphal, p. 159.
1989 *Cyamodus laticeps*, Mazin, p. 733.
1989 *Cyamodus muensteri*, Mazin, p. 733.
1989 *Placodus laticeps*, Nosotti and Pinna, p. 42, Fig. 8, Pl. 4, Fig. 1.
1989 *Placodus münsteri*, Nosotti and Pinna, p. 37, Fig. 4.
1989 *Cyamodus laticeps*, Nosotti and Pinna, pp. 67, 82.
1989 *Cyamodus münsteri*, Nosotti and Pinna, pp. 67, 82.
1990a *Cyamodus münsteri*, Pinna, p. 149, Fig. 1.
1990b *Cyamodus laticeps*, Pinna, p. 11, Table 1.
1993 *Cyamodus laticeps*, Mazin and Pinna, p. 84.
1993 *Cyamodus muensteri*, Mazin and Pinna, p. 84.
1993 *Cyamodus muensteri*, Pinna and Mazin, p. 126, Fig. 1.
1996 *Cyamodus laticeps*, Nosotti and Pinna, p. 36, Fig. 24.
1996 *Cyamodus muensteri*, Nosotti and Pinna, p. 3, Fig. 24.
1997 *Cyamodus münsteri*, Rieppel and Zanon, p. 212.
1999 *Cyamodus laticeps*, Pinna, p. 45.f.
1999 *Cyamodus muensteri*, Pinna, p. 22.f.

**HOLOTYPE**—BSP AS VII 1210; incomplete skull.

**STRATUM TYPICUM**—Trochitenkalk Formation and the lower part of the Meissner Formation (atavus through postspinosus biozone), upper Muschelkalk (mol), uppermost Illyrian, upper Anisian, Middle Triassic.

**LOCUS TYPICUS**—Bayreuth, southern Germany.

**COMMENTS**—As discussed above, the skull of *Cyamodus muensteri* is incomplete and heavily reconstructed. The skull of *Cyamodus laticeps* Owen, 1858, from the same locality is more complete, somewhat larger than that of *C. rostratus*, and distinctly larger than that of *C. muensteri*. According to Kuhn (1933), Meyer (1863) considered *C. laticeps* a junior synonym of *C. muensteri*, but no such indication can be found in Meyer's (1863) text. Drevermann (1928) was the first to claim that *C. laticeps* and *C. tarnowitzensis* are junior synonyms of *C. muensteri*, an arrangement that was also accepted by Huene (1956) for *C. laticeps* and *C. muensteri*. Table 5 summarizes the dentitional characters of the species of the genus *Cyamodus* and shows that the presence of three palatine tooth plates, located entirely behind the posteriormost maxillary tooth, is autapomorphic for *C. rostratus*. All other species have two palatine tooth plates, of which the anterior one is located lateral to and slightly behind the posterior maxillary tooth. The posterior maxillary and anterior palatine teeth thus are aligned in an anteriorly slightly concave arch. *C. muensteri*, *C. laticeps*, and *C. tarnowitzensis* differ from *C. kuhnschuynderi* by the presence of three maxillary teeth and by a slightly (*C. muensteri*, *C. laticeps*) or distinctly (*C. tarnowitzensis*) elongated posterior palatine tooth plate. However, *C. hildegardis* also has three maxillary teeth (four in one specimen) and elongated posterior palatine tooth plates. Whereas similarities in the dentition corroborate Drevermann's (1928) conclusion that *C. laticeps* is a junior synonym of *C. muensteri* in spite of size difference, comparison with *C. hildegardis* indicates that the incomplete and poorly preserved skulls of *C. muensteri* do not permit a diagnosis of the species on the basis of dentitional characters. The skull of *C. laticeps* is unique among its genus in that the posterior (nasal) processes of the premaxillae meet the frontal, thereby separating the nasals from one another; this character is unknown for the holotype of *C. muensteri*. It may therefore be prudent to treat this species as a metaspecies sensu Gauthier, Estes, and DeQueiroz (1988; see also Archibald, 1994).

The synonymy of *C. tarnowitzensis* is less easily resolved. The incomplete skull came from a different horizon and a different locality (lower Muschelkalk, Upper Silesia) than *C. muensteri* (upper Muschelkalk, Bayreuth, southern Germany) and can no longer be located today. The illustrations provided by Gürich (1884) are schematic and not useful in establishing species validity or synonymy. For these reasons, the species *tarnowitzensis* is here treated as nomen dubium.

**Cyamodus rostratus** (Münster, 1839)

1839 *Placodus rostratus*, Münster, p. 119, Pl. 15, Figs. 1–6.
1839 *Placodus rostratus*, Agassiz, Vol. 2, Pl. 71, Figs. 6–12.
1840 *Placodus rostratus*, Braun, p. 74 (fide Pinna, 1999).
1856 \textit{Placodus rostratus}, Owen, p. 170, Pl. 11, Fig. 4.


1890 \textit{Cyamodus rostratus}, Lydekker, p. 7.

1922 \textit{Cyamodus rostratus}, Drevermann, p. 100.


1928 \textit{Cyamodus rostratus}, Drevermann, p. 291 ff., Figs. 1–2, Pl. 23, Figs. 1a–e.

1928 \textit{Cyamodus rostratus}, M. Schmidt, p. 410, Fig. 1150.

1931a \textit{Cyamodus rostratus}, Peyer, p. 5.

1933 \textit{Cyamodus rostratus}, Kuhn, p. 10 f.

1936 \textit{Cyamodus rostratus}, Huene, pp. 110, 129, 147.

1947 \textit{Cyamodus rostratus}, Vialli, p. 112, Table 1.


1956 \textit{Cyamodus rostratus}, Huene, p. 371, Fig. 415.


1960 \textit{Cyamodus rostratus}, Kuhn-Schnyder, p. 92 ff., Figs. 3, 4, 5a, 6a, 7a.


1961 \textit{Cyamodus rostratus}, Kuhn-Schnyder, p. 107, Fig. 7b.

1965a \textit{Cyamodus rostratus}, Kuhn-Schnyder, p. 257 ff., Figs. 1–6, Pls. 116–118.


1969 \textit{Cyamodus rostratus}, Kuhn, p. 14 f., Fig. 7.

1974 \textit{Cyamodus rostratus}, Kuhn-Schnyder, p. 70 f., Fig. 50.

1975 \textit{Cyamodus rostratus}, Schubert-Klempnauer, p. 50, Figs. 7A, 8A.


1987 \textit{Cyamodus rostratus}, Sues, p. 143.

1988 \textit{Cyamodus rostratus}, Westphal, p. 159, Fig. 10.

1989 \textit{Cyamodus rostratus}, Mazin, p. 727, Figs. 2A.

1989 \textit{Placodus rostratus}, Nosotti and Pinna, p. 37, Fig. 4, Pl. 6.

1989 \textit{Cyamodus rostratus}, Nosotti and Pinna, pp. 67, 82, Fig. 14.1.

1990a \textit{Cyamodus rostratus}, Pinna, p. 149, Fig. 1.

1990b \textit{Cyamodus rostratus}, Pinna, p. 11, Table 1.


1993 \textit{Cyamodus rostratus}, Dalla Vecchia, p. 55, Fig. 4C.

1993 \textit{Cyamodus rostratus}, Mazin and Pinna, p. 84.


1993 \textit{Cyamodus rostratus}, Mazin and Pinna, p. 84.

1993 \textit{Cyamodus rostratus}, Pinna and Mazin, p. 126, Fig. 1.

1995a \textit{Cyamodus rostratus}, Rieppel, p. 36.

1996 \textit{Cyamodus rostatus}, Nosotti and Pinna, p. 3 ff., Fig. 24.

1996 \textit{Cyamodus cfr. rostratus}, Nosotti and Pinna, Fig. 20.


**Holotype**—umo BT 748; skull.

**Stratum Typicum**—Trochitenkalk Formation and the lower part of the Meissner Formation (atavus through postspinomus biozone), upper Muschelkalk (mol), uppermost Illyrian, upper Anisian, Middle Triassic.

**Locus Typicus**—Bayreuth, southern Germany.

**Diagnosis**—Grooves on the postorbital part of each frontal converging toward the pineal foramen; maxilla extends backward in lateral view to level well behind the posterior margin of orbit; jugal excluded from the orbital margin in lateral view; anterior palatal process of jugal entering deeply between maxilla and palatine; jugal extending backward along the anteromedial margin of the subtemporal fossa (possibly also present in \textit{Cyamodus kuhnschnyderi}); tip of the posterior dorsal process of the epipterygoid exposed at the dorsomedial corner of the posttemporal fossa in occipital view; occiput with a separate, heterotrophic “epiotic” ossification located between supraoccipital and opisthotic; three palatine tooth plates, located entirely behind the two maxillary tooth plates.

**Distribution**—Upper Muschelkalk (upper Anisian), southern Germany.

**Referred Specimens**—SMNS 17403; incomplete
skull. UMO BT 2172; isolated lower jaw. SMF R-4040; isolated lower jaw.

**Placochelyida, new taxon**


**DIAGNOSIS**—Vertical suture between maxilla and jugal below midpoint of orbit; postorbital with medioventral process abutting the epipterygoid; maxilla with anterolateral process tapering off along lateral margin of rostrum; ventral surface of rostrum concave; palatine extends laterally to meet jugal.

**DISTRIBUTION**—Upper Triassic, central Europe and southern Alps.

**Macroplacus Schubert-Klempnauer, 1975**

**TYPE SPECIES**—*Macroplacus raeticus* Schubert-Klempnauer, 1975, from the Rhaetian of the Bavarian Alps.

**DEFINITION**—A monotypic taxon including the species *raeticus*.

**DIAGNOSIS**—Posterior palatine tooth plates hypertrophied; posterior (nasal) processes of the premaxillaries enlarged and extending backward to reach the frontal, thereby separating the nasals from one another (convergent in *Psephoderma*); posttemporal fossae greatly reduced; a foramen piercing the shaft of the quadrate just above the mandibular condyle.

**DISTRIBUTION**—Rhaetian (Upper Triassic) of the Bavarian Alps.

**Macroplacus raeticus Schubert-Klempnauer, 1975**

1975 *Macroplacus raeticus*, Schubert-Klempnauer, p. 35, Figs. 1–6, 7C, 8C, PIs. 4–5.
1976a *Macroplacus raeticus*, Pinna, pp. 11, 35 f.
1989 *Macroplacus raeticus*, Pinna, pp. 150, 154, Fig. 5.
1990a *Macroplacus raeticus*, Pinna, p. 149.

1990a *Psephoderma raeticus*, Pinna, p. 149, Fig. 1.
1993 *Psephoderma raeticus*, Mazin and Pinna, p. 84.
1993 *Macroplacus raeticus*, Pinna and Mazin, p. 126, Fig. 1.
1995a *Macroplacus raeticus*, Rieppel, p. 17, Fig. 22.

**HOLOTYPE**—BSP 1967 I 324; skull.

**STRATUM TYPICUM**—Kössener Schichten, Rhaetian, Upper Triassic.

**LOCUS TYPICUS**—Hinterstein (Sonthofen), Allgäu, Bavaria, Germany.

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

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

**REFERRED SPECIMENS**—None.

**Unnamed Taxon**

**DEFINITION**—A monophyletic taxon including *Protenodontosaurus* Pinna, 1990b, and the Placochelyidae.

**DIAGNOSIS**—Otic process of squamosal extends beyond the medial margin of the posttemporal fossa; palatine contacts quadrate lateral to palatoquadrate cartilage recess; prootic exposed in posterior view of skull.

**DISTRIBUTION**—Upper Triassic, central Europe and southern Alps.

**Protenodontosaurus Pinna, 1990b**

**TYPE SPECIES**—*Protenodontosaurus italicus* Pinna, 1990b, from the Carnian of Dogna, Udine, Italy.

**DEFINITION**—A monotypic taxon including the species *italicus*.

**DIAGNOSIS**—Single (posterior) maxillary tooth, separated by a wide diastema from premaxillary tooth (teeth?); maxilla almost as high as it is long in lateral view because of distinct ascending pro-
cess; prefrontal not extending far down along the anterior margin of the orbit; orbital margin of frontal rather straight, postorbital not extending beyond the midpoint of the upper temporal fossa along its lateral margin; vomers much enlarged and reaching far anteriorly into rostrum; exoccipitals meet dorsal to the occipital condyle (convergent in Cyamodus); basioccipital tuber and ventral flange of opisthotic meeting each other ventral to the passage of the internal carotid, and meeting the posterior margin of the basicranium (convergent in Placochelys).

**DISTRIBUTION**—Carnian (Upper Triassic) of the southeastern Alps (northeastern Italy).

**Protenodontosaurus italicus** Pinna, 1990b

1990b *Protenodontosaurus italicus*, Pinna, p. 6, Figs. 1–4.
1993 *Protenodontosaurus italicus*, Dalla Vecchia, pp. 51, 53, Fig. 5C.
1993 *Protenodontosaurus italicus*, Mazin and Pinna, p. 84.
1993b *Protenodontosaurus italicus*, Nosotti and Pinna, pp. 110, 112, Fig. 2B.
1993 *Protenodontosaurus italicus*, Pinna and Mazin, p. 126, Fig. 1.
1994 *Protenodontosaurus italicus*, Sirna et al., p. 262.
1996 *Protenodontosaurus italicus*, Nosotti and Pinna, p. 22 ff., Fig. 24.
1997 *Protenodontosaurus italicus*, Rieppel and Zanon, p. 213.
1999 *Protenodontosaurus italicus*, Pinna, p. 28 f.

**Placochelyidae Romer, 1956**

**DEFINITION**—A monophyletic taxon including the genera *Placochelys* Jaekel, 1902, and *Psephoderma* Meyer, 1858.

**DIAGNOSIS**—Skull depressed; rostrum narrow and distinctly elongated; suture between maxilla and jugal located below posterior half of orbit; premaxillary teeth absent; ventral surface of rostrum with distinct grooves leading to internal nares; palatal exposure of pterygoid relatively long; distal tip of paroccipital process abuts squamosal buttress; anterior tip of dentary edentulous.

**DISTRIBUTION**—Upper Triassic, central Europe and southern Alps.

**Placochelys Jaekel, 1902**

**TYPE SPECIES**—*Placochelys placodonta* Jaekel, 1902, from the Carnian of Veszprem, Hungary.

**DEFINITION**—A monotypic taxon including the species *placodonta*.

**DIAGNOSIS**—Three maxillary teeth; posterior process of premaxilla extending backward beyond the level of the anterior margin of the orbit; frontal narrowly exposed between the posterior parts of nasals; anterolateral processes of frontal weakly developed; maxilla flooring the external naris (convergent in *Cyamodus*); squamosal and quadratojugal extending anteriorly within the temporal arch to a level in front of the anterior margin of the upper temporal fossa; foramen piercing the suspensorium between the quadrate, squamosal, and quadratojugal; basioccipital tuber and the ventral flange of the opisthotic meet ventral to the passage of the internal carotid, and meet the posterior margin of the basicranium (convergent in *Protenodontosaurus*, unknown in *Psephoderma*).

**DISTRIBUTION**—Carnian (Upper Triassic) of central Europe (Hungary).

**Placochelys placodonta** Jaekel, 1902

1901 *Placochelys*, Jaekel, p. 57.
1902a *Placochelys placodonta*, Jaekel, p. 4, Figs. 1–5 (fide Pinna, 1999).
1902b *Placochelys placodonta*, Jaekel, p. 127, Fig. on p. 130.
1903 *Placochelys placodonta*, Frech, p. 17, Pl. XV.
1910 Placochelys placodonta, Jaekel, p. 335, Fig. 4.
1911 Placochelys placodonta, Huene, p. 45, Fig. 51.
1915 Placochelys, Drevermann, p. 403 ff.
1921 Placochelys placodonta, Broili, p. 316.
1922 Placochelys placodonta, Broom, Fig. 2C.
1922 Placochelys, Drevermann, p. 292 ff.
1924 Placochelys placodonta, Broom, p. 54, Figs. 4a, 5a.
1928 Placochelys, Drevermann, p. 98 ff.
1930 Placochelys placodonta, Goodrich, p. 333, Fig. 345.
1931 Placochelys placodonta, Huene, p. 7, Pl. I–III.
1933 Placochelys placodonta, Kuhn, p. 12.
1936 Placochelys placodonta Huene, pp. 123, 128, 147.
1947 Placochelys placodonta, Vialli, p. 111, Table 1.
1956 Placochelys placodonta, Huene, p. 373, Figs. 416–417.
1956 Placochelys placodonta, Sacchi Vialli, p. 96.
1957 Placochelys placodonta, Brotzen, p. 167 f.
1959 Placochelys placodonta, Kuhn-Schnyder, p. 186.
1960 Placochelys placodonta, Gorce, p. 23.
1960 Placochelys placodonta, Kuhn-Schnyder, p. 96, Figs. 5b, 6b.
1961 Placochelys placodonta, Kuhn, p. 19.
1961 Placochelys placodonta, Kuhn-Schnyder, p. 107, Fig. 7b.
1963 Placochelys placodonta, Kuhn-Schnyder, Figs. 1b, 2b, 3b, 4.
1965a Placochelys placodonta, Kuhn-Schnyder, p. 257 ff.
1965b Placochelys placodonta, Kuhn-Schnyder, Fig. 8.
1967 Placochelys placodonta, Kuhn-Schnyder, Figs. 7, 11.
1968 Placochelys placodonta, Müller, p. 199, Figs. 235–237.
1969 Placochelys placodonta, Kuhn, p. 15 f., Figs. 3, 6.
1975 Placochelys placodonta, Haas, p. 452.
1975 Placochelys placodonta, Schubert-Klemm, pp. 50, 53, Figs. 7B, 8B.
1975 Placochelys placodonta, Westphal, p. 113, 121, Fig. 11.
1976a Placochelys placodonta, Pinna, pp. 10, 36 ff.
1976 Placochelys placodonta, Westphal, p. 35, Fig. 3C.
1980 Placochelys, Kuhn-Schnyder, p. 164, Fig. 9.6.
1980a Placochelys placodonta, Pinna, p. 298 ff.
1986 Placochelys placodonta, Nosotti, Fig. 2.
1987 Placochelys, Sues, p. 141.
1989 Placochelys placodonta, Mazin, p. 728, Fig. 3.
1989 Placochelys placodonta, Nosotti and Pinna, pp. 50, 83, Pls. XIII–XIV.
1989 Placochelys placodonta, Pinna, pp. 141, 150, 153, Fig. 4.
1990a Placochelys placodonta, Pinna, p. 150 f., Fig. 1.
1990b Placochelys placodonta, Pinna, p. 11, Table 1.
1990c Placochelys placodonta, Pinna, p. 140 ff.
1993 Placochelys placodonta, Dalla Vecchia, pp. 51, 55, Fig. 5A.
1993 Placochelys placodonta, Mazin and Pinna, p. 83 ff, Figs. 7–9.
1993 Placochelys placodonta, Pinna and Mazin, p. 126, Fig. 1.
1994 Placochelys placodonta, Sirna et al., p. 262.
1995a Placochelys placodonta, Rieppel, p. 37, Fig. 47.
1996 Placochelys placodonta, Nosotti and Pinna, p. 4 ff, Fig. 24.
1997 Placochelys placodonta, Rieppel and Zanon, p. 215, Figs. 1D, 2C, 3C.

HOLOTYPE—FAFI Ob/2323/Vt.3; skull and postcranial remains.
STRATUM TYPECUM—Physiocardia-beds (Artha-
ber, 1906), Alsó Keuper (equivalent to the Raibler
Schichten), Carnian, Upper Triassic.
Fig. 35. Skull of *Placochelys alpis sordidae* Broili (holotype, bsp 1921.1.3): A, dorsal view; B, ventral view. Scale bar = 20 mm.

**LOCUS TYPICUS**—Jeruzsalemhegy (Jerusalem Mountain) near Veszprém, Bakony Mountains, Hungary.

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

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

**REFERRED MATERIAL**—MB.R.1765; skull.

**COMMENTS**—*Placochelys placodonta* Jaekel, 1902, is a monotypic genus represented exclusively by the material collected in the Keuper near Veszprém, Hungary. No other vertebrate fossils were ever collected in the same strata. Nonetheless, a number of placodont remains from the Alpine Triassic have been referred to the genus *Placochelys* by various authors, mostly on the basis of stratigraphic considerations.

*Placochelys alpis sordidae* Broili, 1921, is based on an incomplete skull (bsp 1921.1.3; Figs. 35, 36) from the Rhaetian Koessen-Formation of...
the Bavarian Alps (Kothalpe am Wendelstein), which Broili (1921) believed to be of equivalent age as the Keuper of Veszprém. The skull is distinctly smaller than the holotype of *Placochelys placodonta* and is very incomplete, for which reason it is not diagnostic at the species level, nor is its referral to the genus *Placochelys* unequivocal, as was already noted by Broili (1921). The skull is transversely broken through the middle of the orbits, and the anterior part is missing. The maximal length of the preserved (posterior) part of the skull measures 54 mm. The right side of the skull shows the postorbital arch in lateral and dorsal view (Figs. 35A, 36A). Along the posterior margin of the orbit, the postfrontal can be demarcated from the postorbital, and posteroventrally the postorbital can be delineated from the jugal. Unfortunately, it is impossible to ascertain whether the posterolateral margin of the postfrontal was deeply concave and angulated (as in *Placochelys*) or only weakly concave and smoothly curved (as in *Psephoderma*). Likewise, it is impossible to establish whether the postfrontal remained broadly separated from the anteromedial margin of the upper temporal fossa or narrowly approached it.

The right temporal arch is complete but broken and distorted, as is the right upper temporal fossa. Little sutural detail can be made out, but the posterior tip of the postorbital is clearly indicated along the medial margin of the temporal arch at a level behind the midpoint of the longitudinal diameter of the upper temporal fossa. This is an important character shared by *Placochelys* and *Psephoderma* (see below for further discussion).

The skull table is of rather square or weakly rectangular contours as in *Placochelys*, without the constriction in its posterior part that is observed in *Psephoderma*. It shows dental encurtations similar to those of *Placochelys*, that is, two protuberances along each lateral side of the skull table and a posteromedial one in front of which there is another medial protuberance (Figs. 35A, 36A).

The lateral walls of the braincase have undergone breakage and distortion, but the contact of the palate with the quadrate lateral to the palatoquadrate cartilage recess is distinct on the right side (Figs. 35A, 36A). The left side of the skull shows the tilted epitypogid in lateral view, with an indistinct depression, possibly representing the trigeminal incisure, separating the anterior epitypogid from the posterior prootic. The occiput is incompletely preserved. The only identifiable elements are the exoccipitals, which form vertical struts indicating the lateral margins of the foramen magnum. As preserved, the exoccipitals are widely separated from one another. There is certainly no evidence that they may have met above the occipital condyle (basiooccipital). Splints of bone located below the posterior margin of the skull table may represent parts of the supraoccipital.

The ventral view of the skull (Figs. 35B, 36B) displays the palate and pterygoid bones along with the palatal dentition. Sutural details are difficult to determine. The ventral margin of the right temporal arch shows the posterior tip of the jugal, which appears to meet the quadratojugal (?) at an unusually posterior level. The mandibular condyle of the right quadrate is somewhat eroded, but in front of it the suture separating the anteromedial wing of the quadrate from the quadrate ramus of the pterygoid can clearly be identified. The longitudinally oriented flange of the right pterygoid is distinct but deflected toward the midline of the skull, and the anterior tip of the right pterygoid is distinct, located at the level of the posterior third of the longitudinal diameter of the posterior palatine tooth plate. There is no indication of the presence of an ectopterygoid bone. The medioventral suture between the palatinus is distinct; that between the pterygoids is partially obscured. The posterior dental lamina foramina are distinct and located posteromedial to the posterior palatine tooth plates. By comparison with other cyamodontoids, the position of the posterior dental lamina foramina also indicates the position of the transverse suture between palatinus and pterygoids. This in turn allows the estimation of the relative length of the palatal exposure of palatine and pterygoid. Dividing the distance from the posterior margin of the dermal palate to the posterior margin of the posterior dental lamina foramina (10/10.5 mm) by the length of the palate (28.2/27.5 mm) yields a quotient of approximately 0.37. As discussed below, a quotient larger than 0.3 is synapomorphic for *Placochelys* and *Psephoderma*.

Each palatine preserves a small anterior and a much larger posterior palatine tooth plate (Figs. 35B, 36B). The left palatine tooth plate is not completely exposed; its posterolateral part is covered by bone. The right palatine tooth plate is fully exposed. Dividing its longitudinal diameter (18.4 mm) by its transverse diameter (12.8 mm) yields a ratio of 1.44. This ratio is larger than the corresponding value for *Placochelys* yet falls into the lower range of variation for *Psephoderma*, a genus diagnosed by distinctly elongated posterior
palatine tooth plates. As discussed in more detail below, there is a positive allometric size increase in the posterior palatine tooth plate in *Psephoderma*, and the fact that *P. alpis sordidae* is a relatively small skull may explain why the proportions of its posterior palatine tooth plate fall into the lower range of variation observed in *Psephoderma*. The relatively pronounced elongation of the posterior palatine tooth plates, together with the posterior extent of the postorbital along the lateral margin of the upper temporal fossa and the relatively broad palatal exposure of the pterygoid, indicates that specimen bsp 1921.1.3 is best referred to the genus *Psephoderma*. The holotype of the genotypical species, *Psephoderma alpinum* (bsp AS 1 8), likewise comes from the Rhaetian Koessen-Formation of the Bavarian Alps (Winkelmoos Alpe). bsp 1921.1.3 is too incomplete however, to be diagnostic at the species level. The species and subspecies names *alpis* and *sordidae* therefore are *nomina dubia*.

A fragmentary cyamodontoid palate (bsp AS 1 1457) from the Rhaetian Koessen-Formation of the Bavarian Alps (Plankensteinsattel, S-Tegernsee) was preliminarily described as *Placochoelys stoppanii* by Oswald (1930); a full description of the specimen was never published (Fig. 37). The specimen consists of a fragmentary dermal palate that shows a small right anterior, a large right pos-

terior, a small left anterior, and a fragment of the left posterior palatine tooth plates. The right anterior palatine tooth plate has a longitudinal diameter of 7.1 mm and a transverse diameter of 6.5 mm. Dividing the longitudinal diameter (25.1 mm) of the right posterior palatine tooth plate by its transverse diameter (14.5 mm) yields a ratio of 1.73, which indicates a distinct elongation of the tooth plate, a character diagnostic for the genus *Psephoderma*. Zapfe (1950) later referred two isolated tooth plates from the Rhaetian of the Austrian Alps to that same taxon. All of this material is too incomplete, however, to be diagnostic at the species level. The species name *stoppanii* therefore is a *nomen dubium*.

The same is true of an isolated tooth plate, again from the Rhaetian of the Bavarian Alps, which was originally described as *Placodus zitteli* by Ammon (1878) and later referred to the genus *Placochoelys* by Broili (1921). Another isolated tooth from the Upper Triassic (Norian or Rhaetian) of the Austrian Alps was referred to *Placochoelys* by Rosenberg (1935).

The Bayerische Staatssammlung für Paläontologie und historische Geologie holds two dermal ossifications (bsp AS I 1463) from the Rhaetian (Upper Triassic) of Kotalm in the Bavarian Alps, which were referred to *Placochoelys* (Fig. 38). One of these fragments is a conical ossification with a broken tip, a circular cross section, and a lightly striated surface. Its length, as preserved, is 27.8 mm. The second fragment is a triangular ossification, flattened, again with a broken tip. One surface is slightly convex, the opposite surface is slightly concave. The surface of the bone is again slightly striated; the length (as preserved) is again 27.8 mm. Both these ossifications are in fact quite different from the conical tubercular osteoderms of the carapace of *Placochoelys*, which show deep furrows radiating from the apex toward the base of the tubercle. Assignment of the ossifications (bsp AS I 1463) to *Placochoelys* is therefore highly conjectural and certainly not based on close similarity, let alone diagnostic features.

The occurrence of *Placochoelys* in the northern Alpine Triassic cannot therefore be established on the basis of diagnostic material. The same is true for the southern Alpine Triassic. An isolated cyamodontoid tooth plate, almost certainly re-worked, from the Liassic of Arzo was tentatively referred to *Placochoelys* by Peyer (1931b), but again cannot be considered diagnostic. Isolated tooth plates from the Norian, Carnian, and Rhaetian of the southern Alps were tentatively re-
Fig. 38. Dermal ossifications referred to Placochelys (bsp AS I 1463) from the Rhaetian of the Bavarian Alps. Scale bar = 20 mm.

ferred to Paraplagocodon broliii, Psephoderma alpinum, Psephoderma cfr. alpinum, and Placochelys placodonta, by Nosotti (1986), but again, the material is not diagnostic and most probably represents Psephoderma alpinum. Other incomplete cyamodontoid remains (tooth plates, dorsal vertebra, rib fragment), again from the Carnian, Norian, and Rhaetian of northern Italy (Province Bergamo), have been referred to Psephoderma alpinum, Psephoderma cfr. alpinum, and Placochelys placodonta respectively by Nosotti (1987). Because of its incompleteness, all of this material is not diagnostic at the generic or species level. Given the absence of any diagnostic material of Placochelys placodonta from the Upper Triassic of the southern Alps, however, all of this fragmentary material most likely represents Psephoderma alpinum.

Boni (1946 [1947]) reported Placochelys malanchinii from the Rhaetian of Val Sambuco near Valcava (Monte Albenza, Lombardy); the species was based on an incomplete skull that he later described in detail (Boni, 1947 [1948]). The original skull (Pinna, 1976, Pls. IV–V) was in the private collection of Luciano Malanchini of Bergamo, and can no longer be located today. A rather poor cast kept at the Museo Civico di Storia Naturale di Milano indicates that the skull is broken obliquely through the right temporal arch and transversely immediately in front of the orbits. Preserved are the left temporal region of the skull, two teeth on the left maxilla, the posteriormost tooth on the right maxilla, and the anterior tooth plate on the left palatine. The posterior tooth plate on the left palatine is badly broken but still indicates a distinctly elongated (i.e., oval) shape, similar to the posterior tooth plates of Psephoderma alpinum but unlike the more rounded shape of the posterior palatine tooth plates of Placochelys placodonta (measurements for the specimen are given in Table 12; comparative measurements for Placochelys placodonta are presented in Table 1). The dorsal view of the skull shows the presence of a large pineal foramen in an anterior position, close to the frontoparietal suture.

A second, beautifully preserved skull (MSNM V471), collected in 1974 from the Rhaetian of Monte Cornizzolo, Lombardy, was preliminarily identified as that of "Placochelyus malanchinii" by Pinna (1975). In so doing, he referred malanchinii to the genus Placochelyus, following a suggestion made by Kuhn (1969). Later, Pinna (1976) considered the incomplete skull from Monte Albenza (Placochelys malanchinii of Boni, 1946 [1947]), to represent the same taxon as the

| Table 12. Measurements of the maxillary and palatine tooth plates of Placochelys malanchinii Boni, 1947. Cast kept at MSNM. All measurements in mm. |
|---|---|---|---|---|
| | left | | right | |
| | longitudinal | transverse | longitudinal | transverse |
| anterior maxillary tooth | 9.3 | 5.6 | - | - |
| posterior maxillary tooth | 11.6 | 5.3 | 12.1 | 5.8 |
| anterior palatine tooth | 11.0 | 8.0 | 10.1 | 8.4 |
| posterior palatine tooth | 36.0 | 23.2 | (33) | (22) |

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Table 13. Measurements of the maxillary and palatine tooth plates of *Psephoderma alpinum* (MSNM V471). All measurements in mm.

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skull from Monte Cornizzolo, and furthermore treated *malanchinii* as a junior synonym of *stoppanii*, which he referred to the genus *Placochelysanus* Kuhn, 1969. The skull from the Rhaetian of Monte Cornizzolo was thus described as that of *Placochelysanus stoppanii* (new combination, Pinna, 1976). Still later, another fragmentary skull was collected in the Rhaetian of Monte Rena near Bergamo (Pinna, 1978, Pl. LXXI–LXXII) from deposits that also yielded carapace fragments referred to *Psephoderma alpinum* (Pinna, 1978; the specimens are kept at the Museo Civico di Scienze Naturali “E. Caffi” in Bergamo). Pinna (1978) considered the skull fragments to be associated with the carapace fragments, and at the same time established the taxonomic identity of the skull fragments from Monte Rena (again with a large and anteriorly placed pineal foramen and elongated posterior palatine tooth plates) with the skulls from Monte Albenza and from Monte Cornizzolo (MSNM V471; Table 13). *Placochelysanus stoppanii* thus became a junior synonym of *Psephoderma alpinum*. The identification of the well-preserved skull from Monte Cornizzolo as that of *Psephoderma alpinum* has since been corroborated by the discovery of articulated whole skeletons (Pinna & Nosotti, 1989; Renesto & Tintori, 1995). The synonymy of the incomplete skulls from Monte Albenza and Monte Rena with this taxon is likely.

Finally, an incomplete and strongly depressed skull from the uppermost Ladinian or lowermost Carnian of Fusea near Tolmezzo (Province of Udine, northeastern Italy; Zucchi Stolfa, 1975) was identified as *Placochelys placodonta* by Pinna and Zucchi Stolfa (1979). The skull originally belonged to the Museo Friuliano di Storia Naturale in Udine, but can no longer be located today. It shows little morphological detail, and in particular it lacks the rostrum. General resemblance is more with *Cyamodus* than with *Placochelys placodonta*, however. The same layer that yielded this skull also yielded a complete cyamodontoid carapace, carapace fragments, and skull fragments. The carapace is clearly different from that of *Placochelys placodonta* in osteoderm structure and arrangement, suggesting that the material from Fusea represents a new cyamodontoid taxon (Rieppel & Dalla Vecchia, 2001).

The only possible occurrence of *Placochelys placodonta* outside the type locality is in the Muschelkalk of Makhtesh Ramon, Negev, Israel. Isolated osteoderms from that locality, of upper Anisian or lower Ladinian age, have the same structure as the enlarged tubercles arranged in longitudinal rows and surrounded by a ring of smaller tubercles in the carapace of *Placochelys placodonta*. Similarly large tubercles are not known from the dermal armor of any other cyamodontoids, although isolated osteoderms cannot be considered diagnostic of a specific taxon.

**Psephoderma Meyer, 1858**


**TYPE SPECIES**—*Psephoderma alpinum* Meyer.

Table 14. Data matrix for implementation of the Brooks parsimony analysis in the reconstruction of cyamodontoid historical biogeography.

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RIEPEL: THE CRANIAL ANATOMY OF *PLACOCHELYS PLACODONTA*
1858, from the Rhaetian (Upper Triassic) of the Bavarian Alps.

**DEFINITION**—A monotypic taxon including the species *alpinum*.

**DIAGNOSIS**—Squamosal projecting far posteriorly; upper temporal fossa relatively narrow; posterior (nasal) process of premaxilla enlarged and extending backward to reach the frontal, thereby separating the nasals from one another (convergent in *Macroplacus*); frontal narrowly entering the anterior margin of the pineal foramen; pineal foramen located in front of a distinct step in the skull roof; postfrontal small; the posterior palatine tooth plates elongate in adult (convergent in *Macroplacus*, and, to a lesser degree, in *Cyamodus hildegardis*).

**DISTRIBUTION**—Norian to Rhaetian (Upper Triassic) of northern and southern Alps.

**Psephoderma alpinum** Meyer, 1858

1858a *Psephoderma Alpinum*, Meyer, p. 246, Pl. 29.
1858b *Psephoderma Alpinum*, Meyer, p. 646.
1863 *Psephoderma alpinum*, Curioni, p. 268.
1886 *Psephoderma alpinum*, Deecke, p. 195 ff.
1902 *Psephoderma alpinum*, Huene, p. 33.
1902a *Psephoderma alpinum*, Jaekel, p. 16.
1903 *Psephoderma alpinum*, Frech, p. 17.
1905 *Psephoderma alpinum*, Fraas, p. 367.
1907 *Psephoderma alpinum*, Jaekel, p. 52 f., Figs. 36–37.
1915 *Psephoderma alpinum*, Drevermann, p. 404.
1921 *Psephoderma alpinum*, Broili, pp. 317.
1933 *Psephoderma alpinum*, Kuhn, p. 12 f.
1936 *Psephoderma alpinum*, Huene, pp. 134, 147.
1947 *Placochelys* n. f. Boni, Vialli, p. 120, Fig. 1.
1956 *Psephoderma alpinus*, Huene, p. 374, Fig. 419.
1961 *Psephoderma alpinum*, Kuhn, p. 20 f.
1968 *Psephoderma alpina*, Müller, Fig. 238.
1969 *Psephoderma alpina*, Kuhn, p. 16.
1975 *Placochelyanus malanchinii*, Pinna, p. 92, Fig. 1.
1975 *Psephoderma alpina*, Schubert-Klempnauer, p. 53.
1975 *Psephoderma alpinum*, Westphal, pp. 99 f., 121 f., Fig. 1.
1976a *Placochelyanus malanchinii*, Pinna, p. 11, 13, 41.
1976a *Psephoderma alpina*, Pinna, p. 11.
1976b *Placochelyanus stoppanii*, Pinna, p. 108., Figs. 1 a–e.
1976 *Psephoderma alpinum*, Westphal, p. 32, Fig. 1.
1979 *Psephoderma alpinum*, Pinna, p. 195 ff., Fig. 1, Pl. 9.
1980b *Psephoderma alpinum*, Pinna, p. 308 ff., Fig. 1, Pl. 8.
1986 *Psephoderma alpinum*, Nosotti, p. 238 ff., Fig. 1.
1987 *Psephoderma alpinum*, Nosotti, p. 318 ff., Figs. 1a, 2a–b.
1989 *Psephoderma alpinum*, Mazin, p. 728, Fig. 4A.
1989 *Psephoderma alpinum*, Nosotti and Pinna, pp. 48, 83, Figs. 11, 12, Pl. 11.
1989 *Psephoderma alpinum*, Pinna, pp. 150, 154, Fig. 6.
1990a *Psephoderma alpinum*, Pinna, pp. 146, 151, Fig. 1.
1992 *Psephoderma alpinum*, Pinna, p. 4 ff., Fig. 23b.
1993 *Psephoderma alpinum*, Dalla Vecchia, pp. 51, 53, 55, Fig. 5D.
1993 *Psephoderma alpinum*, Mazin and Pinna, p. 83 ff., Figs. 2, 5, 6b.
1993b *Psephoderma alpinum*, Nosotti and Pinna, p. 109 ff., Fig. 2C.
1993 *Psephoderma alpinum*, Pinna, pp. 117, 121, Fig. 12.
1993 *Psephoderma alpinum*, Pinna and Mazin, p. 126, Fig. 1.
1996 *Psephoderma alpinum*, Nosotti and Pinna, p. 19 ff., Fig. 24.
1997 *Psephoderma alpinum*, Rieppel and Zanno, p. 215, Figs. 1E, 2D, 3D.

**HOLOTYPE**—BSP AS 18; carapace.

**STRATUM TYPICUM**—Kössen Schichten, Rhætian, Upper Triassic.

**LOCUS TYPICUS**—Winkelmoos Alpe, Bavarian Alps, Germany.

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

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

**REFERRED MATERIAL**—MSNB 1, carapace fragment. MSNM V467, isolated tooth; V471, skull; V527, articulated skeleton. MSNB S699, isolated tooth; 4614, carapace fragment; 4884, juvenile specimen without carapace; 5114, isolated tooth; 8358, carapace; 8359, tail; MSNB uncatalogued, skull fragment and carapace fragment (original of Pinna, 1978, Pls. 71–73): ST 82003, articulated skeleton.

**COMMENTS**—The species names of *Placochelys alpis sordidae* (Broili, 1921), *Placochelys (Placochelysanus) malanchinii* (Boni, 1947 [1948]), *Placochelys (Placochelysanus) stoppanii* (Osswald, 1930), and *Placochelys zitteli* (Ammon, 1878) are all *nomina dubia* because the holotypes are either lost, or not diagnostic at the species level, or both. The material is, however, referable to the genus *Psephoderma* (see comments on *Placochelys placodonta* above).

The skull from Mte. Cornizzolo, identified as *Placochelysanus malanchinii* (Pinna, 1975), or *Placochelysanus stoppanii* (Pinna, 1976) is diagnostic at the species level, however, and was correctly synonymized with *Psephoderma alpinum* by Pinna (1978), as is indicated in the synonymy listing for the latter taxon.

Meyer (1864, 1867) described *Psephoderma anglicanum* on the basis of six osteoderms from the Holwell fissure fill (Rhætian, Upper Triassic) of Holwell near Frome, Sumerset, Great Britain. Both the original material and numerous additional specimens are kept in the Bath Geological Museum, and casts of the six osteoderms figured by Meyer (1867) are kept at The Natural History Museum, London (BMNH. R. 1511–1514). The material is not diagnostic (Storrs, 1994) and cannot be distinguished from *Psephoderma alpinum* (C. J. Duffin, personal communication).

**Placochelys and Potential Turtle Relationships of the Cyamodontoida**

In his original description of *Placochelys*, Jaekel (1902, 1907) postulated placodont, and specifically cyamodontoid, relationships for turtles, which he based mainly on the presence of a dorsal and ventral dermal armor in some representatives of the Cyamodontoida. Placodont relationships of turtles have been rejected (Gregory, 1946) and papareptilian relationships have been suggested instead, either with pareiasaurs (Gregory, 1946; Lee, 1995, 1997) or with procolophonoids (Laurin & Reisz, 1995; Reisz & Laurin, 1991). Other analyses have recently pointed to sauropterygian affinities of turtles (Rieppel, 1994b; de Braga & Rieppel, 1997), which raises the question of the cyamodontoid relationships of turtles again. Both of these groups, cyamodontoids and turtles, are highly autapomorphic in their cranial anatomy, which renders comparison difficult.

The general appearance of cyamodontoid skulls, in particular that of *Placochelys*, evokes general similarities with turtle skulls, especially those taxa that show some reduction of the dermal bones covering the cheek. Apart from similarities, however, there also exist many differences in the cranial anatomy of cyamodontoids and turtles.

The geologically oldest and most plesiomorphic turtle is *Proganochoelys quenstedti*, which was the focus of a recent monograph by Gaffney (1990). In his description of the skull of *Proganochoelys*, Gaffney (1990) discussed epidermal scale areas that are often associated with projections and bosses. Such are found on the prefrontal and postorbital bones, as well as along the posterior margin of the skull roof. Similar projections and bosses have been described above as dermal encrustations on the prefrontal, postfrontal, postorbital, and parietal skull roof of *Placochelys*. Whether these dermal encrustations reflect areas of epidermal scales in cyamodontoids cannot be as-
certained because of the lack of extant models. Nonetheless, *Proganochelys*, as well as all other turtles, lacks dermal tubercles secondarily fused to dermal bones of the temporal region of the skull.

Several authors have assumed that a horny sheath similar to the rhamphotheca of turtles, might have covered the margins of the edentulous rostrum in cyamodontoids. This character is highly conjectural and, if present, does not represent the plesiomorphic condition of cyamodontoids, which is characterized by a short and broad rostrum formed by tooth-bearing premaxillae.

There are differences in the composition of the dermatocranium of *Proganochelys* and cyamodontoids. *Proganochelys* lacks a postfrontal, which is present in cyamodontoids, yet the supratemporal, absent in cyamodontoids, is present in *Proganochelys*. On the other hand, an ectopterygoid is absent in both groups. All turtles except *Proganochelys* lack a lacrimal bone as well as a lacrimal duct; a lacrimal bone is present in *Proganochelys*, and it alone encloses the lacrimal foramen, which in one specimen appears to be paired (Gaffney, 1990: 41). A lacrimal is absent in all cyamodontoids, as indeed in all sauropтерygians, and the lacrimal foramen is enclosed within the maxillary bone, with a possible contribution from the prefrontal in *Placochelys*. It appears, however, that in some cyamodontoids, the lacrimal duct bifurcates in the anteroventral corner of the orbit (see discussion above), as is also the case in one specimen of *Proganochelys*.

In all stem-group Sauropтерygia, the dermal palate is fused to the basicranium and extends backward up to the occipital condyle, obscuring the basicranium in ventral view except at its posteriormost margin (Rieppel & Werneburg, 1998). This condition represents the basal morphology at the level of Sauropтерygia. In placodonts in particular, the palatines that carry large tooth plates are greatly enlarged within the dermal palate at the expense of the pterygoids. In contrast to other turtles, *Proganochelys* retains an open palatobasal articulation (Gaffney, 1983, 1990). In all other turtles the dermal palate is likewise fused to the basicranium, but the palatines are not enlarged at the expense of the pterygoids, and the basicranium remains exposed in ventral view. Palatal tooth plates are absent in all turtles, including *Proganochelys*.

Fusion of the dermal palate to the basicranium results in an intracranial course of the internal carotid both in cyamodontoids and in turtles. *Proganochelys* itself retains the plesiomorphic condition, with a superficial course of the internal carotid, which pierces the base of the basipterygoid process. In other turtles the internal carotid enters the foramen posterior canalis caroticis interni (Gaffney, 1972), the location of which is variable within the group (Gaffney, 1979; Rieppel, 1980). In derived cryptodires, the foramen posterior canalis caroticis interni lies at the posterior end of the pterygoid. In cyamodontoids, the internal carotid passes through a gap between the basioccipital tuber and a ventral flange of the opisthotic to enter the posterior part of the craniaoquadrate passage. From there it continues in a canal between the basicranium and the otic complex. Although trapped in an intracranial course in turtles (except *Proganochelys*) as well as in cyamodontoids, the passage of the internal carotid into the basicranium is topologically not equivalent in the two groups.

As in other reptiles, the internal carotid bifurcates near the dorsum sellae in cyamodontoids and in turtles. One branch, the cerebral carotid, passes through a foramen in the sella turcica into the cerebral cavity of the braincase. The other branch continues anteriorly as the palatine artery. In *Ctenosaura*, a lizard with an open palate, the palatine artery travels through the pyriform recess, across the transverse process of the pterygoid, and continues on the dorsal surface of the palate into the orbit (Oelrich, 1956). On its way, it supplies the soft palate with vessels, a major one piercing the inferior orbital membrane spanning the inferior orbital foramen (*sensu* Oelrich, 1956; infraorbital foramen of other authors).

In turtles, the palatine artery continues anteriorly in the canalis caroticus lateralis within the pterygoid bone, from which it emerges through the foramen caroticum lateralis, which opens into the sulcus cavernosus directly lateral to the basisphenoid (Albrecht, 1976; Gaffney, 1972). According to Albrecht (1976), a ventral branch of the palatine artery pierces a small foramen in the pterygoid to supply the soft palate in the area of the pterygoid–vomer suture. The inframaxillary artery, a branch of the infraorbital artery (which itself originates from the stapedial artery) passes through the foramen palatinum posterius (Rieppel, 1995c) in turtles and continues anteriorly along the margin of the triturating surface (Albrecht, 1976).

As mentioned above, the palatine artery originates from the internal carotid within a basicranial canal in cyamodontoids. It may have reached soft
palate tissues through small foramina in the palate, which would be difficult to identify in fossils, or through the dental lamina foramina, particularly the large posterior dental lamina foramen.

The homology of the inferior orbital foramen of diapsids (sensu Oelrich, 1956; infraorbital or suborbital foramen of other authors) and the foramen palatinum posterius of turtles is a much debated subject. The different terminology implies an a priori assessment of nonhomology. DeBraga and Rieppel (1997) considered a suborbital fenestra (i.e., an opening in the dernal palate below the orbit) that is bordered laterally by either the maxilla or the jugal to be an autapomorphy of Reptilia, with a reversal in Lanthanosuchoida, within turtles, and in sauropterygians (the latter two considered sister-groups in this study). Exclusion of both the maxilla and the jugal from the lateral border of the suborbital fenestra occurs in Pareiasauria, Rhynchosauria, and in turtles. Turtles have a tendency to close the dernal palate to a degree that may result in the formation of a secondary palate. In the embryonic condition, when the dernal palatal elements have not yet fully ossified, the space that corresponds to the suborbital fenestra (foramen palatinum posterius of Gaffney, 1972) is bounded laterally by the maxilla and jugal (Rieppel, 1995b). As the bones continue to grow, the size of the foramen palatinum posterius is reduced, and it may even be lost (Gaffney, 1979). In some fossil taxa (Plesiochelys, Portlandemys; Gaffney, 1976), the maxilla enters the lateral margin of the foramen palatinum posterius. In Proganochelys, the foramen palatinum posterius is located between the palate and the pterygoid (Gaffney, 1990), which corresponds to the most frequently encountered position in both fossil and extant turtles (Gaffney, 1979).

In cyamodontoid placodonts, a large (posterior) dental lamina foramen is located on the pterygoid–palatine suture, behind the posterior palatine tooth plates. This foramen corresponds to the dental lamina foramen, which in Placodus is located lateral to the posterior palatine tooth plates (i.e., between the maxilla, ectopterygoid, and palatine). Sues (1987) was the first to suggest a homology of the posterior dental lamina foramen of Placodus with the suborbital foramen of other reptiles. The designation of these foramina as dental lamina foramina (Rieppel, 1995a) reflects the consideration that vertical tooth replacement necessitates the presence of dental lamina tissue in the replacement pit below the functional tooth, and vascular supply would reach the dental lamina tissue through the dental lamina foramen. Functional considerations should not bear on assessments of homology, and in cyamodontoids more so than in Placodus, the prominent posterior dental lamina foramina topologically correspond to the foramen palatinum posterius of turtles. In the second specimen of Protenodontosaurus (MFSN 1923GP), the posterior dental lamina foramina open not only to the ventral surface of the palate, but on the dorsal surface as well on both sides of the skull. Although an anomaly in comparison with other cyamodontoids (including the holotype of Protenodontosaurus), this instance may still document the developmental potential for the posterior dental lamina foramen to pierce the palate in a topological position equivalent to the foramen palatinum posterius in turtles. However, in turtles it is the inframandibular artery that passes through the foramen palatinum posterius, whereas in cyamodontoids it is the palatine artery that might have emerged from the posterior dental lamina foramen.

The epitypoid is a prominent element in cryptodire turtles, as it is in cyamodontoids. The structure of the epitypoid in Proganochelys remains incompletely known; the status of the epitypoid in pleurodires cannot be critically evaluated in the absence of embryological studies. In both cryptodires and cyamodontoids, the epitypoid is an elongate (i.e., broad) element that contributes significantly to the closure of the secondary lateral wall of the braincase. The proportional contributions to the secondary lateral wall of the braincase are different in turtles and cyamodontoids, however. In turtles, the epitypoid remains low, and the descensus parietalis is extensive (except in Proganochelys; Gaffney, 1990). In cyamodontoids, the epitypoid is high, and the descensus parietalis relatively narrow. In both groups, the epitypoid participates in the formation of a well-defined posterior margin for the foramen interorbitale. In turtles, the epitypoid contacts the ventral flange of the parietal at the posterior margin of the interorbital foramen; the same is observed in Cyamodus, whereas in Placochelys, the anterior dorsal margin of the epitypoid meets the postorbital.

The foramen interorbitale was defined by Gaffney (1972: 19) as "[t]he paired openings between the orbits, filled in life with cartilage" (which is pierced by the optic nerve and eye muscle nerves). Indeed, the cartilage filling the interorbital foramen corresponds to the interorbital sep-

RIEPEL: THE CRANIAL ANATOMY OF PLACOCHELY S PLACODONTA 89
turn, which remains unossified in turtles and in cyamodontoids. But whereas the interorbital septum (unpaired in turtles) represents an element of the endocranium (neurocranium) proper, the posterior margin of the interorbital foramen, defined by dermal (parietal and/or postorbital) and splanchnocranial (epipterygoid) elements, morphologically represents the secondary lateral wall of the braincase (located lateral to the cavum epiptericum), which is why the foramen is paired. A well-defined foramen interorbitale is absent in *Placodus*.

Posteriorly, the epipterygoid forms the anterior margin of the trigeminal foramen in cyamodontoids, which it may also do in some cryptodire turtles; in other cryptodire taxa, the epipterygoid may be excluded from the trigeminal foramen either by the pterygoid (Gaffney, 1979) or by the parietal (Rieppel, 1980). In cyamodontoids, the epipterygoid always meets the prootic at the dorsal margin of the trigeminal foramen, a contact that may exceptionally occur in turtles (Gaffney, 1979: 98). The epipterygoid may contact the prootic at the ventral margin of the trigeminal foramen in cyamodontoids, but it never does so in turtles. Some turtles show an internal subdivision of the trigeminal foramen by bony processes originating from the surrounding bones (Gaffney, 1979: 127). Among the cranial material of cyamodontoids, only the acid-prepared second specimen of *Protenodontosaurus* (MFSN 1923GP) shows a comparable internal subdivision of the trigeminal foramen.

In turtles, the ventral contact of the epipterygoid is with the crista pterygoidea of the pterygoid. The crista pterygoidea forms the lateral margin of the sulcus cavernosus, a trough on the dorsal surface of the pterygoid extending between the crista pterygoidea and the basisphenoid rostrum, deep to the epipterygoid. The sulcus cavernosus essentially corresponds to the floor of the cavum epiptericum, which in turtles is incorporated into the cavum cranii by the development of a lateral wall of the braincase. Coming from behind, the vena capitis lateralis enters the cavum acustico-jugularis through the fenestra postotica. The cavum acustico-jugularis corresponds to the posterior part of the cranioquadrate passage of other reptiles. From it, the vena capitis lateralis reaches the sulcus cavernosus through the foramen cavernosum, located lateral to the posterior margin of the trigeminal foramen. The lateral head vein continues its course along the sulcus cavernosus and emerges, together with the ophthalmic branch of the trigeminal nerve, from behind the posterior margin of the foramen interorbitale.

In cyamodontoids, the anterior part of the epipterygoid rests on the palatine because of the significant enlargement of this element at the expense of the pterygoid. Again, there is a gap between the ventral margin of the epipterygoid and the rostrum basisphenoidale (exposed in *Placodus*, MBL. 1765), exposing the dorsal surface of the palatine, which here forms the floor of the cavum epiptericum. The cavum epiptericum is again incorporated into the cranial cavity through the formation of a secondary lateral wall of the braincase. The profundus branch of the trigeminal nerve will again have emerged from behind the posterior margin of the foramen interorbitale. The course of the lateral head vein remains unknown for cyamodontoids, however. In particular, the possible entry of the lateral head vein into the cavum epiptericum from behind cannot be explained (see description above).

The posterior part of the epipterygoid of cyamodontoids shows a ventral margin of unfinished bone that overhangs the posterior part of the palatoquadrate recess, floored by the pterygoid. The palatoquadrate cartilage must have persisted in the adult, linking the epipterygoid with the quadrate. In *Placodus*, palatoquadrate cartilage persisted in the gap between the epipterygoid and the anteromedial flange of the quadrate, both overlapping the dorsal flange of the quadrate process of the pterygoid (Huene, 1931; see also the detailed description above). Huene (1931; see also Kuhn-Schnyder, 1960, 1965a) referred to the persisting palatoquadrate cartilage in support of cyodont affinities of placodonts.

However, cryptodire turtles also show the persistence (to a variable degree) of palatoquadrate cartilage in the adult (the epipterygoid and its relation to neighboring bones remains incompletely known in *Proganochelys*; Gaffney, 1990); the result of a persisting palatoquadrate cartilage is the fossa cartilaginis epipterygoidei, located between the posterior process of the epipterygoid and the processus epipterygoideus of the quadrate and floored by the pterygoid. The processus epipterygoideus of the quadrate of turtles is comparable to the anteromedial flange of the quadrate in cyamodontoids, which broadly overlaps the pterygoid and forms the posterolateral margin of the posterior part of the palatoquadrate recess. The persisting cartilage that connects the epipterygoid with the quadrate is thus located in topologically equivalent positions in cryptodire turtles and cy-
amodontoids. The palatine remains restricted to an anterior position in turtles, however, and does not contact the quadrant (processus epipterygoideus) lateral to the fossa cartilaginis epipterygoidei. The fossa cartilaginis epipterygoidei is generally smaller in cryptodires than in cyamodontoids, and no anterior parts of the cartilaginous palatoquadrate persist in turtles as they do in cyamodontoids.

No ossifications in the primary lateral wall of the braincase have so far been reported for cyamodontoids. This contrasts with *Placodus*, where Broili (1912) described a structure that he called an "alisphenoid bridge." Located deep to the dorsal process of the epipterygoid, this ossification must represent the primary lateral wall of the braincase, although its exact nature remains debatable (Rieppel, 1995a).

Ossifications in the primary lateral wall of the braincase in front of the otic capsules are restricted to the clinoid process in turtles. The clinoid process is located lateral to the dorsum sellae and represents the ossified basal portion of the embryonic pila antotica. In *Plesiochelys*, the ossification of the pila antotica reaches up to the dorsal edges of the prootic (Gaffney, 1976). No part of the pila antotica is ossified in the cyamodontoid *Placochelys*.

Other ossifications of the primary lateral wall of the braincase in the orbitotemporal region are absent in turtles with the exception of *Proganochelys* (Gaffney, 1990), where an ossification is found in one skull only. This element most probably corresponds to an ossification that incorporates the pila antotica, pila metotica, and more dorsal elements of the primary lateral braincase wall (Gaffney, 1990, Fig. 48) and as such corresponds to the plesiomorphic sphenethmoid (de Braga & Rieppel, 1997). Depending on the phylogenetic position of turtles, the presence of a sphenethmoid will optimize as an autapomorphy of *Proganochelys* (Gaffney, 1990).

The otico-occipital region of advanced turtles is uniquely derived by the differentiation of a cavum acustico-jugulare and "recessus scalae tympani" sensu Gaffney (1972), located between the quadrant laterally and the otic capsule medially, floored by the pterygoid and bounded dorsally by the paroccipital process (Gaffney, 1972). The structural relations of the cavum acustico-jugulare were reviewed in detail by Rieppel (1980, 1985). Turtles do not have a subdivided fissura metotica, as it is observed in lepidosaurs and archosaurs, and hence lack a true recessus scala tympani (Rieppel, 1985), as do cyamodontoids (and sauropterygians in general). Lack of a subdivided fissura metotica is a plesiomorphic feature of amniotes. The cavum acustico-jugulare of turtles corresponds to the posterior part of the cranioquadrate passage, within which a posteromedial pocket is partially isolated by what Gaffney (1972) described as a ventral process of the opisthotic (processus interfensetralis: Gaffney, 1972); the posteromedial pocket of the cavum acustico-jugulare was designated as "recessus scalae tympani" by Gaffney (1972), with the vagus nerve and the vena cerebralis posterior passing through it.

In fact, however, the processus interfensetralis of Gaffney (1972) corresponds to the posterior wall of the otic capsule. It forms the posterior margin of the fenestra ovalis and in turtles is pierced by the glossopharyngeal nerve (an autapomorphy of Testudines). Behind the otic capsule, between it and the exoccipital, lies the metotic foramen (foramen metoticum of Rieppel, 1985; usually referred to as jugular foramen, but designated as foramen jugulare anterus by Gaffney, 1972). The structure that creates the pocket referred to as "recessus scalae tympani" by Gaffney (1972) is an elaboration of the exoccipital and opisthotic, which provides a posterior wall to the cavum acustico-jugulare and shields the jugular foramen (foramen jugulare anterus of Gaffney, 1972) in the posterior view. As a consequence, this elaboration of the opisthotic and exoccipital traps the vagus nerve in the pocket located between itself and the posterior wall of the otic capsule. The vagus nerve may leave this pocket posteriorly through a secondary foramen, the foramen jugulare posticus of Gaffney (1972), which is formed by the posterior elaboration of the exoccipital bordering on the opisthotic. The foramen jugulare posticus may be confluent with the posterior opening of the cavum acustico-jugulare (i.e., with the fenestra postotica), or it may be absent altogether (Gaffney, 1972).

*Proganochelys* lacks a comparable cavum acustico-jugulare, largely as a result of a lesser development of the quadrate ramus of the pterygoid and lack of a posterior elaboration of exoccipital and opisthotic shielding the foramen jugulare anterus in posterior view. This leaves the middle ear region open posteroventrally (Gaffney, 1990) and prevents the recognition of a "recessus scalae tympani" sensu Gaffney (1972, 1990). Hence, plesiomorphic relations obtain. The fenestra vestibuli opens into the cranioquadrate passage. The posterior margin of the fenestra vestibuli is formed by the opisthotic, which is traversed by

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the glossopharyngeal nerve. Between the opisthotic and the exoccipital lies the jugular foramen (foramen jugulare posterius sensu Gaffney, 1972). The two roots of the hypoglossal nerve leave the exoccipital through separate foramina.

In plesiochelyids, the separation of a “recessus scalae tympani” sensu Gaffney remains incomplete as well (Rieppel, 1980, 1985). There is no foramen jugulare posterius, and because of a lesser elaboration of the exoccipital and opisthotic, the foramen jugulare anterius is exposed in posterolateral view. The cavum acustico-jugulare as well as its posterior opening, the fenestra postotica, is better defined in plesiochelyids as compared with Proganochelys, because of increased development of the quadrate ramus of the pterygoid flooring the posterior part of the craniouquadrate passage.

In all turtles, including Proganochelys, the internal carotid enters the craniouquadrate posteriorly and gives off the stapedial artery within its posterior part or directly in front of the fenestra postotica where differentiated (Albrecht, 1976). The stapedial artery passes dorsal to the stapes (Albrecht, 1976) on its way to the aditus canalis stapedio-temporalis (Gaffney, 1972). The canalis stapedio-temporalis is a canal that pierces the paroccipital process in its anterior part, and allows the stapedial artery to reach the temporal muscles through a foramen (the foramen stapedio-temporale of Gaffney, 1972) located on the dorsal surface of the paroccipital process, most frequently between the quadrate and the prootic. In Proganochelys, the opisthotic forms the posterior margin of the foramen stapedio-temporale, which is bounded anteriorly by the quadrate and medially by the prootic.

With the posterior extension of the pterygoid in cyamodontoid placodonts, the posterior part of the craniouquadrate passage is closed ventrally, resulting in the formation of a space located between the quadrate laterally and the otic capsule medially, which is floored by the pterygoid and bounded dorsally by the paroccipital process. The jugular foramen lies outside this space, however, on the posterior surface of the occipital process, rather than in the posteromedial corner of this space, as in turtles. A ventral opisthotic flange, capturing the internal carotid between itself and the basioccipital tuber as it enters the posterior opening of the craniouquadrate passage, is not known in turtles. In cyamodontoids, the stapedial artery may have passed below and in front of the stapes, but as in turtles, it pierces the paroccipital process on its way to the temporal muscles. The pteroccipital foramen of cyamodontoids is the functional equivalent of the stapedio-temporal foramen of turtles. The only difference is that the anterior margin of the pteroccipital foramen is formed by a neomorphic otic process of the squamosal, whereas the stapedio-temporal foramen borders on the quadrate.

Turtles have a long and slender stapes that contacts the tympanic membrane by means of a cartilaginous extracolumella. In Proganochelys, however, a tympanic membrane appears to have been absent, and the distal end of a somewhat more massive stapes is received in a stapedial recess low on the medial surface of the quadrate in Proganochelys, just as in cyamodontoids.

The splenial is absent in modern turtles, but where it is present in fossil turtles, it remains excluded from the mandibular symphysis (Gaffney, 1979, 1990), unlike Placodus and cyamodontoids, where the splenial enters the mandibular symphysis. The retroarticular process is variably developed in turtles, but where present it is usually relatively short and sloping, as in cyamodontoids.

In summary, cyamodontoid placodonts and turtles share a number of striking convergences in their cranial as well as postcranial anatomy. Morphological similarities are often superficial, however, and do not pass the test of similarity. The stapedial artery, for example, pierces the paroccipital process in both groups, but the bones surrounding the stapedial artery are different in cyamodontoids and turtles. That turtles are, indeed, convergent on cyamodontoid placodonts was recently corroborated on the basis of cladistic analysis (Rieppel & Reisz, 1999).

Paleobiogeography and Paleoecology of Cyamodontoid Placodonts

Analysis of the historical biogeography of cyamodontoid placodonts remains incomplete, mainly because widespread occurrences of the clade in eastern Europe (Romania: Jurcsak, 1982; Huza et al., 1987) and along the northern Gondwanan shelf (Brotzen, 1957; Haas, 1959, 1969, 1975; Goree, 1960; Beltan et al., 1979) are supported only by very fragmentary material that is difficult or impossible to place phylogenetically. On the basis of formally described taxa, the Placodontia remain restricted to the western Tethyan faunal province throughout their existence. Most
recently, cyamodontoid placodonts have been collected, but not yet described, from the Middle and Upper Triassic of southern China, which is not surprising given a fairly strong signal for Asiatic (western Pacific) affinities for the sister group of the Placodontia, the Eosauropterygia (Rieppel, 1999), and its subclade, the pachypleurosaurus (Rieppel, 1998).

Within the western Tethyan realm, the cyamodontoids from the Germanic Basin (*Henodus* and *Cyamodus*) form a clade, the monophyly of which is maintained even after the inclusion of an incomplete skull fragment from the Muschelkalk of Makhtesh Ramon, Israel, and of *Cyamodus hildegardis*. The taxa from the Germanic Basin group as a monophyletic clade to the exclusion of related taxa (other than *Cyamodus hildegardis*) from outside this basin (northern Alpine Triassic and the southern Alpine–Hungarian carbonate platform). This is a pattern of relationship and geographic distribution that in essence is congruent with pachypleurosaurs interrelationships and distribution (Rieppel, 1998). The pattern suggests that there was a radiation of cyamodontoid placodonts (and other sauropterygians) within the Germanic Basin that occurred independently from the Alpine Triassic.

In spite of the incomplete knowledge of the cranial anatomy of *Cyamodus hildegardis*, inclusion of that taxon in the analysis shows it to group with the *Cyamodus* species from the Germanic Basin. The genus *Cyamodus* can thus be interpreted as a radiation of taxa within the Germanic Basin, which at the Anisian–Ladinian boundary gained access to the southern Alpine realm, there giving rise to a separate species. The same pattern of relationships and geographic distribution is again observed among Eosauropterygia, within pachypleurosaur, and within the *Nothosaurus–Lariosaurus* clade. Taxonomic congruence thus provides further support for a scenario that postulates a faunal exchange of sauropterygians, in this case of *Cyamodus*, between the Germanic and the southern Alpine Triassic through a southern gateway, the Burgundy Gate (Rieppel & Hagdorn, 1997).

Other than *Cyamodus hildegardis*, the cyamodontoids from the northern and southern Alpine Triassic are more closely related to each other than to the taxa from the Germanic Basin (with some rather weak indications that the Negev cyamodontoid may be more closely related to the Alpine genera than to the taxa from the German Muschelkalk). The cyamodontoids collected from Middle and Upper Triassic deposits in the northern and southern Alps and in the Balaton area (Hungary: *Placochelys*) are records of a geographic distribution across the Eurasian carbonate platform, which during Triassic times extended along the East European passive margin, between Sardinia and Moesia (Philip et al., 1995). During the Upper Triassic, a broad carbonate shelf dominated the southern Alpine region, extending northward into the Balaton area, the northern Alps, and the Carpathians (Marcoux et al., 1993; Marcoux & Baud, 1995).

Among the cyamodontoids from outside the Germanic Basin, the best supported sister-group relationship is between *Psephoderma*, widespread in the southern Alpine Triassic, and *Placochelys*, from the Alsó Keuper of the Balaton area in Hungary. This sister-group relationship may reflect the distribution of these taxa on the southern Alps–Hungarian carbonate platform (Marcoux et al., 1993; Marcoux & Baud, 1995). The Bakony Mountains from where *Placochelys* comes have been identified as the southern end of the central Hungarian mountain range with Triassic outcrops of a typically southern Alpine-type facies (Dercourt et al., 1984). This finding is corroborated by the close relationships between *Placochelys* and *Psephoderma*.

*Macroplacus* is from the northern Alps, separated from the Hungarian platform by the Hallstatt trough, and *Protenodontosaurus* comes from the eastern part of the southern Alps (Tre Venezie area of northern Italy), which, with respect to eosauropterygian components, shows closer faunal affinities with the northern Alpine and Germanic Triassic than with the more western parts of the southern Alpine Triassic (Rieppel & Dalla Vecchia, 2001). The sister-group relationship of *Psephoderma* and *Placochelys* thus appears to substantiate the biotic unity of the southern Alps–Hungarian platform, and the two taxa may have resulted from a vicariance event on this platform during the Upper Triassic.

To test these paleobiogeographical patterns reconstructed on the Tethys map (Marcoux et al., 1993), the Brooks Parsimony Analysis procedure (Wiley, 1988; Brooks, 1990) was applied to cyamodontoid phylogeny and geographic distribution. Deleting *Cyamodus hildegardis* and the incompletely known taxon from the Negev from the analysis yielded a single area cladogram (Fig. 39), which shows the Germanic Basin in a basal dichotomy with the areas of the Eurasian carbonate platform. Within the Eurasian carbonate platform,
the northern Alpine region is the sister area of the southern Alps–Hungarian platform. The southeastern Alpine realm, however, is not closer to the northern Alps, as might be concluded from overall similarities of osauropterygian faunal components (Rieppel & Dalla Vecchia, 2001, and above) but instead is the sister area of the southwestern Alpine and Balaton realms. Including *Cyamodus hildegardis* in the analysis, and treating all three species of *Cyamodus* as terminal taxa, results in four equally parsimonious cladograms, which in the strict consensus tree retain the basal dichotomy of the Germanic Basin and Eurasian carbonate platform only. Within the Eurasian carbonate platform, all resolution is lost, which may reflect dispersal of *Cyamodus* into the southern Alpine realm (Rieppel & Hagdorn, 1997). Cyamodontoid phylogeny and distribution can thus largely be understood as a sequence of vicariance events that involved an early bifurcation establishing separate clades in the Germanic Basin and on the Eurasian carbonate platform. Subsequent vicariance events established separate clades in the northern Alpine Triassic and on the southern Alps–Hungarian platform, with further subdivision of the clades within the latter.

Throughout their history, cyamodontoid placodonts remained restricted to nearshore habitats, epicontinental seas, or intraplatform basins. They appear to have reached their greatest diversity on the Eurasian carbonate platform and along the northern Gondwanan shelf. The development of extensive dermal armor and large palatine tooth plates indicates that they were predominantly bottom-walking, durophagous animals. Cyamodontoids retaining a premaxillary dentition on a relatively short and robust rostrum probably used these anterior procumbent teeth to pick up epibiotic invertebrate prey from the substrate. By contrast, more advanced cyamodontoids may have used the slender, elongated, and edentulous rostrum to probe the muddy benthos for invertebrate prey. The rostrum of *Psphoderma* in particular may have been too delicate to have been used to seize invertebrate prey and separate it from the substrate. Instead, the elongated and edentulous rostrum of advanced cyamodontoids shows the development of distinct grooves on its ventral surface leading up to the internal nares. It is conceivable that these forms used their rostrum to probe the muddy substrate for olfactory clues, sucking in water and exposing it to the olfactory epithelium through the internal nares. In view of the reduction of both premaxillary and maxillary teeth, suction feeding may in addition have been an important component of underwater feeding in advanced cyamodontoids. Underwater suction feeding has been documented to occur in turtles without much morphological modification. Both pleurodires (Damme & Aerts, 1997) and cryptodires (Lauder & Pendergast, 1992) use essentially the same technique for feeding under water. As the head moves toward the prey item, the esophagus remains compressed during this movement cycle. As the jaws close around the prey item, the esophagus is expanded to maintain the unidirectional water flow until the prey is secured. Mandated by hydrodynamic constraints, aquatic turtles resemble primary aquatic feeders in many aspects of their underwater feeding technique, while at the same time no evolutionary changes other than behavioral ones are necessary to adapt to feeding in the aquatic environment. A similar behavioral mechanism of hyoid depression may have been used by advanced cyamodontoids to probe the muddy bottom water in search of olfactory clues, and perhaps also in support of food intake.

The Upper Triassic intraplatform basins were anoxic in their center, but superficial water layers provided an oxic environment, as did the basin margins with a sandy–muddy bottom (Renesto & Tintori, 1995). Feeding on endobiotic inverte-
brates by marine vertebrates was recently reviewed by Geister (1998), and advanced cyamodontoids with an edentulous rostrum have previously been portrayed as predators on endobiontic shelled invertebrates (Pinna & Nosotti, 1989; Stefani et al., 1992; Mazin & Pinna, 1993). This has been disputed by Renesto & Tintori (1995) with reference to the absence of a “shelly” endofauna in the Calcare di Zorzino. This contradiction would suggest that the reconciliation of functional anatomical and paleoecological interpretations of advanced cyamodontoid placodonts requires further investigation of local differences of ecological and taphonomic conditions in the intraplatform basins of the southern Alps.

During the Upper Triassic, Europe and North America experienced a period of increasing aridity (Robinson, 1973; Tucker & Benton, 1982; Bechstädt & Schweizer, 1991), punctuated by a middle to upper Carnian humid phase (Simms & Ruffell, 1989, 1990; Simms, Ruffell, & Johnson, 1994). Climatological changes during the Upper Triassic may have been triggered by continental rifting (Hay et al., 1982; Manspeizer, 1982) and, perhaps, asteroid impacts (Spray et al., 1998).

The circum-Mediterranean Triassic in particular shows the development of increasingly arid environments in an east–west gradient (Visscher & van der Zwan, 1981) during the Late Triassic. Correlated with these climatological changes are Late Triassic faunal changes (Benton, 1994; Fraser & Sues, 1994), including the extinction of stem-group Sauripterygia (Bardet, 1995). Of these, the last to disappear are the cyamodontoid placodonts. Their latest occurrence is during the Rhaetian transgression (Pinna & Mazin, 1993), with representatives in the southern (Psephoderma) and northern (Macroplacus; “Placochelys alpis sordidae”) Alpine Triassic, and in the British Westbury Formation (Storrs, 1994). Their tolerance for changing climatic conditions may well be correlated with the development of extensive dermal armor, which may have provided not only protection from predators, but also an efficient osmotic barrier (Bentley, 1976). The environmental tolerance of cyamodontoids is perhaps best exemplified by Henodus from the Gipskeuper (Carnian) of Lustinau near Tübingen (southern Germany), which survived in a lagoonal lake environment subject to cycles of marginal rain flooding, hypersalinity, and marginal desiccation (Reiff, 1937; Fischer, 1959). No placodont is known to have survived into the Jurassic (the placo-

codont tooth reported from the Liassic of Arzo [Peyer, 1931b] is almost certainly reworked).

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Appendix I: Character Definitions for the Cladistic Analysis of Cyamodontoid Interrelationships

1. Osteoderms absent (0); osteoderms present (1); carapace present (2). The presence of a carapace is difficult to assess for some of the cyamodontoid taxa. Several skulls, skull fragments, and lower jaws have been collected from the Muschelkalk of Upper Silesia and Bayreuth, but in spite of the availability of extensive collections, including lots of fragmentary material, not a single cyamodontoid osteoderm or carapace fragment has become known from the lower upper Muschelkalk. The presence of a carapace in Cyamodus rostratus is therefore judged questionable. The allocation of carapace fragments to Cyamodus kuhnschneri (Nosotti & Pinna, 1996) is here provisionally accepted. Both Macroplacus and Protenodontosaurus are known from

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skulls only, but these come from deposits from which cyamodontoid carapace fragments have commonly been collected. The carapace is therefore coded present for the latter two taxa.

2. Dividing the total length of the skull by the total height of the skull yields a ratio smaller (0) or larger (1) than 3. Although the skull of Henodus appears to be strongly depressed at first sight, it is to be noted that the facial (orbital and preorbital) region of the skull is set at a distinct angle relative to the skull table, the eyes and external nares facing almost directly anteriorly. This feature, together with the suspensorium, defines a relatively high skull (see also v. Huene, 1936, Pl. 9, Fig. 4a).

3. Rostrum relatively short and broad (0), narrow and distinctly elongated (1), or spatulate (2). The rostrum of Henodus is extremely short and broad, and although it could be coded (0) under the broad character definition given above, it is still distinct from the rostrum of other cyamodontoids and hence considered autapomorphic (spatulate).

4. The ventral surface of the premaxilla is level with the ventral surface of the maxilla (0) or the rostrum is distinctly downturned (1) (Merck, 1997).

5. The premaxilla extends backward for more (0) or less (1) than half of the length of the ventral margin of the external naris (Merck, 1997).

6. Nasals in contact along midline of skull (0) or separated from one another by large posterior (nasal) processes of the premaxilla.

7. Anterior end of maxilla does not (0) or does (1) expand medially to form most of the dermal floor of the external naris.

8. Anterior tip of the jugal does (0) or does not (1) extend anteriorly along the ventral margin of the orbit beyond the midpoint of the longitudinal diameter of the orbit.

9. The jugal does not (0) or does (1) extend backward along the anteromedial margin of the subtemporal fossa.

10. Pineal foramen placed in center of parietal skull table (0), displaced anteriorly on parietal skull table (1) or is displaced anteriorly with frontal entering its anterior margin (2).

11. Anterolateral processes of frontals well developed (0) or reduced (1).

12. Parietal without (0) or with (1) distinct anterolateral processes embraced by postfrontal and frontal.

13. Frontals do not (0) or do (1) reach posteriorly beyond the level of the anterior margin of the upper temporal fossa. Although the upper temporal fossa is vestigial or obliterated in Henodus, the posterior tip of the frontal (posterolateral process) lies well in front of the level where the posteromedial and posterolateral rami of the postorbital separate, indicating the level of the anterior margin of the original upper temporal fossa. Henodus is therefore coded (0) for this character.

14. Parietal skull table constricted in its posterior part (i.e., with concave lateral margins) (0) or square (i.e., with straight lateral margins in its posterior part) (1). This character remains unknown for Henodus because the upper temporal fossa is completely obliterated, or nearly so.

15. Posterolateral margin of postfrontal weakly concave and evenly curved (0) or deeply concave and angulated (1).

16. Postfrontal enters upper temporal fossa (0) is excluded from upper temporal fossa by a narrow (1), or broad (2) contact of the postorbital with the parietal. Unknown for Henodus, for the same reason as stated above.

17. Postorbital extends along lateral margin of temporal fossa to a level in front of or at the midpoint of the longitudinal diameter of the upper temporal fossa (0) or further back (1). Unknown for Henodus, for the same reason as stated above.

18. The vertical part of the suture separating the maxilla from the jugal is located behind the level of the posterior margin of the orbit (0), behind the level of the midpoint of the longitudinal diameter of the orbit but in front of the posterior margin of the latter (1), or at the level of the midpoint of the longitudinal diameter of the orbit (2). The exact configuration of the maxillary–jugal suture remains unknown in Henodus, especially in its approach to the ventral margin of the skull.

19. Dorsal process of the epitypogold is narrow (0) or broad (1).

20. Base of the epitypogold is sutured predominantly to the pterygoid (0) or to the palatine (1).

21. The postorbital does not (0) or does (1) form a medioventral process, which abuts against
the lateral surface of the epipterygoid at the posteroventral margin of the foramen interorbitale.

22. Dividing the basicranial length (tip of snout to occipital condyle) by the transverse diameter of the upper temporal fossa yields a ratio which is larger (0) or smaller (1) than 3. Unknown for *Henodus*, for the same reason as stated above.

23. Dividing the longitudinal diameter of the upper temporal fossa by the longitudinal diameter of the orbit yields a ratio that is smaller (0) or equal or larger (1) than 2 (in the adult).

24. The epipterygoid does not (0) or does (1) form a posterior dorsal process that contacts the squamosal at the anterodorsal corner of the posttemporal fossa.

25. The epipterygoid is always fully ossified in the adult (0) or may be incompletely ossified in the adult (1).

26. The (neomorph) otic process of the squamosal is absent (0), extends to the midpoint of the ventral margin of the posttemporal fossa (1), or extends beyond the level of the medial margin of the posttemporal fossa (2) (in lateral view of the skull).

27. A palatoquadrate cartilage recess is absent (0) or present (1) (see discussion on p. 65).

28. A basi orbital furrow is absent (0) or present (1).

29. The palatine does not (0) or does (1) contact the quadrat along the lateral margin of the palatoquadrate cartilage recess.

30. The pterocipital foramen is absent (0) or present (1).

31. The prootic is not (0) or is (1) exposed in occipital view of the skull.

32. Premaxillary teeth are present (0) or absent (1). The premaxillary "dentition" of *Henodus* is here considered autapomorphic (i.e., not comparable to the premaxillary dentition of other placodonts).

33. Anterior premaxillary and dentary teeth pointed (0), chisel-shaped (1), or bulbous with anterior transverse ridge (2).

34. A diastema separating premaxillary and maxillary teeth is absent (0) or present (1).

35. Four or more (0), three (1), two (2), one (3), or no (4) maxillary teeth (tooth).

36. More than three (0), three (1), two (2) or one (3) pair(s) of palatine teeth.

37. Anterior palatal tooth plate(s) small and rounded (0), or transversely enlarged (1).

38. The ratio of the longitudinal to the transverse diameter of the posterior palatine tooth plate less (0), or equal or more (1) than 1.4 (in the adult).

39. Maxilla without (0) or with (1) anterior process extending into rostrum in ventral view.

40. Ventral surface of rostrum flat (0) or concave (1).

41. Ventral surface of rostrum without (0) or with distinct grooves leading up to internal nares (1).

42. Internal nares separated (0) or confluent (1).

43. Ectopterygoid present (0) or absent; if absent, palatine extends laterally at the anterior margin of the subtemporal fossa to meet the jugal (1) or jugal extends medially to meet the palatine (2).

44. The ratio of the length of palatal exposure of pterygoid relative to length of palatine is less (0) or more (1) than 0.3.

45. The ventral pterygoid flange has a single (0) or a double (1) ventral projection.

46. The posttemporal fossae are relatively large (0) or reduced (1) because of expansion of occipital exposure of parietal, squamosal, and opisthotic.

47. The squamosal buttress against which abuts the distal tip of the paroccipital process is absent (0) or present (1).

48. The posteroventral tubercle is absent (0) or present (1) at the distal tip of the paroccipital process.

49. The exoccipitals do not (0) or do (1) meet above occipital condyle (above the basioccipital.

50. The basioccipital tuber and the ventral opisthotic flange remain separate (0) or meet each other (1) ventral to passage of internal carotid.

51. Anterior tip of dentary with teeth (0) or edentulous (1) (Merck, 1997).

52. The coronoid remains well separated from lower margin of the mandible (0) or closely approaches the lower margin of mandible (1). Although the position and shape of the coronoid bone relative to the coronoid process of the lower jaw in *Henodus* is more similar to other cyamodontoids than to *Placodus*, it remains widely separated from the ventral margin of the lower jaw and has been coded accordingly.

53. The retroarticular process is long and slender
(0) or short with a sloping surface (1). Although the retroarticular process of the lower jaw is longer in *Henodus* than in other cyamodontoids, it is robust and has a sloping surface, as in other cyamodontoids except *Placodus*.

54. Tubercular osteoderms, secondarily fused to the underlying bone, are absent (0), present along the posterior margin of the upper temporal fossa only (1), or present on lateral surface of posterior part of temporal arch also (2).