**INTRODUCTION**

Research on marine reptiles of the Middle Triassic Germanic Basin began with descriptions of articulated skeletal finds from non-dinosaurians and mainly marine sauropods (e.g., Münster, 1830; Agassiz, 1833-1843; Meyer, 1847-55, 1863; Dames, 1890; Fraas, 1893; Huene, 1952; Rieppel, 2000a). Most of the finds were isolated bones and teeth of pachypleurosaurs, placodonts, nothosaurs, pistonosaurs and even terrestrial lepidosaurs in the “Bayreuther” Upper Muschelkalk bonebeds at six quarries in the Lainecker Mountain chain at Hegnabrunn, Laineck and Bindlach in northern Bavaria (Münster, 1830; Meyer, 1847-55, 1863; Rieppel, 2000b; Diedrich, 2012). Later, the rich Germanic Basin Muschelkalk/Keuper-boundary bonebeds became known, especially during the basal Upper Muschelkalk transgression, and *Paraplacodus*, together with the genera *Placodus* and *Cyamodus*, are recorded from Heimhausen, Bad Sulza and other sites near Bayreuth (all Germany), also are represented by palatine and isolated teeth from Tarnowice of Upper Silesia (Poland). The skeleton of *Paraplacodus broili* Peyer, 1931 from Monte San Giorgio (Switzerland) is of Anisian/Ladinian boundary (Upper Muschelkalk) age. This was the time of maximum flooding, during which these reptiles were more widely distributed. The few articulated skeletons of adult and juvenile individuals from the Monte San Giorgio lagoon and the one from Brasov may have been carcases that drifted a short distance from their original habitats. These habitats were most likely shallow marine, macroalgae-rich carbonate platforms and swells surrounding lagoons, as in the Muschelkalk of the Germanic Basin, in which the placodonts fed on sea plants.

Abstract—New cranial remains and isolated teeth of *Paraplacodus* from Europe at different stratigraphic levels of the Triassic and from several localities demonstrate a wide distribution in the northern Tethys and Germanic Basin and a time range from the Aalcean to Longobardian. The earliest worldwide records of this placodont are described here from the Carpathian Gate with new postcranial remains from Brasov, Southern Carpathian Mountains (Romania) that are dated as Aalcean (lowermost Anisian, Middle Triassic). Another vertebral column (basal placodont) is from the Bithynian (lower Anisian, Middle Triassic), found in intertidal biolaminates at Winterswijk, Netherlands, west of the Germanic Basin. Isolated teeth and some postcranial bones are recorded from Central German sites, especially from the reptile rich locality Freyburg a. d. U., which were found in carbonate sand bar shallow marine deposits of the Lower Muschelkalk Jena Formation ("Saurierkalk," Schaumkalk Member, Pelsonian). Placodonts disappeared from the Germanic Basin during deposition of the Middle Muschelkalk as a result of basinal changes to evaporitic paleoenvironments and the disappearance of macroalgae, their primary food source. Placodonts again dispersed with emigration during the basal Upper Muschelkalk transgression, and *Paraplacodus*, together with the genera *Placodus* and *Cyamodus*, are recorded from Heimhausen, Bad Sulza and other sites near Bayreuth (all Germany), also are represented by palatine and isolated teeth from Tarnowice of Upper Silesia (Poland). The skeleton of *Paraplacodus broili* Peyer, 1931 from Monte San Giorgio (Switzerland) is of Anisian/Ladinian boundary (Upper Muschelkalk) age. This was the time of maximum flooding, during which these reptiles were more widely distributed. The few articulated skeletons of adult and juvenile individuals from the Monte San Giorgio lagoon and the one from Brasov may have been carcases that drifted a short distance from their original habitats. These habitats were most likely shallow marine, macroalgae-rich carbonate platforms and swells surrounding lagoons, as in the Muschelkalk of the Germanic Basin, in which the placodonts fed on sea plants.

**DISTRIBUTION OF BASAL MIDDLE TRIASSIC FOSSIL REPTILE PLACODONTS IN THE GERMANIC BASIN AND NORTHERN TETHYS**

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tioned as “not being diagnostic” (cf. Rieppel, 2000b). *Paraplacodus* was then reported, but not well illustrated, from postcranial bones, especially vertebrae from the Aleş region in the Apuseni Mountains of western Romania (Jurcsák, 1973, 1975, 1976, 1977, 1978), to which new skeletal remains from the Southern Carpathian Mountains will be added here. This rare placodont was then reported from a single lower jaw tooth from a historical collection of the Lower Muschelkalk site Freyburg a. d. U. in Central Germany (Diedrich and Trostheide, 2007). Cranial and postcranial material can be added now from different Lower and Upper Muschelkalk sites in the Netherlands, Germany and Poland of the Germanic Basin (Figs. 1-2) and from the Braşov (German = Kronstadt) region in the Romanian Southern Carpathian Mountains of the northern Tethys, close to the Carpathian Gateway. Those overlooked historical finds from Germany are from the famous sites Bindlach, Laineck and Hegnabrunn near Bayreuth, where Münster (1830), and Meyer (1847-55, 1863) collected, described and illustrated the first placodont records, but these were only *Placodus* and *Cyamodus*. In those collections the small oval palatine and maxillary teeth of *Paraplacodus* were misidentified as fish teeth ("Colobodus"), whereas the anterior teeth were found in between *Placodus* teeth.

The purpose of this article is to revise the known historically or newly collected *Paraplacodus* finds. It summarizes the known sites and their stratigraphic positions in the Lower and Upper Muschelkalk of the Middle Triassic, and describes the paleobiogeographic facies related distribution in the Northern Tethys and Germanic Basin. Therefore, the few skeletons and important and characteristic cranial elements are described and discussed here.

**GEOLOGY AND ENVIRONMENT**

The *Paraplacodus* skeleton from Winterswijk was found in Bithynian-age sediments of the uppermost Bunter to Lower Muschelkalk (Diedrich, 2001), now called the Winterswijk Formation (Fig. 2). The Winterswijk Formation consists of a series of mainly Aegean-age, intertidal biolaminates rich in vertebrate tracks, including a bonebed, and the skeleton remains described here. In the upper part the layers are more massive dolomitic limestone beds that are deposits of a lagoon in which ceratite finds of *Beneckaia buchii* date the middle part of the section as Bithynian of the basal Lower Muschelkalk (Diedrich, 2001).

The *Paraplacodus* skeletal remains in the Romanian Southern Carpathian Mountains were found in the easternmost part of the Getic Nappe in the Triassic Braşov Series, particularly in the Anisian section from Vulcan in the Braşov region (Fig. 2). The outcrop is located on an old road connecting the villages of Vulcan and Holbav villages, on the Gorgan Hill (Romanian = dealul Gorganului) (GPS location: 45°38’53.59”N, 25°24’36.00”E, alt. 675 m). The bone-bed, a 5-cm thick dark gray bituminous limestone, occurs in brown-yellowish marly shales and platy marly limestones, alternating upsection with platy, bituminous limestones in the topmost part of the *Costatoria costata praegoldfussi*–bearing Plattenkalk-type sequence. Palynomorphs typical of the *Triadispora crassa* biozone (Antonescu et al., 1976) and the bivalve assemblage including *Costatoria costata praegoldfussi* Patrulius, *Anodontophora fassaensis* Bittner, *Liomyophoria elegans* (Dunker), and *Hoernesia socialis* (Schlotheim), support the assigned age (e.g., Patrulius, 1971; Kovács et al., 2010). This sequence can be correlated with the Lower Anisian (Aegean) marine Germanic Basin Myophoria Formation (central to eastern Germany) and the Gogolin Formation (Upper Silesia, Poland) and also with the terrestrial Germanic Rot Formation to the west. Higher, the Plattenkalk-type sequence grades into Gutenstein-type medium to thick-bedded, dark gray, bituminous limestones (Kovács et al., 2010). The whole succession was deposited in a restricted lagoon. Unfortunately, the section is no longer accessible.
The sediments in which Paraplacodus and other placodonts were found in the Germanic Basin are mainly in the Lower and Upper Muschelkalk and are carbonate sand or shell-rich, shallow, subtidal carbonates. The Lower Muschelkalk (Jena Formation, Pelsonian) carbonate sands are shallow marine bar deposits indicating a few meters of water depth (e.g., Knaust, 1997). These were widely distributed over the western Germanic Basin, building the Schaumkalk Beds, the so-called “Saurierkalk” (Diedrich and Trostheide, 2007).

The taphonomic situation of reptile carcasses found on intertidal biolaminates of Bithynian age, such as at Winterswijk within the Winterswijk Formation, or the Karlstadt Formation (basal Middle Muschelkalk; cf. Diedrich and Trostheide, 2007) is different. Here, in an intertidal setting, the animals seem to have been flooded far onto the intertidal flats by tsunami or storm events; even those that survived would not have been able to walk dozens of kilometers over the intertidal zone back to the water (Diedrich, 2002, 2009a). In the Upper Muschelkalk, the finds are not in the biolaminates and intertidal deposits, but instead they occur in shallow marine carbonate sand bar deposits, such as at Bad Sulza and in the sediments of Bindlack, Laineck and Hegnabrunn (near Bayreuth, Germany). In the Upper Muschelkalk, the Paraplacodus remains are from bioclastic, dominantly terebratulid shell-rich layers of the shallow subtidal marginal facies (Diedrich, 2010b), and not from massive rich crinoidal limestones (= “Trochitenkalk;” cf. Aigner and Bachmann, 1991). As described for Placodus, the layers represent a palaeoenvironment with benthic mollusc communities (Diedrich, 2009b).

MATERIAL AND METHODS

Fieldwork in the 1970s in the Brașov region in the Romanian Southern Carpathian Mountains resulted in the discovery of one articulated skeleton in the Anisian (Middle Triassic) section from Vulcan (FGGUB no. R.236-242). This was extracted from the Lower Anisian (Aegean) bituminous impregnated limestone beds by chemical dissolution with diluted acetic acid. The most massive bones survived, but the gastrals were damaged, as were the thin-plated pectoral/pelvic and other fragile bones, which were impossible to prepare well (Fig. 4). Previously, a few isolated bones of Paraplacodus were collected in the Apuseni Mountains at Aleșd, Bihor County, in upper Anisian (Illyrian) age carbonates (Fig. 1). This material was published by Jurcsák (1973, 1975, 1976, 1977, 1978) and is stored at the Natural Sciences Department in Muzeul Tarii Crisurilor (Museum of the Three Rivers Land) in Oradea, Romania, but was not accessible during our studies.

Another find included in this study is from Winterswijk, Netherlands. On a slab from the biolaminates of the Lower Muschelkalk (Bithynian), skeletal remains of two different reptiles were found (ME No. Wi-1, cast). The first one is a mostly articulated pachypleurosaur sauropterygian Serpianosaurus skeleton, and the second consists of only a part of the dorsal vertebral column of Paraplacodus. The Serpianosaurus skeleton can be well-identified based on the humeri, which are similar to those figured for a postcranial skeleton of the basal Middle Muschelkalk (Karkstadt Formation, Illyrian) of Heteborn, Central Germany (Diedrich and Trostheide, 2007). The neural arches are disarticulated and some had drifted onto the Serpianosaurus skeleton. The neural arches of Paraplacodus are very different from those of Serpianosaurus and have very long lateral processes. Also, the elongated vertebral centra are deeply amphicoelous only in placodonts, and not in any of the sauropterygians such as pachypleurosaurus or nothosaurs.
FIGURE 3. Paraplacodus cf. P. broilii Peyer, 1931 cranial remains from the Germanic Basin and Polish Carpathian Gate. 1, Lower jaw anterior tooth from the muS of the upper Lower Muschelkalk (Pelsonian) from Freyburg a. d. U., Central Germany (MB no. 4736), lateral. 2, Lower jaw anterior tooth from the muS of the upper Lower Muschelkalk (Pelsonian) from Jena, Central Germany (MLU:IFG no. 2007.26), a, lateral, b, lingual. 3, Upper jaw premaxillary tooth of the mo2 of the Upper Muschelkalk (Illyrian/Fassania) from Bindlach near Bayreuth, southeastern Germany (U-MO no. 1204), lateral. 5, Palatine with five teeth (one damaged) of the Upper Muschelkalk from Tarnowice of Upper Silesia, Poland (MB no. R. 4418), a-b, ventral. 6, Upper jaw premaxillary tooth of the upper Lower Muschelkalk (Pelsonian) from Freyburg a. d. U., Central Germany (MB no. R.4420), lateral. 7, Upper jaw premaxillary tooth of the mo1 of the lower Upper Muschelkalk (Illyrian) from Bad Sulza, Central Germany (NME no. 78/518), lateral. 8, Palatine, maxillary or dentary tooth of the lower Upper Muschelkalk (Illyrian/Fassanian) from Bindlach near Bayreuth, southeastern Germany (U-MO no. 68), occlusal. 9, Palatine, maxillary or dentary tooth of the lower Upper Muschelkalk (Illyrian/Fassanian) from Bindlach near Bayreuth, southeastern Germany (U-MO no. 75), a, occlusal, b, ventral. 10, Palatine, maxillary or dentary tooth of the upper Lower Muschelkalk (Illyrian/Fassanian) from Bindlach near Bayreuth, southeastern Germany (U-MO no. 69), occlusal. 11, Palatine, maxillary or dentary tooth of the lower Upper Muschelkalk (Illyrian/Fassanian) from Bindlach near Bayreuth, southeastern Germany (U-MO no. 75), a, occlusal, b, ventral. 11, Palatine, maxillary or dentary tooth of the Upper Muschelkalk from Tarnowice of Upper Silesia, Poland (MB no. R. 4419), occlusal. 12, Palatine, maxillary or dentary tooth of the lower Upper Muschelkalk (Illyrian) from Laineck near Bayreuth, southeastern Germany (MB no. 4417), occlusal. 13, Tooth wear stages, A, wear stage 2, and B, wear stage 3, of the Paraplacodus palatine teeth from the Upper Muschelkalk of Tarnowice of Upper Silesia, Poland (cf. Fig. 5; MB no. R. 4418), occlusal. 14, Tooth wear stages, A, wear stage 1, B, wear stage 2, and C, wear stage 3, of Placodus palatine and dentary teeth from the Upper Muschelkalk of Bayreuth in Bavaria, Germany (MB and NMB without no).
FIGURE 4. *Paraplacodus* cf. *P. broilii* Peyer, 1931 postcranial skeletal remains consisting mainly of a dorsal vertebral column and a few forelimb and pectoral girdle bones from the Aegean found in Vulcan in the Carpathian Mountains of Romania. 1, Part of the articulated specimen after acid treatment and before separation in the following single bones. 2, Strongly incomplete pelvic/pectoral bone (FGGUB R.236), ventral. 3, Fibula (FGGUB no. R.237), dorsal. 4, Outer gastral rib (FGGUB no. R.238), cranial. 5, Thoracic vertebra neural arch (FGGUB no. R.239): a, cranial; b, lateral. 6, Thoracic vertebra neural arch (FGGUB no. R.240): a, cranial; b, lateral. 7, Thoracic vertebra centrum (FGGUB no. R.241): a, cranial; b, dorsal; c, lateral. 8, Thoracic vertebra and centrum connected (FGGUB no. R.241): a, cranial; b, lateral. 9, Thoracic vertebra arch (FGGUB no. R.242): a, caudal; b, lateral.
They have vertebral centra that are only slightly amphicoelous, and are also much shorter, as can be compared well on the centra found on the slab of Winterswijk.

In addition to those skeletal remains, historical German Museum collections from famous bone-rich localities such as Jena, Freyburg a.d. U. (Lower Muschelkalk), Bad Sulza and Bayreuth and other southwestern German sites such as Heimhausen, as well as Upper Silesian sites such as Tarnowice (Upper Muschelkalk) were checked for the possible presence of isolated cranial and postcranial Paraplacodus material. In total, several thousand teeth and bones were studied, all from non-systematic collecting activities, of which finally only a very few can be determined to belong to this placodont genus; postcranial bones are difficult to distinguish from those of other placodonts, especially in juvenile individuals.

The bone material examined in this study is housed in the Geological Department of Martin-Luther-Universität Halle/Saale (=MLU), the Humboldt-Museum of Natural History in Berlin University (=MB), the Bayrische Staatsammlung für Paläontologie, Universität München (=BSP), the Staatliche Museum für Naturkunde Stuttgart (=SMNS), the Museum für Natur und Umwelt Osnabrück (=NMO), the Urwelt-Museum Oberfranken in Bayreuth (=U-MOB), the Muschelkalkmuseum in Ingelfingen (=MHI), Museum in Enschede (=ME), the Naturals in Leiden (=NMNH), Naturkundemuseum Bamberg (=NMB), and the Naturkundemuseum in Erfurt (=NME). The Romanian material is housed in the University of Bukarest, Faculty of Geology and Geophysics (=FFGUB).

Finally, bonebed material consisting of about 2500 vertebrate remains from Lamenring in western Germany (enodis/possecker/Biozone, Anisian) was used for the comparative faunal analyses to understand the paleoenvironment and possible presence of macroalgae, and therefore the palaeoecology of placodonts. The northwestern German Bissendorf compressus Bonebed (Anisian/Ladinian boundary) site, with several hundred systematically excavated bones and teeth, was integrated into the taphonomy and palaeoecology analyses. Also included was the reptile fauna of the Bayreuth region, which included about 1600 bones and teeth.

The direct comparisons of anterior and other teeth to the holotype skull of P. broili (cf. Fig. 1), as well as comparisons of isolated postcranial placodont remains, allowed the determinations presented here. The anterior teeth of Paraplacodus were found in the collections labelled as “Tholodus” ichthyosaur teeth, whereas palatine and isolated teeth from Upper Silesian sites were misidentified as “Colobodus” remains.

SYSTEMATIC PALEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
   Order PLACODONTIA Cope, 1871
   Suborder PLACODONTOIDEA Cope, 1871
   Family PARAPLACODONTIDAE
   Peyer and Kuhn-Schnyder, 1955
   Genus Paraplacodus Peyer, 1931
   Paraplacodus cf. P. broili Peyer, 1931
   Figs. 3-5

Cranial material: Cranial remains consist of isolated teeth and a palatine. The dentary or maxillary teeth cannot be assigned to their exact positions. Two lower jaws and one premaxillary upper jaw (Figs. 3.1-2, 6) are from the Lower Muschelkalk muS (Jena Formation, Pelsonian) of Jena and Freyburg a.d. U. (Central Germany). From similar, old Lower Muschelkalk layers (muS, Pelsonian) a single premaxillary tooth is from Heimhausen (southwestern Germany) (Fig. 3.4). A third upper jaw premaxillary tooth is from the Upper Muschelkalk mol1 (Bad Sulza Formation, upper Illyrian) of Bad Sulza (Central Germany). One anterior tooth is from Bindlach near Bayreuth (Central Germany) (Fig. 3.3).

A palatine with four preserved teeth and one damaged tooth (Fig. 3.5) and one isolated maxillary, palatine or dentary tooth (Fig. 3.11) was found in the Upper Muschelkalk of Tarnowice in Upper Silesia (Poland). Four similar teeth were found in the mol of the lower Upper Muschelkalk (Bad Sulza Formation, Illyrian) in Bindlach and Lanneck near Bayreuth (Central Germany) (Figs. 3.8-10, 12).

Postcranial material: Skeletal remains from the Aegean layers (lowermost Anisian, Middle Triassic) from the Romanian Southern Carpathian Mountains (Fig. 4) consist of some pelvic and pectoral bones, a few limb bones and mainly vertebrae, and some fragmentary gastrail ribs. The pectoral or pelvic elements (Fig. 4.1) are too fragmentary for clear identification. A fibula is nearly complete (Fig. 4.2). The thoracic remains are illustrated here only by the largest fragment of a gastrail element (Fig. 4.3). Most remains are vertebrae (Figs. 4.4-8), of which the neural arches and centra are in most cases non-fused, although in one they are connected (Fig. 4.7).

A second postcranial Paraplacodus skeleton mainly consisting of the dorsal vertebral column with disarticulated centra and neural arches comes from intertidal biolaminates at Winterswijk, Netherlands (Fig. 5). The vertebral column of Paraplacodus was found associated with another carcase, of the pachypleurosaur Serpianosaurus (Fig. 5). The skeleton is from the lower Bithynian (lowermost Middle Triassic). The total number of bones and vertebrae is unclear because many of the bones are embedded in sediment, so they cannot clearly be determined. At least 18 neural arches and four centra can be distinguished, as can one incomplete coracoid and one complete radius (Fig. 5).

DISCUSSION

Systematic Attribution

The material described here is referred to Paraplacodus, whereas historical descriptions of material of the possibly synonymous Saurophargis are far from resolved, and Eusaurophargis also is based on incomplete remains, as in Nosotti and Rieppel (2003), who state that the original specimen of “Saurophargis voltzi” had deeply amphicoelous centra. The positions of Eusaurophargis and Saurophargis remain unclear, and these might represent Paraplacodus. Conversely, some of the material described here might reflect those species.

The slab from Winterswijk consists of two distinguishable skeletal remains, although the large pachypleurosaur is much better articulated. In the postcranial skeleton from Heeteborn, central Germany (cf. Diedrich and Trotshede, 2007), the humeri and pectoral girdle are very similar to that of the Winterswijk specimen. Whereas the Winterswijk Serpianosaurus skeleton is of early Bithynian age, the one from Heeteborn is of latest Pelsonian age. This material was also compared to the Fassani/Norwegian-age holotype skeleton of Serpianosaurus mirigiolensis, 1989 (cf. Rieppel, 1989).

The few anterior teeth and skull fragment and two postcranial skeleton remains described here can be attributed to the genus Paraplacodus after comparisons to the Monte San Giorgio specimens and to other placodont skull and isolated tooth remains (cf. Peyer, 1931; Kuhn-Schnyder, 1942; Nosotti, 1986; Zanon, 1989; Rieppel, 2000b).

The anterior teeth in Paraplacodus are much different and longer and more slender compared to those of Placodus (cf. also Dreverman, 1933; Diedrich, 2010b and Fig. 3). Also, the enamel surface in Paraplacodus is stronger and has a more fine, parallel-ridge ornamentation. The only similar teeth are the anterior teeth of Cyamodus, but those are half the length. This comparison of the anterior teeth of all three placodonts was illustrated recently (Diedrich, 2010a-b). The lower jaw anterior teeth seem in Placodus to be less thick basally than the upper jaw anterior teeth (cf. Figs. 3.2 and 3.6).

The palatine, maxillary and dentary teeth of Paraplacodus are also described by Peyer (1931) and Rieppel (2000b) as slightly conical and in oval to slight rectangular outline and have in the non-use stage (wear stage 1 after Diedrich, 2010b) a radial enamel structure similar to
FIGURE 5. Basal placodont (*Paraplacodus* or *Saurosphargis*) postcranial skeleton remains consisting mainly of a dorsal vertebral column and a few forelimb and pectoral girdle bones from the Bithynian, mixed with another marine large pachypleurosaur *Serpianosaurus* sp. skeleton found on intertidal biolaminates at Winterswijk, Netherlands in the western Germanic Basin (cast in the ME no. Wi-1, original in the NL no. NMNHL RGM 449487).
Placodus (cf. Figs. 3.14.A-C). The palate teeth are much less conical, and more or less oval to rectangular. Their maximum diameter is less than one cm, and this is likely the cause of their misidentification as Colobodus fish teeth, although Colobodus teeth are much smaller (maximum 3 mm in diameter) and often polygonal in occlusal outline. Possibly some of the here figured worn teeth (most in wear stage 2) are Cyamodus maxillary teeth, or maybe maxillary teeth of very juvenile Placodus (cf. Diedrich, 2010b).

The preserved palate from Tarnowice (Poland) (Fig. 5.4) has polished teeth in three different wear stages. Whereas the anterior damaged one is unused (wear stage 1), the second is worn in the enamel (wear stage 3; Fig. 3.13.B), and the last two are polished without any enamel structure (wear stage 2; Fig. 3.13.A). Similar different wear stages and tooth replacement can be seen in Placodus (Figs. 2-14A-C) and in the figures of the Monte San Giorgio (Switzerland) Paraplacodus specimens (cf. Peyer, 1931; Kuhn-Schnyder, 1942; Nosotti, 1986; Zanon, 1989; Rieppel, 2000b), which caused confusion about the number of palate teeth in Paraplacodus. The palate remains from Poland are important for the systematic and anatomic discussion of Paraplacodus. In the original skull reconstruction of P. broilii, only five teeth were illustrated. In the redescriptions of several specimens and one complete skull from Monte San Giorgio (Rieppel, 2000b), seven maxillary and five palate teeth are preserved. In the incomplete specimen from Upper Silesia five teeth are preserved in the palate, and a sixth was damaged; this is the smallest and most posterior tooth (cf. Fig. 3.5). Compared to the described material from Monte San Giorgio (holotype PIMUZ T4773), the specimen from the northern Tethys is damaged exactly in this region on the right palate, and seems to have had also an empty sixth and small alveolar groove. This individual was undergoing tooth replacement at different tooth positions, and is missing three teeth in the right palate, including the last posterior one. This tooth change stage is documented by empty alveolar grooves. In the descriptions of Peyer (1931) and Rieppel (2000b) the number of palate teeth vary between four to five, but six appears to be the real total in this genus and the species P. broilii, if all are in their fully erupted position. Therefore, the skull in ventral view is presented here slightly modified after the presentations of Kuhn-Schnyder (1960) with one smaller posterior tooth in the palate (cf. Fig. 3.5b).

The postcranial remains from Vulcan (Romania) also match well with the unfortunately poor illustrations and descriptions of finds of Paraplacodus in the Apuseni Mountains of western Romania, which were therefore proposed to be “non-diagnostic” (Rieppel, 2000b). Thus, the former suggestions by Jurcsák (1973, 1975, 1978) about the presence of Paraplacodus in the northern Tethys close to the Carpathian Gateway in the Carpathians of Romania can be supported by the important diagnostic postcranial skeleton remains illustrated here from the Brașov region. They do not allow further systematic discussions or revisions of the postcrania of Paraplacodus.

The postcranial remains from Winterswijk (Netherlands) (Fig. 4) are similar to those and to the holotype skeleton, and typically have small vertebrae similar in size to those of the Romanian specimen. The centra are elongated and, as is typical for placodonts, deeply amphicoelous on their terminal articular surfaces (cf. Kuhn-Schnyder, 1942; Rieppel, 2000b), as in the vertebrae of the Romanian specimen (cf. Figs. 4.6-7). This differs from the vertebrae of Serpianosaurus, which are nearly as long, wide, smooth and slightly amphicoelous on their terminal articular surfaces (cf. also Rieppel, 2000a). Therefore, the vertebrae are readily distinguished on the “bone slab” from Winterswijk as two distinct carcases. An incomplete coracoid and complete radius appear to be the only preserved additional pectoral and appendicular bone elements of Paraplacodus on the Romanian specimen (Figs. 4.2-4.3).

**TAPHONOMY AND BIOSTRATIGRAPHY**

In the taphonomic record, Paraplacodus remains have been found with isolated teeth and possibly postcranial bones in central Germany, mainly in the Jena “Saurierkalk” and Freyburg a. d. U. “Schaumkalk” carbonate sand-bar deposits (muS member, Lower Muschelkalk, Pelsonian). One tooth illustrated here (Fig. 3.4) from the Pelsonian layers was already mentioned by Hagdorn and Rieppel (1999) from Heimhausen (southwestern Germany). Other discoveries come from the Upper Muschelkalk coastal shallow marine carbonates near Bayreuth (Diedrich, 2012). In contrast to these shallow marine marginal deposits, placodont bones and teeth are almost absent from terrestrially influenced sediments of the uppermost Upper Muschelkalk bone beds of northern Germany, as has recently been demonstrated for the enodis/posseckerti (Lower Ladinian) bone bed (Diedrich, 2003). This taphonomic distribution therefore provides evidence of “facies adaptation” in these reptiles. Placodont remains are well represented in carbonate sands and biolecsediments but less so in crinoidal limestones of the Germanic Basin such as at Bissendorf, whereas in more clay-rich and terrestrial (low carbonate) facies such as those at Lamerden they are rare or even absent (cf. Diedrich, 2009b). The dominance of single teeth, which were replaced and dropped during the life of the reptiles, and not transported far, also supports the interpretation of the original habitat of placodonts in this macroalgae-rich facies.

The Paraplacodus remains found at Vulcan, seem to be similar to those in the Winterswijk specimen, a slightly disarticulated specimen. Bones were isolated by acid preparation, but the slab contained only a part of the individual skeleton (due to modern damage). It was fossilized in an oil-impregnated carbonate micrite; the bituminous material originated from the black shale layers. The partly anoxic conditions of the carbonate/black shale series were generated by the decay of the macroalgae mass, a situation that resembles the paleoenvironments of the anoxic lagoons of Monte San Giorgio (Furrer, 1995). As a whole, the early Anisian (Aegean) was mostly characterized by anoxic environments in the central-eastern part of the Getic domain of the Romanian South Carpathian Mountains (e.g., Patrulius, 1971; Kovács et al., 2010).

**PALEOECOLOGY AND PALEOBIOGEOGRAPHY**

Whereas seagrass is not known from pre-Tertiary times, there is indirect evidence of macroalgae in the Germanic Basin (Figs. 7-8) in the Jena Formation (Lower Muschelkalk) and the Bad Sulza, Trochitenkalk to Meissner formations (Upper Muschelkalk), and also in the northern Tethys Cassina Formation (Upper Muschelkalk equivalent) of the Alps (Fürsich, 1981; Hagdorn, 2004). Benthic communities of bivalves and gastropods are well known in the “Lower Muschelkalk,” where the gastropod genera Wortheniella, Omphalophtyca and Polygrinina, often enriched with other shells in storm shell beds of the “Wellenkalk facies,” indicate the presence of larger macroalgae meadows (cf. Hagdorn, 2004; Diedrich, 2010b). In the Upper Muschelkalk, benthic communities again provide evidence for the existence of macroalgae in both the Germanic Basin and the northern Tethys; gastropods such as Neritaria are the indicators in the Germanic Basin (cf. Hagdorn, 2004), whereas in the Tethys it is Rhaphistomella and Anoptychia (cf. Fürsich, 1981).

The placodont Paraplacodus lived among those macroalgae benthic communities, in sand bar to shelf-enriched paleoenvironments, supporting the hypothesis that Paraplacodus also was an algal feeder like all other placodonts (Diedrich, 2010a), and not a durophagous, shell-crushing sauropterygian. This paleoenvironmental adaptation finally explains the paleobiogeographic distribution of placodonts in all areas of the marine facies surrounding Pangaea. Other calcareous green algae groups have been documented from those shallow marine Tethyan habitats (e.g., Furrer, 1995), but those with calcareous skeletons would not have provided the appropriate plant food-sources for placodonts. This facies adaptation is important to explain the paleobiogeographical distribution of placodonts, so the model of Rieppel and Hagdorn (1997) must be revised and modified for several reptile groups.

Paraplacodus was the smallest of the three Germanic Basin placodonts and had unique thoracic ribs, which were enlarged with distal, flat, wing-like extensions (cf. Peyer, 1931) to enhance the body weight in
a quite unique way. The general body proportions and general osteology and anatomy were closer to *Placodus* than to *Cyamodus*, therefore *Paraplacodus* is the most primitive known placodont (Kuhn, 1969; Sues, 1987; Rieppel and Zanon, 1997; Rieppel, 2000b).

The *Paraplacodus* occurrence in the late Anisian (Illyrian) in the Apuseni Mountains of western Romania (Jurcsák, 1973-1978; Patrulius, 1979), and the newly reported occurrence here of the *Paraplacodus* remains in the early Anisian (Aegean) from Vulcan in the Romanian South Carpathian Mountains, document that placodonts inhabited the north-western shore of the Tethyan Sea and migrated via the Carpathian Gate seaway connection between the Tethyan Sea and the Germanic Basin.

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