BioOne COMPLETE

The evolution of the temporal region of placodonts (Diapsida: Placodontia) – a problematic issue of cranial osteology in fossil marine reptiles

Author: Maisch, Michael W.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The evolution of the temporal region of placodonts (Diapsida: Placodontia) – a problematic issue of cranial osteology in fossil marine reptiles

Michael W. Maisch

Abstract

The osteology of the temporal region of placodonts is re-investigated. The elements identified as quadrates by previous descriptions of the basal taxa *Palatodonta bleekeri* and *Paraplacodus broilii* are re-interpreted to represent entirely or in part the quadratojugal. A new interpretation and reconstruction of the best preserved skull of *Paraplacodus broilii* is presented. In *Placodus*, the squamosal and quadratojugal are fused into a compound bone, as proposed by some previous authors. The structure of the upper zygomatic arch in cyamodontoids, which possess a large quadratojugal that even enters the margin of the fenestra supratemporalis, cannot be satisfactorily explained by the current evolutionary scenario, which assumes a total loss of the quadratojugal in basal placodontiforms and basal placodonts and a re-appearance and unique enlargement in the highly derived cyamodontoids. With the new interpretation, this apparent disagreement between proposed phylogenetic relationships within placodonts and osteological observations is resolved. The quadratojugal was never lost in the ancestral line of placodonts or in early members of the group. It probably continuously increased in size in derived placodonts. This led to a strengthening of the single remaining zygomatic arch of these animals. As most peculiar features in the skull of these reptiles, this unusual condition also may represent an adaptation to the shift in diet to durophagy.

K e y w o r d s : Placodontia, Diapsida, Triassic, cranium, osteology, anatomy, evolution.

1. Introduction

The Placodontia, an important clade of Triassic marine amniotes, are universally regarded as part of a major radiation of secondarily marine diapsids by recent studies which supposedly also includes ichthyosaurs, thalattosaurs, saurosphargids and a number of less well-known forms (e.g., Chen et al. 2014; Neenan et al. 2013, 2015). Many recent studies even include Placodontia in Sauropterygia (Neenan et al. 2013, 2015; Neenan & Scheyer 2014; de Miguel Chaves et al. 2018), despite the major osteological differences (both cranial and postcranial) of the two groups. Placodontia are here regarded as a group clearly distinct from sauropterygians, although probably closely related to them (Chen et al. 2014; Neenan et al. 2013, 2015).

The purpose of this study is to address a particularly problematic issue regarding the cranial osteology of placodonts, the osteology and evolution of the temporal region. Interpretations by previous studies turn out to pose major difficulties at closer inspection that are not easily explained by the results of current phylogenetic analyses.

The cranial structure of placodonts and sauropterygians is widely different with regards to this region of the skull, as well as in many other major features. Among sauropterygians there is also a variety of cranial morphologies in early taxa that are also not easily explained by current phylogenetic hypotheses, but this does not form part of the present investigation. The interpretation of several placodont taxa as found in the literature is at any rate problematic and the present study attempts to resolve the existing discrepancies between phylogenetic hypotheses and osteological observations.

A n a t o m i c a l a b b r e v i a t i o n s : a = angular, c = coronoid, d = dentary, fr = frontal, j = jugal, mx = maxilla, n = nasal, o = osteoderm, p = parietal, pal = palatine, pmx = premaxilla, pof = postfrontal, prf = prefrontal, q = quadrate, qj = quadratojugal, sa = surangular, sq = squamosal

I n s t i t u t i o n a l a b b r e v i a t i o n s : SNSB-BSPG – Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; GMPKU – Geological Museum Peking University, Beijing, China; GPIT – Paläontologische Sammlung des Instituts für Geowissenschaften der Universität Tübingen, Germany; MBI – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; PIMUZ – Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SMNS – Staatliches Museum für Naturkunde Stuttgart, Germany.

2. Material

In the past 20 years, many placodont specimens were investigated personally at several occasions, the most important ones being listed here:

- *Paraplacodus broilii*: PIMUZ T4773 (holotype), PIMUZ T 4775, SNSB-BSPG 1953 XV 5 (referred specimens)
- *Placodus gigas*: SNSB-BSPG AS VII 108 (holotype), SNSB-BSPG 1968 I 75, SMNS 59434 cast of SMF R-1035 (the Drevermann skeleton) at the GPIT, uncatalogued (referred specimens).

- *Placodus inexpectatus*: GMPUK P-1054 (holotype)
- *Cymodus rostratus*: SMNS 17403 (referred specimen)
- *Cyamodus kuhnschnyderi*: SMNS 15855 (holotype), SMNS 16270 (paratype).
- *Cymaodus hildegardis*: PIMUZ T4763 (holotype)
- *Cyamodus muensteri*: SNSB-BSPG AS VII 1210 (holotype)
- *Placochelys placodonta*: cast of holotype, GPIT uncatalogued, paratype MB.R 1765
- *Placochelys alpissordidae*: SNSB-BSPG 1921 I 3 (holotype)
- *Henodus chelyops*: GPIT uncatalogued, all available specimens.
- *Macroplacus raeticus*: BSP SNSB-BSPG 1967 I 324 (holotype)

3. Review of current interpretations of the temporal region of placodonts

3.1. The skull of *Palatodonta* (Fig. 1)

Palatodonta bleekeri NEENAN et al., 2013 was briefly described on the basis of a tiny, crushed and somewhat disarticulated skull from the Lower Muschelkalk (Vossenfeld Formation, early Anisian, Middle Triassic) of Winterswijk, the Netherlands (Fig. 1). The taxon was found as the sister-group of placodonts in the accompanying phylogenetic analysis. It was interpreted as a juvenile specimen by NEENAN et al. (2013) because of its small size. The very large orbits and the relatively weak sutures of the dermal skull elements may be seen as further evidence of its juvenile status, although without comparative material this remains difficult to assess.

The temporal region of *Palatodonta* is that of a typical derived diapsid which has secondarily lost the lower zygomatic arch (Fig. 1A, B). There is a rounded fenestra infratemporalis, which is bordered by the jugal anteriorly, the squamosal dorsally and (allegedly) the quadrate posteriorly. According to NEENAN et al. (2013) the quadratojugal is entirely absent. The processus subtemporalis of the jugal is reduced, it is represented in most rudimentary form by a very small triangular expansion along the posteroventral margin of the jugal. This is a condition generally similar to that found e.g. in thalattosaurs or squamates, other diapsids with a strongly reduced or absent lower zygomatic arch. The "quadrate" is dorsally capped by the squamosal and the contact between the two bones does not appear to have been a very strong one. The postorbital is excluded from the dorsal border of the fenestra infratemporalis. Instead the squamosal forms an anteroventral process that contacts the ramus postorbitalis of the jugal at the anterodorsal corner of the fenestra. Although unusual, this morphology is not unique. An almost identical configuration was described and figured by WU et al. (2011) in the probable basal sauropterygian *Wumengosaurus delicato-*
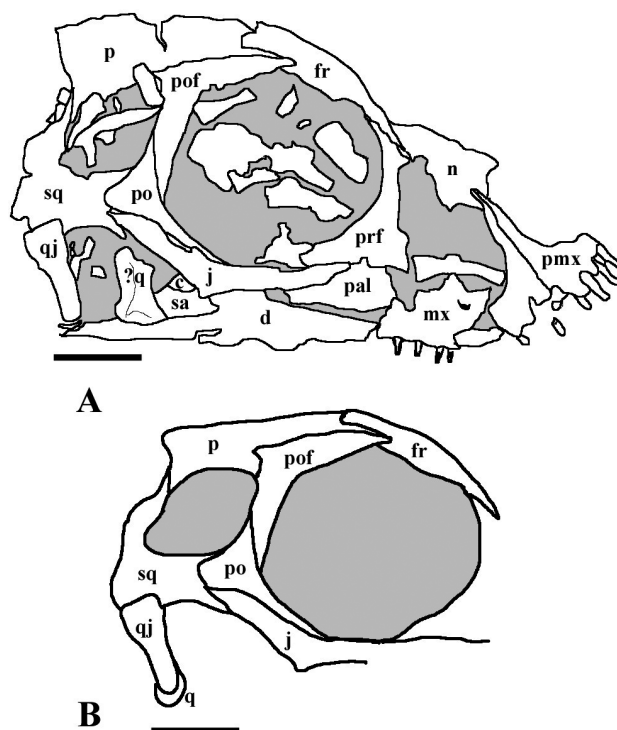
Fig. 1. A – Interpretative drawing of the type skull of *Palatodonta bleekeri* NEENAN et al., 2013. **B** – Reconstruction of the temporal region. Based on data provided by NEENAN et al. 2013. Scale bar equals 3 mm.

mandibularis. Similar conditions are widespread among sauropterygians and occur in several nothosaurids, such as in material attributed to the problematic species *Nothosaurus marchicus* (e.g. the holotype of *Nothosaurus raabi*, see RIEPPEL & WILD 1996) and in *Nothosaurus winkelhorsti* (KLEIN & ALBERS 2009). It also occurs in *Simosaurus* (VON HUENE 1921) and plesiosaurs.

The upper zygomatic arch is mostly formed by the postorbital and squamosal. The postorbital shows a small but well-developed subtriangular posterior process which is dorsally and ventrally sutured to the squamosal and, as indicated above, also meets the jugal ventrally.

The fenestra supratemporalis is bordered by the squamosal and postorbital ventrally, the postorbital and postfrontal anteriorly, the parietal medially and the squamosal posteriorly, as in many other diapsids and indeed in many sauropterygians. The fenestra is small, much smaller than the orbit, which to a certain degree is surely a condition due to the very small size of the skull.

The entire osteology of the temporal region of *Palatodonta* is well in line with that of many other diapsids, particularly sauropterygians. The morphological features as described can be easily derived from a diapsid ancestor with

a reduced lower zygomatic arch, such as *Claudiosaurus* (Carroll 1981) from the Upper Permian of Madagascar. *Palatodonta* agrees with sauropterygians and placodonts in the loss of the supratemporal, a bone that is retained in other lineages of Triassic secondarily marine reptiles (ichthyosaurs, thalattosaurs, saurosphargids, hupehsuchians). It shows no particular similarity in the temporal region to any other well-known placodont, except *Paraplacodus* as described by Rieppel (2000), which is discussed below.
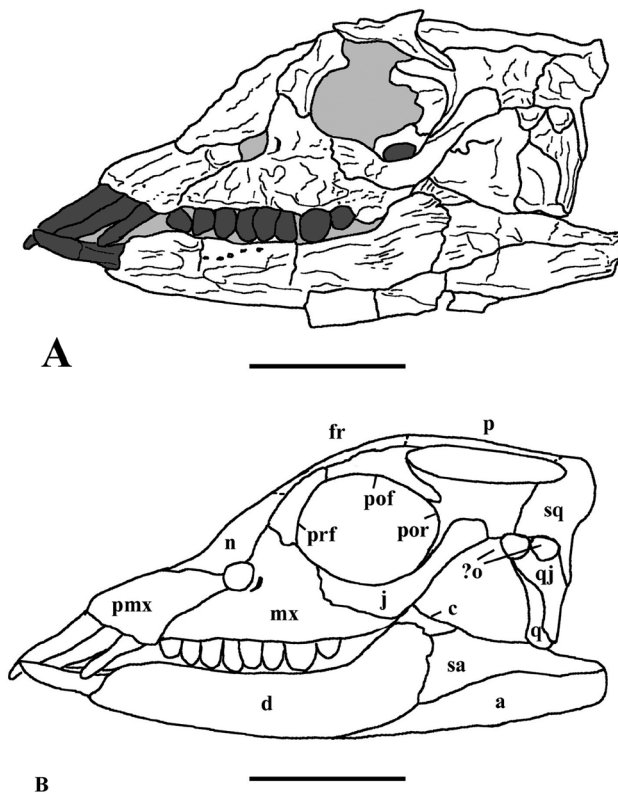
3.2. The temporal region of *Paraplacodus* (Fig. 2)

Paraplacodus broilii, originally described by Peyer (1931), was most recently discussed by Rieppel (2000), who also provided a reconstruction of the single moderately well preserved skull of the taxon (see Fig. 2A, B for a new interpretation). *Paraplacodus* originates form the Grenzbitumenzone (Besano Formation, Anisian-Ladinian boundary, Middle Triassic) of Monte San Giorgio, Switzerland, and is thus distinctly younger than the early Anisian *Palatodonta*. Rieppel (2000) discusses alleged older records of the genus described from various localities, but dismisses all of them as undiagnostic.

At first sight, the skull of *Paraplacodus* as interpreted by Rieppel (2000) is strikingly similar in the temporal region to that of *Palatodonta*. Both genera share the complete loss of the lower zygomatic arch, the complete loss of the quadratojugal, the more or less rounded fenestra infratemporalis, which is distinctly smaller than the orbit, the complete lack of a subtemporal process of the jugal and a wide, plate-like upper zygomatic arch formed mainly by the postorbital and squamosal. The fenestra supratemporalis of *Paraplacodus*, although much larger than in *Palatodonta*, is nonetheless still considerably smaller than in more derived placodonts. The major difference between the two genera is the contact of the postorbital to the dorsal margin of the fenestra infratemporalis in *Paraplacodus*. The anteroventral squamosal process, which meets the ramus postorbitalis of the jugal in *Palatodonta*, is absent. The squamosal of *Paraplacodus* also extends considerably further ventrally along the posterior margin of the "quadrate" than in *Palatodonta*, which may be the result of an earlier ontogenetic stage or simple incomplete preservation in *Palatodonta*. Otherwise differences are rather minimal.

Some new observations on *Paraplacodus*, based on specimen SNSB-BSPG 1953 XV 5, may be added here. As shown already by Rieppel (2000, although not in the skull reconstruction) the specimen has eight, not seven maxillary teeth as other specimens of the taxon. The maxilla bears an enlarged anterior supraalveolar foramen, as in *Placodus*, behind the external naris. Two small pieces of bone, already indicated by Rieppel (2000) but not interpreted, are found in the temporal region at the junction of the squamosal and "quadrate". They could possibly represent small osteodermal ossifications, although the thick layer of varnish with which the specimen is coated (and which makes most interpretations risky) does not allow for a definite decision (see Fig. 2 for more details). The new interpretation of the temporal region of *Paraplacodus* favoured here is discussed in more detail below.

3.3. Comparison of *Palatodonta* and *Paraplacodus*

From the available data it appears to be a well-founded hypothesis that *Palatodonta* and *Paraplacodus* belong to the same clade. The initial development of a placodont-like dentition described by Neenan et al. (2013) in *Palatodonta* is in line with this interpretation. Another important feature shared by the two taxa is the presence of strongly procumbent premaxillary teeth. There are four in *Palatodonta* and three in *Paraplacodus*. The premaxillary teeth of *Paraplacodus* are larger, longer and more "chisel-shaped" than those of *Palatodonta*. This more derived con-

Fig. 2. *Paraplacodus broilii* Peyer, 1931. **A** – Interpretative drawing of the skull (SNSB-BSPG 1953 XV 5). **B** – Reconstruction of the skull. Based on personal observation. Scale bar equals 20 mm.

dition is in line with the later stratigraphic occurrence of *Paraplacodus*. The lower jaw of both genera is relatively elongate and slender if compared to *Placodus* or the cyamodontoids. It is distinguished in both by a distinct processus coronoideus, smaller than in derived placodonts. The dentition, apart of the premaxillary teeth, is highly different, as noted by NEENAN et al. (2013). Whereas *Palatodonta* retains about 14 small, elongate, peg-like teeth in the dentary, the mandibular dentition of *Paraplacodus* is much more specialized. It contains two anterior dentary teeth that are strongly procumbent, as are the premaxillary teeth, followed by a reduced number of seven crushing teeth. Both tooth regions are separated by a distinct diastema.

The maxillary dentition of *Palatodonta* consists of teeth similar to those of the dentary. They show none of the specialisations seen in placodonts and the number appears to be similar to that of the dentary teeth. In *Paraplacodus*, there are seven to eight teeth of subspherical shape, which are separated from the premaxillary teeth by a distinct diastema.

The palatine of *Palatodonta* shows a single row of teeth, a condition shared with *Paraplacodus* and other placodonts, whereas palatal dentition is entirely reduced in sauropterygians. There are ten pointed, narrow teeth in *Palatodonta*. *Paraplacodus* has at least four strongly flattened palatine crushing teeth generally similar to those of other placodonts.

Although the dentition of *Palatodonta* is widely different from that of *Paraplacodus* and other placodonts, it shows a condition that can be well interpreted as one from which the specialized dentition of more derived placodonts could have evolved. Shared characters include: a reduction in the number of dentary and maxillary teeth as compared to most other diapsids, particularly the secondarily aquatic ones; few strongly procumbent premaxillary teeth with flattened tips; and a single row of teeth on the palatine. This is an array of similarities that, together with the almost identical structure of the temporal region, is strongly indicative of a close relationship between *Palatodonta* and *Paraplacodus*, as envisaged by NEENAN et al. (2013). Problems only start to arise when both are compared to the core of the Placodontia, the genus *Placodus* and cyamodontoids.

3.4. The temporal region of *Placodus* (Fig. 3A)

The skull of *Placodus* differs markedly in many features from that of both *Palatodonta* and *Paraplacodus*. The most striking difference is the complete closure of the fenestra infratemporalis. The ventral margin of the skull is practically straight in the postorbital region up to the mandibular articulation, where the quadrate protrudes some-
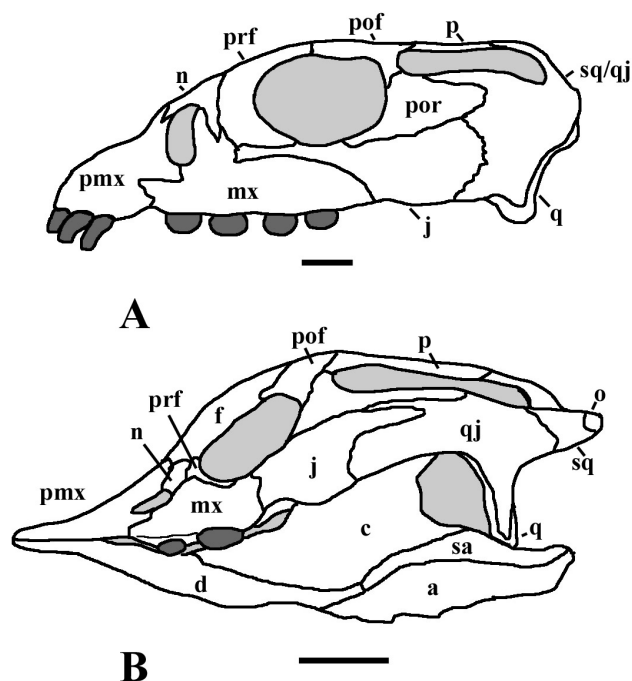
Fig. 3. Cranial reconstructions of derived placodonts in lateral view. **A** – *Placodus gigas* AGASSIZ, 1839, based on SUES (1987), RIEPPEL (1987) and personal observation. Scale bar equals 20 mm. **B** – *Psephochelys polyosteoderma* LI & RIEPPEL, 2002, modified from NEENAN et al. (2015). Scale bars equal 20 mm.

what ventrally. The fenestra supratemporalis is bordered ventrally largely by a very high bony plate. The homology of this ossification has been debated in the literature for more than a century, despite a wealth of well-preserved skulls of the taxon available, mostly from the Middle Triassic (Muschelkalk) of Germany. The recently described *Placodus inexpectatus* from China (JIANG et al. 2008) is here regarded as a placodontid that probably represents a separate genus, as also indicated by the results of the phylogenetic analysis of NEENAN et al. (2015). The temporal region of the type specimen is badly preserved (pers. obs., see also NEENAN et al. 2015: 417, fig. 2) and adds no data relevant to the present discussion.

The major point of disagreement among authors is the presence or absence of a separately ossified quadratojugal in *Placodus*. Whereas SUES (1985) in his detailed study of the cranial osteology of *Placodus* found an extensive quadratojugal, RIEPPEL in his revision of the genus (1995) did not accept the interpretation of SUES (1987) and identified only one very large squamosal in the position where SUES (1987) had indicated two elements. In this, RIEPPEL (1995) followed BROILI (1912). VON HUENE (1911) suggested the presence of two elements already, but he could not clearly identify them as separate ossifications.

SUES (1987) confirmed VON HUENE's (1911) interpretation. PINNA (1989) provided yet another version (while summarizing the earlier ones), indicating a quadratojugal of even larger size than envisaged by VON HUENE (1911) and SUES (1987) and broadly entering the lower margin of the fenestra infratemporalis. This was strongly doubted by RIEPPEL (1995). Since then, excellently preserved cyamodontoid skull material from China (NEENAN et al. 2015) has confirmed the presence of just such a morphology of the quadratojugal in cyamodontoids. Of course this has no direct bearing on the interpretation of the skull of *Placodus*, but it should be kept in mind during the following discussion.

Apart from this major issue, existing cranial descriptions of the *Placodus* skull, particularly the detailed accounts of SUES (1987) and RIEPPEL (1995), agree in most major points. RIEPPEL (1995) concluded that the quadratojugal was either entirely absent or alternatively fused to the squamosal in *Placodus*. With respect to the structure of the temporal region in cyamodontoids (discussed in detail below) the latter interpretation, already suggested by BROILI (1912), appears the more plausible. The main argument for fusion of these elements is, that the so-called "squamosal" of *Placodus* occupies exactly the same position and has the same topological relationships to the surrounding cranial elements as the squamosal and quadratojugal of cyamodontoids (compare Fig. 3A and B). The squamoso-quadratojugal of *Placodus* contacts the postorbital and jugal anteriorly and the parietal posteromedially. It caps the quadrate dorsally and also covers it laterally. Even a remnant of the conspicuous ventral process of the quadratojugal seen in cyamodontoids along the lateral margin of the jugal is present, although only small, due to the secondary closure of the fenestra infratemporalis of *Placodus*. If the quadratojugal was entirely reduced in *Placodus*, it should be expected that the squamosal showed at least a somewhat different morphology and somewhat different relations to the surrounding elements than the squamosal + quadratojugal in cyamodontoids. This is evidently not the case.

3.5. The temporal region of cyamodontoids (Fig. 3B)

The type genus of the family Cyamodontidae, *Cyamodus*, is represented by several species the taxonomy of which is not completely clear. RIEPPEL (2001) recognized *C. rostratus* MÜNSTER, 1839, *C. muensteri* AGASSIZ, 1839, *C. hildegardis* PEYER, 1931 and *C. kuhnschnyderi* NOSOTTI & PINNA, 1993, all from the Middle Triassic of Central Europe, as valid. *C. orientalis* WANG et al., 2019 has recently been added from China. *C. tarnowitzensis* GÜRICH, 1884 is of particular interest, because of its early stratigraphic age. It is early Anisian in age, being almost

coeval to *Palatodonta bleekeri* and indicating that highly derived cyamodontids were already present that early in the Middle Triassic.

Unfortunately, the single known specimen is incomplete and the type skull is lost, only a cast of it remains (GÜRICH 1884; DIEDRICH 2011, see SCHEYER et al. 2012 for corrections regarding the provenance of the specimen). *C. tarnowitzensis* does not play any further role in the present discussion, as it shows no details of its temporal region. Due to incomplete knowledge of its osteology, its referral to the genus *Cyamodus* is not beyond doubt.

Although the most completely preserved European species, the skull of *Cyamodus hildegardis* is inadequately known (PEYER 1931; PINNA 1980; RIEPPEL 2001; SCHEYER 2010) and does not show the temporal region in sufficient detail.

Cyamodus orientalis, although based on an almost complete and articulated skeleton, was described and illustrated rather briefly by WANG et al. (2019) and offers no new data to the debate. A large quadratojugal is reconstructed, but its outline is all conjectural as indicated by dotted lines in the figures (WANG et al. 2019: 5, fig. 2).

The type-species of the genus, *Cyamodus rostratus*, is mainly represented by the holotype skull described in great detail by several authors (DREVERMANN 1924; KUHN-SCHNYDER 1965; RIEPPEL 2001). Unfortunately, the zygomatic arches are very incompletely preserved on both sides of the skull, but a separate quadratojugal element is clearly identifiable in the remaining posterior parts of the temporal region (RIEPPEL 2001, fig. 12). Its suture towards the squamosal is clearest in occipital view, where the dermal skull roof is not covered with osteoderms. A second specimen (SMNS 17403) which may represent the same species was discussed by NOSOTTI & PINNA 1993a (as *C.* cfr. *rostratus*) and RIEPPEL 2001 (as *C. rostratus*), who provided divergent interpretations of the temporal region. Again, RIEPPEL (2001) assumed a quadratojugal of only moderate size to be present, but NOSOTTI & PINNA (1993a) argued for the quadratojugal being by far the dominant element in the zygomatic arch of *C. rostratus*.

The available skulls of *C. muensteri* are inadequately preserved (RIEPPEL 2001; DIEDRICH 2011).

The best cranial material is available for *C. kuhnschnyderi*, described by NOSOTTI & PINNA (1993b, 1996) and RIEPPEL & HAGDORN (1999). Of the few known specimens, none preserves the zygomatic arches completely and they have also been heavily restored (as also noted by NOSOTTI & PINNA 1996 and RIEPPEL 2001). The identification of sutures in the zygomatic arches is therefore highly difficult and it is no wonder that, again, interpretations by NOSOTTI & PINNA (1996) and RIEPPEL (2001) are at variance.

In summary, the cranial osteology of the genus *Cyamodus* is incompletely known in the temporal region, exist-

ing interpretations are at variance, but they at least agree in the presence of a separately ossified quadratojugal element which is best documented in the type skull of *Cyamodus rostratus* and the holotype of *C. kuhnschnyderi*.

Placochelys placodonta JAEKEL, 1902 from the late Middle Triassic of Hungary, was described in great detail by JAEKEL (1902, 1907), VON HUENE (1931) and RIEPPEL (2001). The structure of its skull was also discussed by PINNA (1989), who provided a summary of previous interpretations.

The holotype skull of *Placochelys placodonta* is one of the most complete and best preserved cyamodontoid skulls available. Observations on the osteology of the temporal region are severely hampered, as in many cyamodontoids, by the encrustation of the dermal skull bones with osteoderms in that region. RIEPPEL (2001) confirmed the presence of a separately ossified quadratojugal that had also been identified by previous authors, but, as in *Cyamodus rostratus*, its suture towards the squamosal could be only clearly identified in the occipital surface of the skull, leaving the question open on how far the element extended laterally onto the zygomatic arch and whether it entered the border of the fenestra supratemporalis or not.

Henodus chelyops VON HUENE, 1936 is still the best known cyamodontoid. Eight skeletons, including seven skulls, were excavated in the Carnian of Tübingen-Lustnau and described in great detail by VON HUENE (1936, 1938, 1958) and REIFF (1942). The skull was later reinterpreted by STEIN (1993) (partially published in REIF & STEIN 1999) and RIEPPEL (2001). All existing descriptions are again at variance in several important points, although they all agree on the presence of a separately ossified quadratojugal. Both STEIN (1993) and RIEPPEL (2001) refrained from clearly delineating the element, though, and its extent remains in fact obscure.

The briefly described *Parahenodus atancensis* DE MIGUEL CHAVES et al., 2018 from the Upper Triassic of Spain, based on an incomplete skull, appears to possess a quadratojugal (DE MIGUEL CHAVES et al. 2018: 570, fig. 1) quite similar in its position and extent to the one indicated by VON HUENE (1936) in *Henodus chelyops*.

Protenodontosaurus italicus is based on a well preserved and almost complete three-dimensional skull from the Carnian of Dogna near Udine, northern Italy. It was described by PINNA (1990), NOSOTTI & PINNA (1998) and RIEPPEL (2001). Again, RIEPPEL (2001) indicates the presence of a quadratojugal but refrains from delineating it against the surrounding skull elements.

Macroplacus raeticus was originally described by SCHUBERT-KLEMPNAUER (1975) on the basis of an isolated, but quite complete and well-preserved skull from the latest Triassic (Rhaetian, Kössen Formation) of Hinterstein near Sonthofen, Bavaria. SCHUBERT-KLEMPNAUER (1975: 43, fig. 4) tentatively identified a separate quadratojugal and

squamosal in the specimen. The suture is indicated only by dotted lines and cannot be followed for the entire length of the upper zygomatic arch. PINNA (1989: 154, fig. 5) identified a huge quadratojugal in the specimen, forming most of the zygomatic arch and broadly entering the lower margin of the fenestra supratemporalis. In his interpretation, the squamosal remains a rather small element confined to the uppermost part of the temporal skull region and only forming the posterior margin of the fenestra. RIEPPEL (2001: 50, fig. 26) identified the quadratojugal-squamosal suture exactly at the position where SCHUBERT-KLEMPNAUER (1975) had indicated it, but also could not follow it further posteriorly. The question of the extent of the quadratojuagl and its contribution to the fenestra supratemporalis in the taxon is therefore unresolved. All authors (SCHUBERT-KLEMPNAUER 1975; PINNA 1989; RIEPPEL 2001) agree, however, that there is a sizeable quadratojugal in the taxon that extends far anteriorly and is sutured to the squamosal dorsally and the jugal anteriorly.

Psephoderma alpinum VON MEYER, 1858 is, apart of *Henodus chelyops*, the best represented European placodont. Articulated specimens were described by PINNA & NOSOTTI (1986a) and RENESTO & TINTORI (1985). Cranial anatomy was described in detail by several authors (PINNA 1976; PINNA & NOSOTTI 1986; RIEPPEL 2001; NEENAN & SCHEYER 2014). Again existing descriptions are at variance. The most recent one (NEENAN & SCHEYER 2014: 352, fig. 2) shows a very extensive quadratojugal that widely enters the ventral margin of the fenestra supratemporalis, in agreement to the long-standing argument of PINNA that the quadratojugal was a very extensive element in cyamodontoids that did enter the temporal margin (contra RIEPPEL's interpretation). This highly important confirmation of PINNA in this decade-long debate is not mentioned in the text or commented any further. PINNA reconstructed the temporal region of *Psephoderma* completely correctly already in 1989 without the help of micro-CT or other modern technology, just by means of exact anatomical observation.

Further confirmation of PINNA's hypothesis was more recently provided by additional descriptions of the skulls of several newly discovered Chinese cyamodontoids by NEENAN et al. (2015), which had only been briefly described previously (LI 2000; LI & RIEPPEL 2002; ZHOU et al. 2008). In *Sinocyamodus xinpusenis* LI, 2000 the extensive quadratojugal clearly forms much of the zygomatic arch and separates postorbital and squamosal. The same condition is seen in the very well-preserved skulls of *Glyphoderma kangi* ZHOU et al., 2008 and *Psephochelys polyosteoderma* LI & RIEPPEL, 2002. Particularly in the latter taxon the configuration of the temporal elements reproduces PINNA's (1989) tentative reconstruction of *Macroplacus raeticus* so exactly that it can hardly be coincidental.

4. Discussion

4.1. The present scenario – an osteological and evolutionary conundrum (Fig. 4)

From the discussion provided above, the following points must be considered as well-established facts:

1: The quadratojugal is present in all adequately preserved cyamodontoid placodonts.

2: In all cyamodontoids, it is an extensive element that forms a large part of the zygomatic arch and is tightly sutured to the jugal anteriorly.

3: In adequately preserved cyamodontoids (*Sinocyamodus*, *Psephochelys*, *Glyptoderma*, *Psephoderma*) the quadratojugal widely enters the lower margin of the fenestra supratemporalis and completely separates the postorbital and the squamosal, a condition extremely different to sauropterygians, which only retain rudimentary quadratojugals or have lost the element altogether.

The configuration of the zygomatic arch in cyamodontoids is unique among known diapsids. It also does not bear close resemblance to the lower zygomatic arch of synapsids, as envisaged by VON HUENE (1931) and KUHN-SCHNYDER (1960). In synapsids – the somewhat enigmatic caseids aside- the quadratojugal is never involved in the formation of the lower zygomatic arch. The construction of the zygomatic arch in cyamodontoids also does not correspond to the configuration of the primitive diapsid lower zygomatic arch, which is formed by jugal and quadratojugal exclusively with no involvement of either the postorbital or squamosal.

This leaves only two possible evolutionary explanations. Firstly, the cyamodontoid zygomatic arch is a completely new structure that is highly autapomorphous and does not find its counterpart in any other known diapsid (the explanation favoured here). Secondly, the cyamodontoid zygomatic arch is a product of fusion of the upper and lower zygomatic arches and the lower temporal fenestra has been secondarily closed in these animals. The second possibility appears unlikely, as it cannot explain the large size and contribution of the quadratojugal to the fenestra supratemporalis adequately.

There can be little doubt that placodonts are diapsids and as such are derived from an ancestor which possessed both infra- and supratemporal fenestrae. The crania of *Palatodonta* and *Paraplacodus*, which effectively retain a large, ventrally open fenestra infratemporalis (found, usually to a somewhat lesser degree, also in cyamodontoids) illustrate this beyond reasonable doubt. The osteology of the temporal regions of these taxa, as well as *Placodus*, are however certainly not in line with the temporal osteology of cyamodontoids and therefore have to be explained.
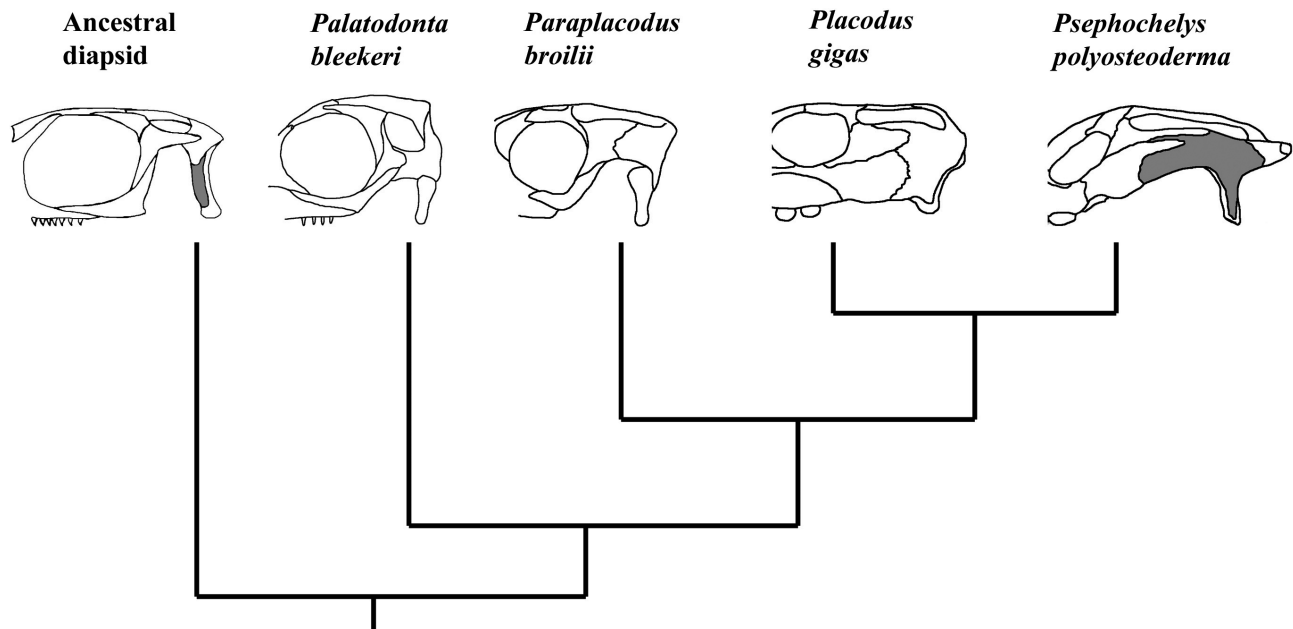
Fig. 4. Standard model of the evolution of the temporal region of placodonts. The quadratojugal is shaded in grey. Note the complete disappearance in basal placodonts and reappearance of a quadratojugal element of uniquely large size in the most derived placodonts (Cyamodontoidea). Reconstructions of the skull of *Palatodonta* based on NEENAN et al. (2013), and that of *Paraplacodus* based on RIEPPEL (2000). Reconstructions are not to scale for ease of comparison.

The traditional evolutionary scenario looks like this:

1. The basalmost known placodontiform, *Palatodonta*, retains a ventrally open fenestra infratemporalis. Its upper zygomatic arch is somewhat expanded dorsoventrally, strengthening that region of the skull. It is mainly formed by the squamosal and postorbital, as in "canonical" diapsids. The lower temporal fenestra, possibly autapomorphously, is not bordered by the postorbital dorsally, and instead the jugal and squamosal get into contact, as in many sauropterygians, both basal and derived. The jugal lacks almost any trace of a processus subtemporalis and the quadratojugal is entirely absent. The lower zygomatic arch is completely reduced, as in squamates.

2. In *Paraplacodus* basically the same condition is seen, except that it retains a postorbital contribution to the dorsal margin of the fenestra infratemporalis. Placodonts therefore lost the quadratojugal entirely in their early evolution.

3. *Placodus* shows a highly autapomorphous skull. It has lost any trace of the original presence of a fenestra infratemporalis. There does not even remain a ventral emargination of the temporal region. Instead its postorbital skull shows a strongly dorsoventrally expanded, plate-like zygomatic arch which is formed by the postorbital, jugal and – according to Broili (1912) and Rieppel (1995) – a very large squamosal. The quadratojugal is equally absent.

4. In all other derived placodonts (cyamodontoids) the quadratojugal, which literally reappears after complete reduction, is not only retained as a large element but it also forms a major portion of the zygomatic arch. In well-known forms it autapomorphously enters the lower margin of the fenestra supratemporalis and separates postorbital and squamosal completely. The temporal region is slightly to strongly emarginated ventrally in cyamodontoids as a clear indication of the original presence of a fenestra infratemporalis.

This scenario is highly problematic. It is considered exceedingly unlikely that the quadratojugal disappeared completely in basal placodonts, just not only to return in cyamodontoids, but to actually become the largest quadratojugal element found in any known diapsid reptile.

4.2. A new parsimonious evolutionary scenario (Fig. 5)

That the quadratojugal can be reduced in size in diapsids which open the lower zygomatic arch ventrally and can regain its original size when they close it again secondarily is evidenced in many other groups. Rhynchosaurs provide a well-documenetd case. In the basal rhynchosaur *Mesosuchus* (Dilkes 1998), which only incipiently shows the dental and cranial adaptations of later taxa to

dealing with fibrous plant material, the lower zygomatic arch is broken and the quadratojugal has lost its anterior process. It nonetheless is retained as an element of respectable size. In later rhynchosaurs, the lower zygomatic arch is secondarily closed and the quadratojgal regains its anterior process, the lower zygomatic arch is expanded and the quadratojugal increases further in size in the most derived forms like *Hyperodapedon* (Benton 1983). The only hint that this construction is derived from the one seen in *Mesosuchus* is the relatively shorter contribution of the quadratojugal to the lower zygomatic arch if compared to basal diapsids such as *Youngina,* which never lost the contact between the two bones (Müller 2003).

The situation in cyamodontoids is not strictly comparable to that seen in rhynchosaurs. The cyamodontoid quadratojugal does not only regain its previous size and topology, as it does in rhynchosaurs, but it is actually much expanded and its topology changes thoroughly. Nonetheless rhynchosaurs are at least an analogous case that illustrates the "reactivation" of a quadratojugal already in the process of being reduced (*Mesosuchus*) due to constructional necessities connected with a major shift in diet. In the case of the rhychosaurs this was the shift to herbivory. In the placodonts it was the shift to a durophagous way of feeding. Durophagy in placodonts is probably responsible for the majority of peculiarities seen in the skulls of these animals (discussed in detail, e.g. by Nosotti & Pinna 1996). Some of the most dramatic changes, apart from the obvious ones in the dentition, include:

- the short mandible with the high coronoid process, which provides an additional and effective area of attachment of the mandibular adductor musculature.

- the enlargement of the fenestra supratemporalis, which had to accommodate the increased adductor mass.

- the completely akinetic palate and the loss of the interpterygoid vacuities.

- the high degree of ossification of the side wall of the brain case and the strong connection between palate, brain case and dermal skull roof.

These modifications are all in line with an adaptational re-construction of the skull in the course of the shift to a strictly duraphagous diet, which necessitated a particularly well-ossified, akinetic and stable cranial skeleton as well as particularly powerful mandibular adductors.

Understood in this context, the cranial construction of *Placodus* is easily explained. *Placodus* is, as shown by its dentition, certainly one of the most extremely durophagous placodonts. It shows a considerable degree of fusion of cranial elements in the skull roof, including a complete fusion of the frontals (not seen in cyamodontoids) and parietals. It is therefore conceivable that, as proposed originally by Broili (1912) and also considered possible by Rieppel (1995), the quadratojugal and squamosal in this genus are also actually fused to provide even more stabi-
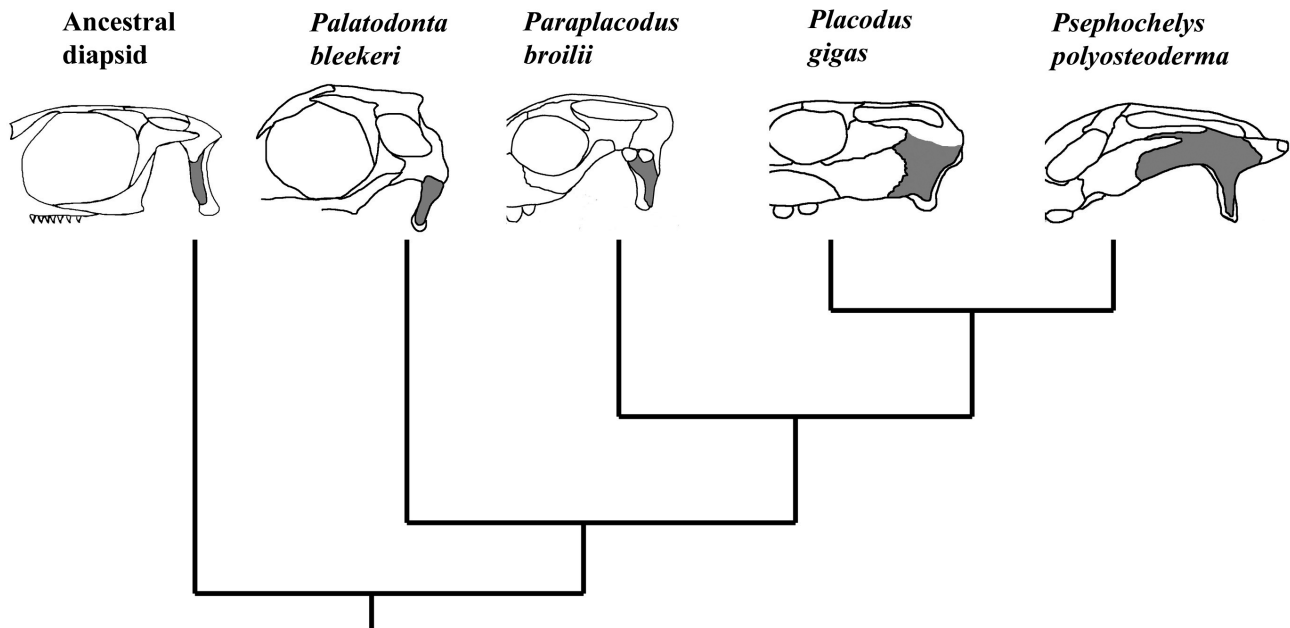
Fig. 5. New model of the evolution of the temporal region of placodonts. Quadratojugal shaded in grey. Note that no disappearance-reappearance of the quadratojugal is required and that the element steadily increases in size during evolution of the group. Skull reconstructions of *Palatodonta, Paraplacodus* and *Placodus* based on the present study. The quadratojugal of *Placodus* is here interpreted as fused to the squamosal. The shading represents a compromise solution between existing interpretations in the literature discussed in the text. Reconstructions are not to scale.

lity to the uniquely high and robust zygomatic arch of that particular genus.

This leaves the condition in *Palatodonta* and *Paraplacodus* as traditionally interpreted still unexplained.

Concerning *Paraplacodus*, available skull material is limited and not well preserved. RIEPPEL's (2000) reconstruction of the skull of the genus may have been influenced by his detailed study of *Placodus*, in which he couldn't find a separately ossified quadratojugal in that genus. PINNA (1989,: 155, fig. 7) provided a different interpretation of the *Paraplacodus* skull. He identified an extensive quadratojugal in that taxon which even contacts the jugal anteriorly and excludes the postorbital from the fenestra infratemporalis. However, this would mean that evidence for the ventral emargination of the temporal region of *Paraplacodus* as being a true fenestra infratemporalis would become questionable. A rupture of the lower zygomatic arch would not be evident from such a construction of the skull. It could also be explained as just a ventral embayment, with no involvement of a true fenestra infratemporalis whatsoever, as it is, e.g., seen in *Nyctiphruretus* (SÄILÄ 2010) and owenettids (REISZ & SCOTT 2002), among parareptiles. The position of the quadratojugal as envisaged by PINNA (1989) also appears rather odd. It is situated extremely far dorsally and would also be positioned at least in part posterior to the quadrate (the

posterior process interpreted as part of the squamosal by RIEPPEL 2000, which is considered correct here).

In fact it appears rather conceivable that the quadratojugal is represented by part of the element identified as quadrate by both PINNA (1989) and RIEPPEL (2000). In that case the quadratojugal would be a dorsoventrally extensive element situated ventral to the squamosal, forming the posterior margin of the fenestra infratemporalis and covering the quadrate laterally. It does exactly the same in cyamodontoids. In these, the quadratojugal is always posteroventrally extended into a styliform process that covers the quadrate laterally (compare, e.g. JAEKEL 1907; VON HUENE 1931; KUHN-SCHNYDER 1965; NOSOTTI & PINNA 1986, 1996; RIEPPEL 2001; NEENAN et al. 2015).

The situation in *Palatodonta* is here interpreted accordingly. The element identified as quadrate by NEENAN et al. (2013) which is situated directly ventral to the squamosal is here also reinterpreted as a quadratojugal. As shown by the accompanying CT-scans in their publication, the element is plate-like and tapering ventrally. The quadrate of all known placodonts, including *Paraplacodus* (see Fig. 2), is mediolaterally expanded for its entire height and forms an anteroposteriorly short and mediolaterally wide condyle that is approximately yoke-shaped in posterior and anterior view. The element labelled as quadrate in *Palatodonta* by NEENAN et al. (2013) is mediolaterally

narrow for its entire height and does not form any kind of condyle for articulation with the mandible (it is also is not preserved in articulation with the mandibular ramus, as best seen in the CT-scans). It therefore cannot represent the quadrate. The large, robust element, labelled with a question mark by Neenan et al. (2013) situated in close proximity to the mandibular joint (see Fig. 1A) anterior to the quadratojugal (and also in close proximity to the quadrate ramus of the pterygoid, as seen in the CT-scans) which bears an articular condyle ventrally and a dorsal articulation facet may be interpreted as a potential candidate for the true quadrate of *Palatodonta*, although it appears to be a bit too short dorsoventrally. Alternatively, the quadrate may have been dislocated and lost taphonomically.

In this way the evolutionary scenario would be extremely parsimonious and simplified. Placodonts arose from diapsids with both temporal fenestrae, but, as in sauropterygians, thalattosuchians, hupehsuchians and other marine diapsids (ichthyosaurs are a different matter that will not be discussed here) the lower zygomatic arch was broken. The quadratojugal and jugal lost contact. The quadratojugal was retained as an ossified element of considerable size which bordered the fenestra infratemporalis posteriorly in *Palatodonta* and *Paraplacodus*. In *Placodus*, the fenestra infratemporalis was completely obliterated by the dorsoventral expansion of the zygomatic arch. To strengthen the zygomatic arch further, squamosal and quadratojugal autapomorphically fused in this taxon. In cyamodontoids, the zygomatic arch was also strengthened, although not to the extreme degree seen in *Placodus*. The quadratojugal was secondarily enlarged, but not, as in rhynchosaurs, its anteroventral portion, leading to a secondarily ventrally closed fenestra infratemporalis. Instead the anterodorsal part of the quadratojugal increased in size and eventually formed a large part of the zygomatic arch and even gained contact to the ventral border of the fenestra supratemporalis.

This scenario explains the various, in part highly autapomorphic constructions of the temporal region of the placodont skull much more parsimoniously than the assumption of a complete loss and re-appearance of the quadratojugal, which after being lost completely incidentally becomes one of the largest skull elements in cyamodontoids. As in the most basal sauropterygians, the quadratojugal was not lost but retained in basal placodonts. The construction of this important region of the skull is therefore essentially similar in basal taxa of the two groups. Placodonts deviated from the ancestral pattern mainly due to adaptations to durophagy. The predatory and largely piscivorous or teuthophagous sauropterygians, on the other hand, soon lost the quadratojugal entirely and developed their skulls further along different evolutionary pathways.

5. References

Broili, F. (1912): Zur Osteologie des Schädels von *Placodus*. – Palaeontographica, **59**: 147–155.

Benton, M. J (1983): The Triassic reptile *Hyperodapedon* from Elgin, functional morphology and relationships. – Philosophical Transactions of the Royal Society of London, (B), **302**: 605–717.

Carroll, R. L. (1981): Plesiosaur ancestors from the Upper Permian of Madagascar. – Philosophical Transactions of the Royal Society, London, (B), **293**: 315–383.

Chen, X.-H., Motani, R, Cheng, L., Jiang, D.-Y. & Rieppel, O (2014): The enigmatic marine Reptile *Nanchangosaurus* from the Lower Triassic of Hubei, China and the Phylogenetic Affinities of Hupehsuchia. – PLoS ONE, **9**: e102361. doi:10.1371/journal.pone.0102361

de Miguel Chaves, C., Ortega, F. & Pérez-Garcia, A. (2018): A new placodont from the Upper Triassic of Spain provides new insights on the acquisition of the specialized skull of Henodontidae. – Papers in Palaeontology, **4**: 567–576.

Diedrich, C. (2011): The shallow marine placodont *Cyamodus* of the Central European Germanic Basin: its evolution, paleobiogeography and paleoecology. – Historical Biology, **23**: 391–409.

Dilkes, D. M. (1998): The Early Triassic Rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. – Philosophical Transactions of the Royal Society, (B), **353**: 501–541.

Drevermann, F. (1924): Die Placodontier. 1. Schädel und Unterkiefer von *Cyamodus*. – Abhandlungen der Senckenbergischen naturforschenden Gesellschaft, **38**: 291–309.

Drevermann, F. (1933): Die Placodontier. 3. Das Skelett von *Placodus gigas* Agassiz im Senckenberg-Museum. – Abhandlungen der Senckenbergischen naturforschenden Gesellschaft, **38**: 319–364.

Gürich, G. J. E. (1884): Über einige Saurier des oberschlesischen Muschelkalkes. – Zeitschrift der Deutschen Geologischen Gesellschaft, **36**: 126-144.

Jiang, D.-Y., Motani, R., Hao, W.-C., Rieppel, O., Sun Y.-L., Schmitz, L. & Sun Z.-Y. (2008): First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the Eastern Tethys. – Journal of Vertebrate Paleontology, **28**: 904–908.

Huene, F. von (1911): Über *Erythrosuchus*, Vertreter der neuen Reptil-Ordnung Pelycosimia. – Geologische und Paläontologische Abhandlungen, Neue Folge, **10**: 3-60.

HUENE, F. VON (1921): Neue Beobachtungen an *Simosaurus*. – Acta Zoologica, **1921**: 201-239.

HUENE, F. VON (1931): Ergänzungen zur Kenntnis des Schädels von *Placochelys* und seiner Bedeutung. – Geologica Hungarica, Series Palaeontologica, **9**: 1–18.

HUENE, F. VON (1936): *Henodus chelyops*, ein neuer Placodontier. – Palaeontographica, (A), **84**: 99–148.

HUENE, F. VON (1938): Der dritte *Henodus*. – Palaeontographica, (A), **89**: 105–115.

HUENE, F. VON (1958): Nachträge zur Kenntnis von *Henodus chelyops* aus dem Tübinger Keuper. – Palaeontographica, (A), **110**: 165–169.

JAEKEL, O. (1902): Über *Placochelys* n. g. und ihre Bedeutung für die Stammesgeschichte der Schildkröten. – Neues Jahrbuch für Geologie, Mineralogie und Paläontologie, **1902**: 127–144.

JAEKEL, O. (1907): *Placochelys placodonta* aus der Obertrias des Bakony. In: HORNYANSZKY, V. (ed.): Resultate der wissenschaftlichen Erforschung des Balatonsees. Vol. 1, Part 1, Paläontologischer Anhang: 1–91; Budapest (K. u. K. Hofbuchdruckerei).

KLEIN, N. & ALBERS, P. (2009): A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the Western Germanic Basin, Winterswijk, the Netherlands. – Acta Palaeontologica Polonica, **54**: 589–598.

KUHN-SCHNYDER, E. (1960): Über Placodontier. – Paläontologische Zeitschrift, **34**: 91–102.

KUHN-SCHNYDER, E. (1965): Der Typus-Schädel von *Cyamodus rostratus* MÜNSTER. – Senckenbergiana Lethaea, **46**: 257–289.

LI, C. (2000): Placodont (Reptilia: Placodontia) from Upper Triassic of Guizhou, Southwest China. – Vertebrata PalAsiatica, **38**: 314–317.

LI, C. & RIEPPEL, O. (2002): A new cyamodontoid placodont from Triassic of Guizhou, China. – Chinese Science Bulletin, **47**: 403–407.

MÜLLER, J. (2003): Early loss and multiple return of the lower temporal arcade in diapsid reptiles. – Naturwissenschaften, **90**: 473–476.

NEENAN, J. M., KLEIN, N. & SCHEYER, T. M. (2013): European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. – Nature Communications, **4** (1621): 1–7.

NEENAN, J. M., LI, C., RIEPPEL, O. & SCHEYER, T. M. (2015): The cranial anatomy of Chinese placodonts and the phylogeny of Placodontia (Reptilia: Sauropterygia). – Zoological Journal of the Linnean Society, **175**: 415–428.

NEENAN, J. M. & SCHEYER, T. M. (2014): New specimen of *Psephoderma alpinum* (Sauropterygia, Placodontia) from the Late Triassic of Schesaplana Mountain, Graubünden, Switzerland. – Swiss Journal of Geosciences, **107**: 349–357.

NOSOTTI, S. & PINNA, G. (1993a): *Cyamodus kuhn-schnyderi* n. sp., nouvelle espèce de Cyamodontidae (Reptilia, Placodontia) du Muschelkalk supérieur allemand. – Comptes Rendues de l'Académie des Sciences, Paris, **317**: 847–850.

NOSOTTI, S. & PINNA, G. (1993b): New data on placodont skull anatomy. – Paleontologia Lombarda, Nuova Serie, **2**: 109–114.

NOSOTTI, S. & PINNA, G. (1996): Osteology of the skull of *Cyamodus kuhnschnyderi* Nosotti & Pinna 1993 (Reptilia, Placodontia). – Paleontologia Lombarda, Nuova Serie, **6**: 1–42.

NOSOTTI, S. & PINNA, G. (1998): Skull anatomy of *Protenodontosaurus italicus* PINNA, 1990 (Reptilia: Placodontia). – Paleontologia Lombarda, Nuova Serie, **11**: 1–17.

PEYER, B. (1931): *Paraplacodus broilii* nov. gen. nov. sp., ein neuer Placodontier aus der Tessiner Trias. Vorläufige Mitteilung. – Centralblatt für Mineralogie, Geologie und Paläontologie, (B), **1931**: 570–573.

PINNA, G. 1980. Lo scheletro postcraniale di *Cyamodus hildegardis* PEYER, 1931, descritto su un esemplare del Triassico Medio Lombardo. – Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, **26**: 275–306.

PINNA, G. (1992): *Cyamodus hildegardis* PEYER 1931 (Reptilia, Placodontia). – Memoire della Società Italiani di Scienze Naturali e del Museo Civico die Storia Naturale Milano, **131**: 1–21.

PINNA, G. (1989): Sulla regione temporo-jugale dei rettili placodonti e sulla relazione fra placodonti e ittiotterigi. – Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, **130**: 149–158.

PINNA, G. (1990): *Protenodontosaurus italicus* n. g., n. sp., un nuovo placodonte del Carnio italiano. – Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, **131**: 137–141.

PINNA, G. & NOSOTTI, S. (1989): Anatomia, morfologia funzionale e paleoecologia del rettile placodonte *Psephoderma alpinum* MEYER, 1858. – Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, **25**: 17–50.

REIF, W.-E. & STEIN, F. (1999): Morphogeny and function of the dentition of *Henodus chelyops* HUENE, 1936 (Placodontia, Triassic). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1999**: 65–80.

REIFF, W. (1942): Ergänzungen zum Panzerbau von *Henodus chelyops* VON HUENE. – Palaeontographica, (A), **94**: 31–42.

REISZ, R. R. & SCOTT, D. (2002): *Owenetta kitchingorum* n. sp., a small pararreptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. – Journal of Vertebrate Paleontology, **22**: 244–256.

RENESTO, S. & TINTORI, A. (1995): Functional morphology and mode of life of the Late Triassic placodont *Psephoderma alpinum* MEYER from the Calcare di Zorzino (Lombardy, N Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **101**: 37–48.

RIEPPEL, O. (1995): The genus *Placodus*: systematics, morphology, paleobiogeography, and paleobiology. – Fieldiana (Geology), New Series, **31**: 1–44.

RIEPPEL, O. (2000): *Paraplacodus* and the phylogeny of the Placodontia (Reptilia: Sauropterygia). – Zoological Journal of the Linnean Society, **130**: 635–659.

RIEPPEL, O. (2001): The cranial anatomy of *Placochelys placodonta* JAEKEL, 1902, and a review of the Cyamodontoidea (Reptilia, Placodonta). – Fieldiana (Geology), New Series, **45**: 1–104.

RIEPPEL, O. & HAGDORN, H. (1999.): A skull of *Cyamodus kuhnschnyderi* NOSOTTI and PINNA 1993, from the Muschelkalk of Wasselonne (Alsace, France). – Paläontologische Zeitschrift, **73**: 377–383.

RIEPPEL, O. & WILD, R. (1996: A revision of the genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. – Fieldiana (Geology), New Series, **34**: 1–82.

SÄILÄ, L. K. (2010): The phylogenetic position of *Nyctiphruretus acudens*, a pararreptile from the Permian of Russia. – Journal of Iberian Geology, **36**: 123–143.

SCHEYER, T. M., NEENAN, J. N., RENESTO, S., SALLER, F., HAGDORN, H., FURRER, H., RIEPPEL, O. & TINTORI, A. (2012): Revised

paleoecology of placodonts – with a comment on 'The shallow marine placodont *Cyamodus* of the central European Germanic Basin: its evolution, paleobiogeography and paleoecology' by C.G. Diedrich. – Historical Biology, **24**: 257–267.

Schubert-Klmepnauer, H. (1975): *Macroplacus raeticus* n. g., n. sp. – Ein neuer Placodontier aus dem Rät der Bayerischen Alpen. – Mitteilungen der Bayerischen Saatssammlung für Paläontologie und historische Geologie, **15**: 33–55.

Stein, F. (1993): Der "Einzahn" mit den vielen Zähnen – Die Osteologie des Schädels von *Henodus chelyops* Huene (1936) (Placodontia, Reptilia) mit besonderer Berücksichtigung der Bezahnung. – Diplomarbeit Universität Tübingen: 78 pp. [unpublished].

Sues, H.-D. (1987): On the skull of *Placodus gigas* and the relationships of the Placodontia. – Journal of Vertebrate Paleontology, **7**: 138–144.

Wu, X.-C., Cheng, Y.-N., Li, C., Zhao, L.-J. & Sato, T. (2011): New information on *Wumengosaurus delicatomandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon. – Journal of Vertebrate Paleontology, **31**: 70–83.

Zhao, L.-J., Li, C., Liu, J. & He, T. (2008): A new armored placodont from the Middle Triassic of Yunnan Province, southwestern China. – Vertebrata PalAsiatica, **46**: 171–177.

Address of the author:

Dr. habil. Michael W. Maisch, Wieslesweg 7, D-72461 Albstadt-Tailfingen, Germany; e-mail: maisch@uni-tuebingen.de