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NEW INTERPRETATION OF THE POSTCRANIAL SKELETON AND OVERALL BODY SHAPE OF THE PLACODONT *CYAMODUS HILDEGARDIS* PEYER, 1931 (REPTILIA, SAUROPTERYGIA)

Torsten M. Scheyer

ABSTRACT

The enigmatic cyamodontoid placodont *Cyamodus hildegardis* from the Besano Formation (Middle Triassic) of the Alpine area of Switzerland and northern Italy has previously been reconstructed with a broad, laterally expanded main armour (carapace) and a separate smaller pelvic shield, lending this species a fairly sprawling appearance. A re-examination and a literature review of the postcranial dermal armour and endoskeletal elements of the three best preserved articulated specimens of the species leads to new interpretations of the dermal armour and associated underlying postcranial bones, as well as a new life reconstruction. The carapace of *C. hildegardis*, carrying a series of similar-sized, enlarged lateral armour plates, is rounder and less laterally expanded than previously hypothesised. The separate pelvic shield, also carrying a smaller set of lateral armour plates that decrease in size with an anteroposterior gradient, covers mainly the pelvic girdle and the base of the tail. The rather short tail is armoured by four series of armour plates that show a simple anteroposterior gradient of size reduction in keeping with an equivalent size reduction in the caudal vertebrae. Until further fossils are recovered, the internal organisation of dermal plates within the two armour shields of *C. hildegardis* remains little known.

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INTRODUCTION

Cyamodontoid placodonts (Eureptilia, Sauropterygia), sometimes referred to as the ‘reptilian rays’ (cf. Naish 2004) and recently proposed to share a convergent lifestyle with modern sirenians (Diedrich 2009), possess a turtle-like armour. The cyamodontoid armour and the turtle shell evolved convergently and are only superficially similar. In contrast to turtle shells, the cyamodontoid dermal armour is not connected to the underlying postcranial endoskeleton (Gregory 1946; Peyer and Kuhn-Schnyder 1955; Westphal 1975, 1976; Pinna 1999; Rieppel 2002). Aside from the other species of

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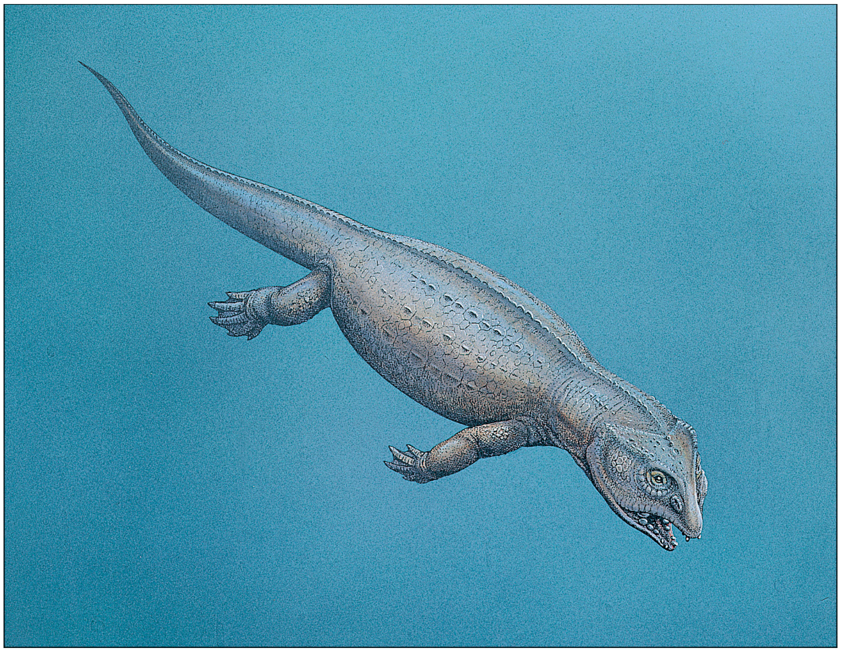

FIGURE 1. Previous life reconstruction of *Cyamodus hildegardis* with a single piece of armour covering the trunk of the animal (Image by Beat Scheffold, Paläontologisches Institut und Museum, Universität Zürich).

Cyamodus, *Cyamodus hildegardis* Peyer 1931 is known from both cranial and postcranial material, mainly because of the exceptional preservation conditions of fossils in the UNESCO world heritage site of Monte San Giorgio, Ticino, southern Switzerland, from which the majority of specimens has been recovered (e.g., Peyer 1931, 1944; Kuhn-Schnyder 1964, 1979; Pinna 1980; Furrer 2003).

Nosotti and Pinna (1996) and Pinna (1999) proposed *Cyamodus hildegardis* to be a junior synonym of *Cyamodus "laticeps"* (Owen 1858), more closely related to the placochelyid *Protenodontosaurus italicus* Pinna 1990 than to *Cyamodus* material from the Germanic Triassic. According to Rieppel (2001), however, *C. hildegardis* forms a monophyletic group with *Cyamodus kuhnschnyderi* Nosotti and Pinna, 1993 and *Cyamodus rostratus* (Münster 1839) from the Germanic Triassic of Germany. Postcranial characters could not yet be included into analyses for the three species of *Cyamodus*, because remains are insufficiently known for the Germanic species (Rieppel 2001).

There are only three specimens of *C. hildegardis* in which the postcranium, especially the dermal armour, is preserved in articulation: two presumably adult specimens (holotype PIMUZ T4763; referred specimen PIMUZ T58) and a juvenile specimen (MSNM V458). For an overview of published specimens referred to *C. hildegardis* see Pinna (1992) and Rieppel (2002). Specimens PIMUZ T58 and MSNM V458, the latter first described by Pinna (1980), were previously figured in part by Westphal (1975, 1976) on the constructional aspects and development of the placodont armour, as well as in the comparative work on cyamodontoid armour by Rieppel (2002).

Skeletal and life reconstructions are substantial for understanding the anatomy of extinct vertebrates. Earlier life reconstructions of *C. hildegardis*, so far mainly published for museum exhibition purposes (e.g., Kuhn-Schnyder 1979; Furrer 2003; Figure 1), implied that the trunk of the animal was covered only by a single continuous main piece of dorsal armour (see also Diedrich 2009 for a recent skeletal reconstruction of *C. rostratus*). Pinna`s (1992) schematic reconstruction based on both the PIMUZ and MSNM specimens on the other hand, already showed a separate shield covering the pelvic region and the base of the tail in *C. hildegardis*. This way, *C. hildegardis* was shown for the first time to have a similar body outline as *Psephoderma alpinum* for which such a bipartite armour structure is best known (Pinna and Nosotti 1989; Rieppel 2002). Pinna (1992) and later Rieppel (2000, 2002) pictured and discussed the various aspects of the postcranial armour of *C. hildegardis*. However, as is discussed below, several problems with their respective interpretations were encountered. The latest life reconstruction of *C. hildegardis*, an aquarelle painting by Fabio Fogliazza, was presented by Nosotti and Teruzzi (2008, figure 46), who underlined difficulties in reconstructing the general morphology of the armour. Although it is by far the best life reconstruction of the species and an artful piece of work in its own right which should not be belittled in any way, it is still deemed appropriate to point out that it is based mainly on earlier, partly erroneous, interpretations.

Herein, a re-examination and novel interpretation of the postcranial skeleton, especially the dermal armour, of *C. hildegardis* based on the two adult PIMUZ specimens is presented, resulting in a novel life reconstruction of the overall body shape of this placodont. On the other hand, matters of scalation patterns, the nature of the dermal armour or the functional role of individual armour plates and their intrinsic role in the general development of the armour are not engaged.

MATERIALS AND METHODS

The holotype PIMUZ T4763 and the referred specimen PIMUZ T58 from the Upper Besano Formation (‘Obere Grenzbitumenzone’; Anisian/Ladinian boundary) of Monte San Giorgio, both presumably adult specimens (Figure 2) and the only material of *Cyamodus hildegardis* showing largely articulated postcranial armour were reinvestigated. Data from the juvenile specimen MSNM V458 from the “Scisti Bituminosi” (=‘Grenzbitumenzone’) of Pogliana near Besano, Lombardy, previously described and pictured by Pinna (1980, 1992) were taken into account as well, although the armour is yet in an early stage of development (Figure 3). The PIMUZ material was further compared to the published accounts on the postcranium of adult specimens of *Psephoderma alpinum* (Pinna and Nosotti 1989; Renesto and Tintori 1995; Rieppel 2002).

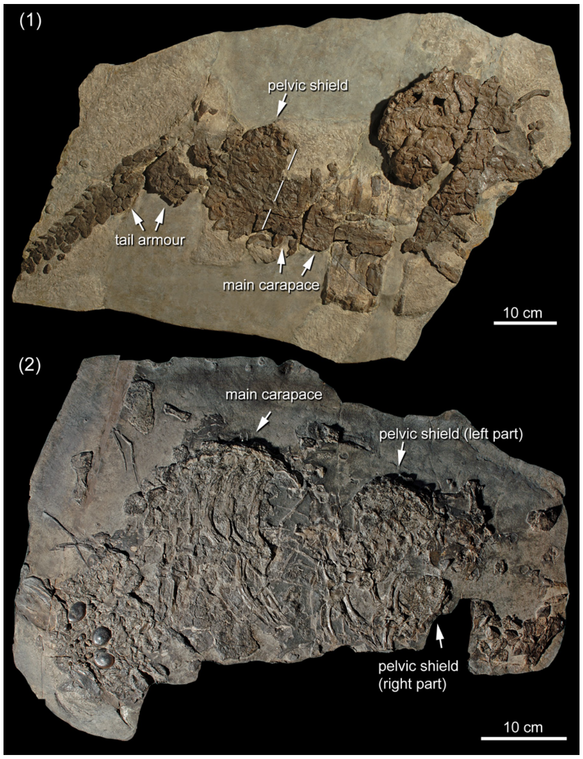

FIGURE 2. Composite picture of (1) the holotype PIMUZ T4763 (dorsal view) and (2) referred specimen PIMUZ T58 (ventral view) of *Cyamodus hildegardis*. Note that the light source had been positioned in a low angle to best indicate the relief of the armour in both specimens.

Institutional Abbreviations

BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **FAFI**, Magayar Allami Földtani Intézet (Geological Institute of Hungary, Budapest) Budapest, Hungary; **Gmr**, specimens collected by the Geological Survey of Guizhou, Guiyang, China – currently with the government of Guanling County, southwestern Guizhou Province, China; **GPIT**, Geologisches und Paläontologisches Institut der Universität Tübingen, Germany; **MCSNB**, Museo di Scienze Naturali di Bergamo, Italy; **MSNM**, Museo Civico di Storia Naturale di Milano, Italy; **PIMUZ**, Paläontologisches Institut und Museum, Universität Zürich, Switzerland; **ZMNH**, Zhejiang Museum of Natural History, Hangzhou, China.

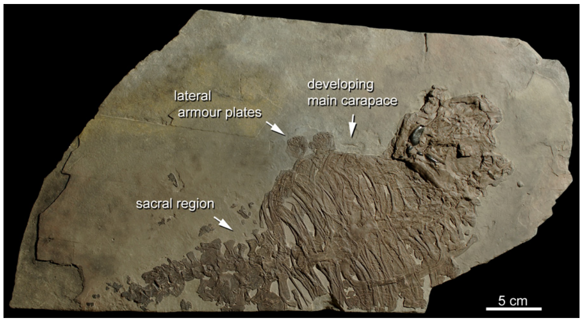

FIGURE 3. Photograph of a cast (PIMUZ A/III 729) of the juvenile specimen MSNM V458 of *Cyamodus hildegardis* in ventral view. Note the developing main carapace with its large prominent lateral armour plates, whereas the sacral region is largely devoid of armour plates yet.

POSTCRANIAL ANATOMY: OVERVIEW AND NEW INTERPRETATIONS

Despite the incomplete or disturbed nature of the specimens, many anatomical details of the postcranium of *C. hildegardis* have been aptly described by Peyer (1931), Westphal (1975) and Pinna (1980, 1992) and thus do not have to be repeated here. In the following, an overview of the underlying endoskeletal elements (i.e., vertebrae, transverse processes, ribs, and elements of the girdles) and the associated units building the post-cranial armour in *C. hildegardis* is given, while highlighting the features essential to the discussion and the new interpretation of the material.

General Overview of the Body Armour

Pinna's (1992) observations that the body of *Cyamodus hildegardis* is covered by three parts of dorsal armour ('corazza dorsale', Pinna 1992) and that a plastron ventral to the gastral apparatus is not developed in the trunk region, were confirmed (Figure 2.2, 3). The dorsal armour consists of an anterior piece of armour covering the main part of the trunk region, the carapace, a posterior situated separate smaller shield ('piastra caudale', Pinna 1992) covering parts of the pelvic region and the base of the tail (Figure 4) as well as armour covering the rest of the tail ('ossificazioni dermiche della coda', Pinna 1992; Figure 5). Rieppel (2002) also pointed out a separation between a 'dorsal shield' and a 'tail shield', although it is unclear if the 'tail shield' indeed refers to the 'piastra caudale' of Pinna (1992), referred to as the pelvic shield herein. In the accompanying figure (Rieppel 2002, figure 10), the part of the armour labelled as 'tail shield' is situated anterior to the part of the armour labelled as 'dorsal shield'. However, as seen in the holotype (Figure 2.1), the tail is situated on the left margin of the image. Following Pinna (1980, 1992; see also Pinna and Nosotti 1989 on fused transverse processes and ribs in *Psephoderma alpinum*), the main part of the armour in *C. hildegardis* is regarded as being underlain by the vertebral centra and thick transverse processes, whereas the more slender and more strongly curved ribs are restricted to the lateral body wall of the trunk region.

Vertebral Column

As noted by Pinna (1992), none of the specimens of *Cyamodus hildegardis* shows a complete vertebral column. The juvenile specimen MSNM V458 (Figure 3) presents the most complete continuous vertebral section, including twelve dorsals, three sacrals and eight caudals. The vertebral column of the holotype specimen PIMUZ T4763 further indicates that there were also at least three cervicals and probably a few more than 18 caudals present (Peyer 1931). In PIMUZ T58, the specimen with the best preserved armour, the elements posterior to the well recognizable seven anterior dorsals (Figure 6) are dislocated. It is tentatively confirmed that the posteriorly situated isolated vertebrae and transverse processes are indeed the following dorsals 8-11 (sensu Pinna 1992), but a different sequence based on the size of the transverse processes is regarded more plausible (Figure 7). Furthermore, the presence of the twelfth dorsal centrum lying anterior to the sacrals is recognized, which fits in size and shape in comparison to the three vertebrae preserved in articulation below the pelvic shield ('piastra caudale', Pinna 1992), previously hypothesized as being sacrals 1-3 (Pinna 1992). The generally poor preservation

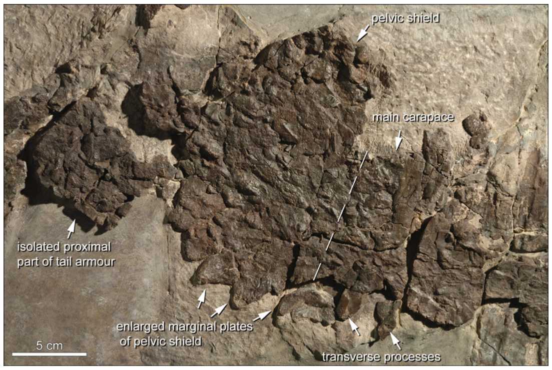

FIGURE 4. Image of the pelvic shield of the holotype specimen PIMUZ T4763 of *Cyamodus hildegardis* in dorsal view.

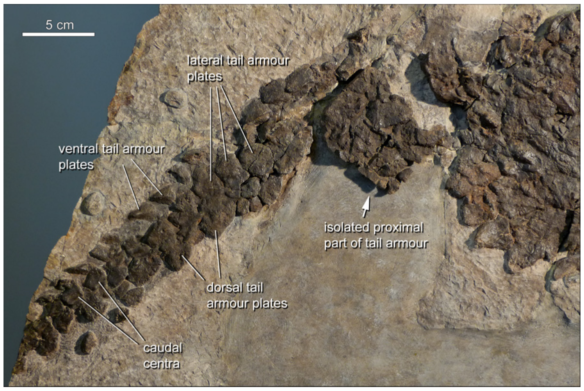

FIGURE 5. Image of the tail armour of the holotype specimen PIMUZ T4763 of *Cyamodus hildegardis* in dorsal and left lateral view.

FIGURE 6. Close-up of the main carapace region of specimen PIMUZ T58 of *Cyamodus hildegardis* in ventral view. (1) Photograph of specimen. Note that because of technical reasons, the image is rotated 90° clockwise to the overview image in Figure 2.2. (2) Interpretative sketch of skeletal elements. Black arrows indicate the two elements previously identified as coracoids by Pinna (1992), here interpreted as being the anterior-most lateral armour plates of the main carapace. Colour code: brown: armour elements; blue: vertebral centra and transverse processes; purple: appendicular elements; grey: girdle elements; green: ribs; yellow: elements of gastral apparatus; red: unidentified elements. Abbreviations: a: armour plates; dv: dorsal vertebra; g: gastral rib; r: rib; ra: radius; sc: scapula; tp: transverse process; ul: ulna; ?: unidentified.

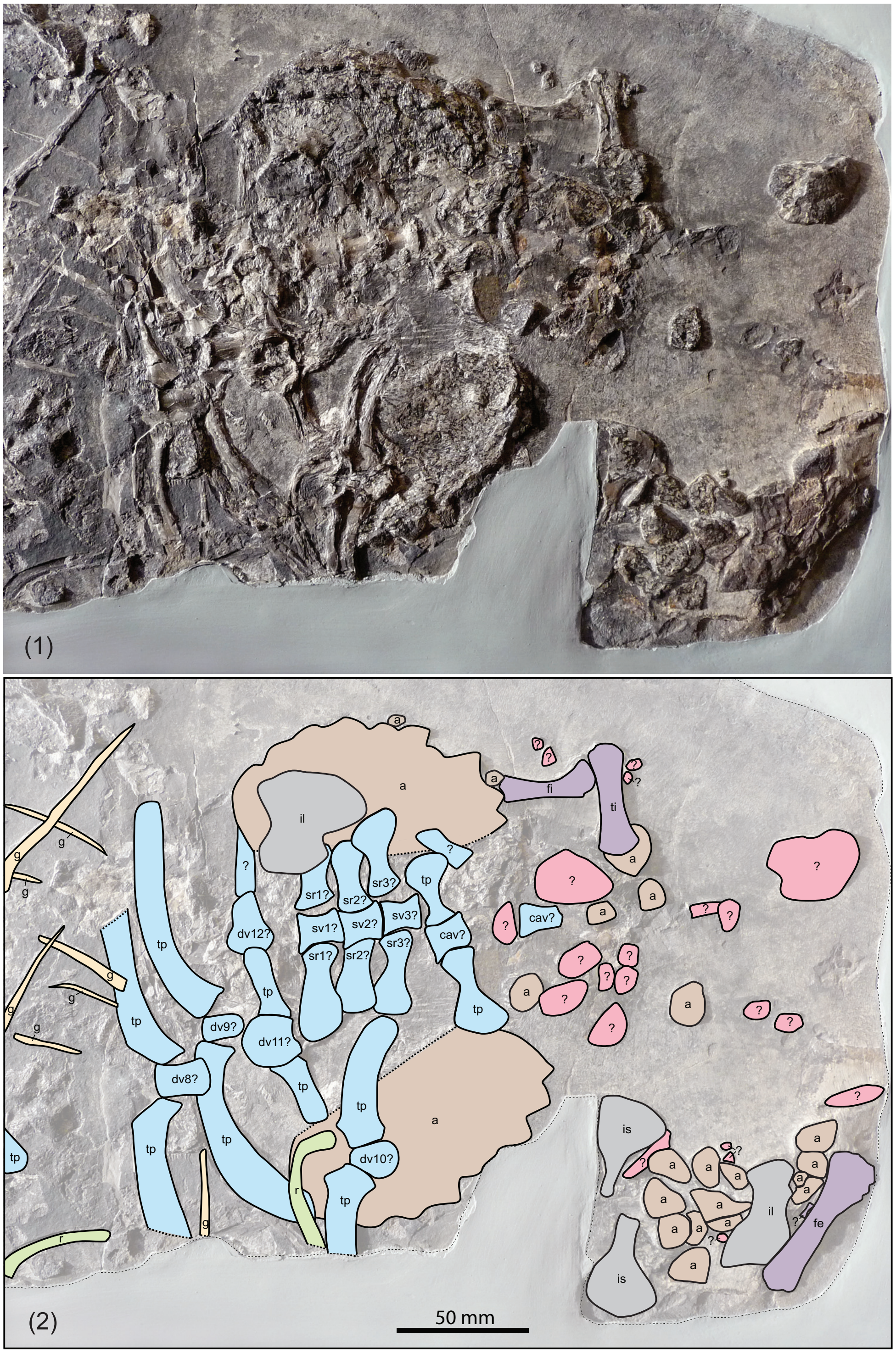

FIGURE 7. Close-up of the pelvic shield region of specimen PIMUZ T58 of *Cyamodus hildegardis* in ventral view. (1) Photograph of specimen. (2) Interpretative sketch of skeletal elements. Note that many of the isolated elements being marked as unidentified may pertain to the pelvic shield or tail armour, but identification was not unambiguous. Colour code: brown: armour elements; blue: vertebral centra and transverse processes; purple: appendicular elements; grey: girdle elements; green: ribs; yellow: elements of gastral apparatus; red: unidentified elements. Abbreviations: a: armour plates; cav: caudal vertebra; dv: dorsal vertebra; fe: femur; fi: fibula; g: gastral rib; il: ilium; is: ischium; r: rib; sr: sacral rib; sv: sacral vertebra; ti: tibia; tp: transverse process; ?: unidentified.

and distortion of the bones in the pelvic region, as well as a rotation of the twelfth dorsal about 90° to the rest of the vertebral column might be the reason why it had been overlooked before (Figure 7). Only the first sacral vertebra was considered to have a transverse process between centrum and sacral rib 1 (Pinna 1980). Taking a conservative approach, however, the exact positions of all preserved vertebrae and their associated transverse processes and/or ribs in PIMUZ T58 cannot be confidently identified.

Pectoral and Pelvic Girdles

Based on the juvenile specimen MSNM V458 a reconstruction of both girdles was presented by Pinna (1980). Few girdle bones, although not preserved in articulation, are recognizable in the referred specimen PIMUZ T58. The pectoral and pelvic girdles are not well visible in the holotype specimen PIMUZ T4763 (Peyer 1931).

As seen in the juvenile specimen, the pectoral girdle is composed of seven bones: the unpaired clavicle and the paired clavicles, scapulae and coracoids (Pinna 1980). Pinna's (1992) identification of the pectoral bones in specimen PIMUZ T58 is highly schematic, with outlines of individual bones often missing. Although badly preserved, the two scapulae of PIMUZ T58 (Figure 6) are recognisable. I do not concur however with Pinna's (1992) identification of the two coracoids. Instead these elements are interpreted to be enlarged dermal armour plates (Figure 6) from the anterior portion of the main carapace that have been dislocated and in which the visceral surface of the bone is now seen. Because all elements of the pectoral girdle have been dislocated, no further information concerning the relation between these bones and the main carapace is available from this specimen.

Similarly, the elements of the pelvic girdle are best discerned in the juvenile specimen MSNM V458 (Pinna 1980; see also Westphal 1975). As depicted by Pinna's (1980) reconstruction, the pelvic girdle is composed of the ventrally situated platy elements, the anterior pubes and the posterior ischia. The ilia lie dorsolaterally to these elements and articulate with the sacral ribs. In PIMUZ T58, the left ilium is well recognisable and it has not shifted far from its natural position (Figure 7). The fragmentary right ilium, on the other hand has been shifted far posteriorly to lie next to the right femur (Figure 8). I disagree with the identification of the pubic bone supposedly associated with the ischium in the interpretative drawing of PIMUZ T58 by Pinna (1992, figure 1). A pubic bone could not be identified with certainty anywhere on the stone slab. Only a small isolated armour plate was found in the place of the supposed ´pubis`. Anterior to this small isolated armour plate, the clear imprint of a transverse process is present, which was not noted before (Figure 7). The two ischia rotated and shifted posteriorly and to the right of their natural positions so that they now lie close to each other with the flat, strongly convex medial parts facing in opposite direction (Figure 8).

Main Carapace

The lateral outline of the main carapace can be inferred based on the specimens PIMUZ T58 and MSNM V458, whereas the anterior and posterior margins of the main carapace are not preserved sufficiently in any of the three specimens. Given the length of the transverse processes 1-12 and curvature of the dorsal ribs 3-12 in the juvenile specimen (Pinna 1980, 1992) and the well preserved festooned margin in PIMUZ T58 (Figure 6) consisting of enlarged pointed armour plates, the main carapace shield was round to slightly ovoid in shape (with the anteroposterior axis being only slightly shorter). In this regard, *C. hildegardis* had a length to width ratio of the carapace of approximately 0.93-0.95 (Table 1) most similar to the Chinese cyamodontoids *Psephochelys polyosteoderma* (Li and Rieppel 2002a, 2002b) and *Glyphoderma kangi* (Zhao et al. 2008). Note that these taxa carry only a main carapace shield but no separate pelvic shield. In *P. polyosteoderma* there are two tapering 'horns' or protrusions at the anterior margin of the carapace, laterally framing a narrow nuchal region and enclosing the pectoral girdle. However, these 'horns' or protrusions are not as strongly developed as the flange-like anterior lobes of the carapace of *Henodus chelyops* (Huene 1936, 1938). According to Zhao et al. (2008, figure 3) *Glyphoderma kangi* lacks tapering 'horns' or flange-like lobes and instead shows only two enlarged osteoderms framing a wide and gently concave nuchal region of the carapace.

Already noted by Peyer (1931; see also Rieppel 2002), the external (dorsal) surface of the dermal armour plates in the holotype PIMUZ T4763 has a granular texture and the elements are shallowly pitted (Figures 4, 5). The internal (visceral) surface of the plates, well visible in PIMUZ T58 (Figure 6.1), has a rough texture caused by elevated, often highly regularly arranged cross-hatching mineralized fibres (e.g., Westphal 1975, 1976; Pinna 1992; Rieppel 2002).

FIGURE 8. Close-up of pelvic, appendicular, and dermal armour elements of specimen PIMUZ T58 of *Cyamodus hildegardis*, the latter possibly pertaining to the tail region. (1) Photograph of specimen. (2) Interpretative sketch of skeletal elements. Colour code: brown: armour elements; purple: appendicular elements; grey: girdle elements; red: unidentified elements. Abbreviations: a: armour plates; fe: femur; il: ilium; is: ischium; ?: unidentified.

TABLE 1. Measurements of the main carapace armour in cyamodontoid placodonts. All values are based on straight measurements (rounded to the nearest full millimetre), not including carapace curvature. *: The carapace of *Placochelys placodonta* Jaekel, 1902 consists only of few fragments thus the given ratio is solely based on the interpretative drawing of the animal by Jaekel (1907: plate 10). Note that specimens MCSNB 8358 and BSP AS I 8 may give LC/WC ratios which are too low, based on their flattened taphonomic preservation.

Taxon and accession number	Length of carapace (LC)	Width of carapace (WC)	Ratio LC/WC	Measurements obtained from:
Cyamodus hildegardis (PIMUZ T58)	~215 mm / ~205 mm	~230 mm / ~215 mm	~0.93 / ~0.95	specimen , Figure 2 / Figure 10.1 (this paper)
Glyphoderma kangi (ZMNH M 8729)	243 mm	262 mm	0.93	Zhao et al. (2008, figure1, table 1)
Henodus chelyops (GPIT uncat., “specimen no. 3”)	640 mm	830 mm	0.77	Huene (1938, figures 5, 6, table); cast (this paper)
Placochelys? minutus (Gmr005)	142 mm	136 mm	1.04	Yin et al (2000, p. 12); see also Li and Rieppel (2002b, p. 407)
Placochelys placodonta (FAFI)	-	-	1.4* (7:5)	Jaekel (1907, plate 10)
Psephoderma alpinum (MCSNB 8358)	207 mm / 210 mm	254 mm / 253 mm	0.81 / 0.83	Pinna and Nosotti (1989, plate XXIX, p. 35) / Rieppel (2002, p. 16)
Psephoderma alpinum (MSNM V527)	250 mm	225 mm	1.11	Pinna and Nosotti (1989, plate XXVI, p. 35)
Psephoderma alpinum (BSP AS I 8)	375 mm / 375 mm	423 mm / 425 mm	0.89 / 0.88	Meyer (1858, plate 29, p. 246) / Rieppel (2002, p. 14)
Psephochelys polyosteoderma (IVPP V 12442)	265 mm	271 mm	0.98	Li and Rieppel (2002a, p. 157; 2002b, p. 404)
Sinocyamodus xinpuensis (IVPP V 11872)	130 mm	175 mm	0.74	Li (2000, plate 1); Li and Rieppel (2002b, p. 407)

Pelvic Shield

The pelvic shield is present in the holotype PIMUZ T4763 and the referred specimen PIMUZ T58. In the holotype, the right lateral margin of the pelvic shield is well preserved, whereas the left margin is partly missing (Figure 4). At the left margin, five enlarged triangular dermal plates are visible. The anterior and posterior margins of the pelvic shield are partly covered and fused to armour plates from the main carapace and plates from the caudal armour respectively, thus the exact borders of the shield are obscured. Within the pelvic shield, it is not possible to identify the delineation between individual osteoderms. As noted already by Peyer (1931), few dermal plates show a flat keel, which is generally oriented in anteroposterior fashion. In PIMUZ T58, the pelvic shield is seen in ventral view, so the main part of the internal organisation of the dermal plates is not visible. However, especially under strongly oblique light conditions (Figures 2.2, 7), the left and right crescent-shaped lateral margins of the pelvic shield are observable. The right part of the shield has been slightly disarticulated from the left part leaving a gap of about 30 mm. The anterior part of the right portion of the pelvic shield is partly hidden beneath four transverse processes and associated vertebrae as well as an isolated rib, which presumably shifted here from the posterior margin of the carapace region. As in the holotype, the margins of the pelvic shield are composed of enlarged triangular dermal armour plates (Figure 7). The left margin shows seven or possibly eight of these lateral plates. By rotating and translocating the right part of the pelvic shield back into its natural position, the anterior and posterior margins of the shield would be straight to very slightly concave (Figure 7). Ventral to the pelvic shield, three articulated and three isolated vertebrae and associated, more or less well preserved transverse processes were identified. A single bone fragment, presumably from a caudal centrum, lies directly adjacent to the posterior margin of the pelvic shield. The isolated pubis and ischium that according to Pinna (1992, figure 1) should be at least partly covered by the posterior margin of the pelvic shield, could not be identified here.

Caudal Armour

The caudal armour is best preserved in the holotype PIMUZ T4763. Only the posterior-most part of the tail and the last vertebrae and associated armour plates of the tip of the tail, and according to Peyer (1931) no more than three distal caudals, are missing. The tail is angled sharply towards the right, thus losing connection with the pelvic shield. A single squared isolated fragment of caudal armour and possibly associated underlying proximal caudals lies between the main part of the tail and the pelvic shield (Figure 5). Although no bone contact exists, the exact position of this armour piece is given by the exactly fitting sediment matrix (Peyer 1931).

The tail armour plates generally become reduced in size in an anteroposterior gradient. Because the tail of the specimen is inclined to the right side, its armour was embedded in left lateral view. On the right side of the caudal vertebrae, a dorsal row of posteriorly tapering armour plates is visible. Laterally, the tail was covered on its left and right side by a single row of tubercular armour plates, similar in size to the dorsal series. At the proximal part of the tail, the caudals are largely covered by the lateral row of dermal plates; only in the distal part of the tail the lateral plates have been dislocated enough to reveal the underlying caudal vertebrae exposed in left lateral view. Ventrally, the tail was armoured by an unpaired series of more tapering plates whose apices were sharply inclined towards posterior. Hemapophyses between this ventral series of armour plates and the caudal centra are not visible. Individual positions to the respective caudals and/or associated armour plates in the tail cannot be assigned with accuracy, because only the posterior-most caudals are visible, and a clear contact with the pelvic shield is missing.

Gastral Apparatus

As indicated by Pinna (1992, figure 2) the gastral apparatus, consisting of two lateral rows and a medial row of rod-like gastral ribs, is best preserved in the juvenile specimen MSNM V458. In PIMUZ T58, the other specimen exposing the ventral side, the arrangement of gastral ribs is largely disturbed. Pinna's (1992) assessment that the open v-shaped gastralia in PIMUZ T58 belong to the medial row is correct, whereas the only slightly recurved gastralia pertain to the lateral series.

DISCUSSION

The present study shows that the basic shape of the dorsal armour of the cyamodontoid *Cyamodus hildegardis* is much narrower than previously reconstructed, with the main carapace having the length-width ratios comparable to the new Chinese cyamodontoids, instead of that of the well-known European forms *Psephoderma alpinum* and *Henodus chelyops*. *C. hildegardis* was thus a medium-sized cyamodontoid placodont (Figure 9), which had a rather round carapace and a separate smaller ovoid and laterally expanded pelvic shield with straight to slightly concave anterior and posterior margins that mainly covered the pelvic region and the base of the tail. The rather short tail itself was armoured with prominent single dorsal and paired lateral series, as well as a more flattened ventral series of dermal plates, all becoming reduced in size in an anteroposterior gradient. Both the anterior shields carrying few enlarged spiked armour plates as well as the armoured tail lend this species a well-fortified character at least as adults. Without new fossil specimens, however, the internal structures and arrangement of the dermal armour of *C. hildegardis* still remain poorly known to date.

Main Carapace

Because of superficial similarities, the armour of *Cyamodus hildegardis* is often compared to that of *Psephoderma alpinum*, and reconstructions of the former often refer to the latter, a well-known species from the Upper Triassic. However, based on the new interpretations and carapacial length-width ratios presented herein, *P. alpinum* might not

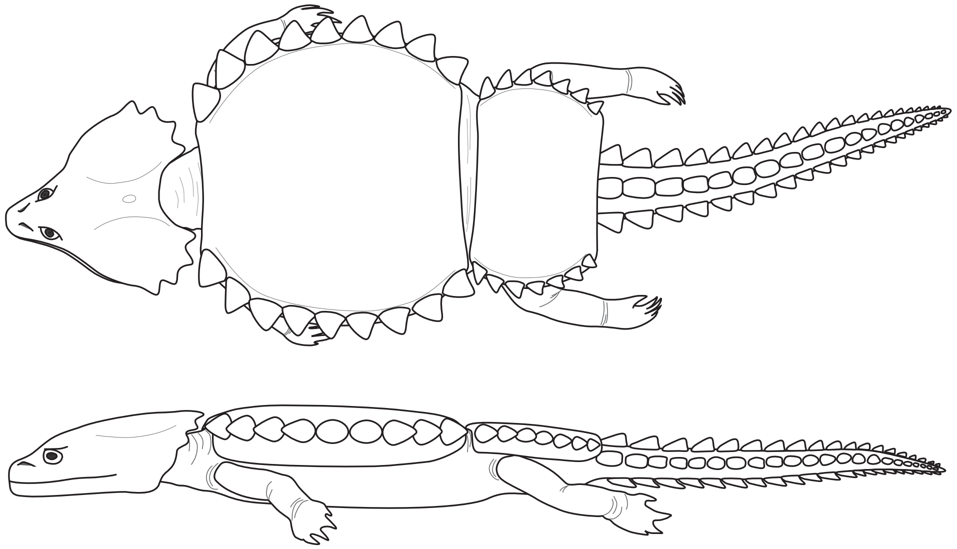

FIGURE 9. New interpretative life reconstruction of *Cyamodus hildegardis*. Skeletal proportions are taken from the holotype specimen PIMUZ T4763 and referred specimen PIMUZ T58. Note that the autopodials are not known for this species.

be such a good reference model for the reconstruction of the postcranium and overall body shape of *C. hildegardis*, as maybe *Glyphoderma kangi* and *Psephochelys polyosteoderma* from China, although these so far lack a separate hip shield. Although several complete or well articulated specimens of *P. alpinum* are known, the carapace appears dorsoventrally compacted during fossilisation in most of these specimens (Meyer 1858: BSP AS I 8; Pinna and Nosotti 1989: MCSNB 8358; Renesto and Tintori 1995: ST82003 stored in the Museo della Vicaria di S. Lorenzo, Zogno, Bergamo, Italy), resulting in a much broader appearance of the carapace than in life. In their emended diagnosis for *Psephoderma*, Renesto and Tintori (1995: p.39) stated the main carapace to be “rounded, stout, wide and very flat […]”. Because only the length of 420 mm and not the carapace width was given for specimen ST82003 in that paper, it is not listed in Table 1. Other specimens, however (e.g., Pinna and Nosotti 1989: MSNM V527; undescribed specimen in PIMUZ, H. Furrer, personal commun.), show much less lateral extension of the carapace, resulting in a more anteroposteriorly elongated oval body shape (Pinna and Nosotti 1989, pl. XXVI, XXVII). This is also underlined by the well articulated gastral apparatus in MSNM V527, indicating that the carapace was not broadly expanded. It cannot be ruled out, however, that intraspecific, ontogenetic, or sexual dimorphic variation instead of (or in addition to) taphonomic compaction is at least partly responsible for the different carapace shapes in these specimens as well. Until new material is discovered that clearly indicates the association of the main dermal armour and underlying skeletal elements, it is hypothesized that the three dimensionally preserved specimens like MSNM V527 are better suited for skeletal reconstruction in *P. alpinum*. In contrast to the condition seen in *P. alpinum* (Pinna and Nosotti 1989), the main outline of the carapace in *C. hildegardis* is interpreted to be round to slightly ovoid.

For the schematic reconstruction of *C. hildegardis*, though, a fairly broad carapace was previously hypothesized with a length-width ratio of about 0.7 (Pinna 1992, figure 19); a value that is lower even than that for *H. chelyops* (Table 1). Furthermore, based on these differences in the development and orientation of armour, it cannot be implied that the same endoskeletal regions are covered by armour in *C. hildegardis* and *P. alpinum* (Pinna and Nosotti 1989: posterior cervicals to sacral 1).

Pelvic Shield

The pelvic shield is situated posterior to the carapace in *Cyamodus hildegardis*, but again it is not sure whether the same endoskeletal regions are covered as in *Psephoderma alpinum* (Pinna and Nosotti 1989: sacral 3 to caudal 8). In *C. hildegardis*, at least part of the sacrum is covered by the pelvic shield, but as the shield is much narrower, it cannot cover the proximal tail region back to the eighth caudal. Pinna (1992, p.13) assumes that “[…] la seconda vertebra caudale occupi lo spazio non corazzato compreso fra questi due margini,” meaning the second caudal vertebra occupies the non-armoured space comprised between the posterior edge of the carapace and the anterior edge of the pelvic shield. This assumption would indicate, however, that the complete sacrum is covered by the main carapace, and only the proximal tail region is covered by the pelvic shield. Assuming that Pinna (1992) actually meant ‘second sacral’ instead of ‘second caudal’, the pelvic shield would then have covered almost the same portions of the sacrum and the tail as reported by Pinna and Nosotti (1989) for *P. alpinum*.

Although the articulated vertebral centra and associated fragmentary lateral bones below the pelvic shield cannot be unambiguously identified as sacrals and sacral ribs, it is still plausible to hypothesise that the complete pelvic shield and the associated vertebral elements were dislocated posteriorly, thus slightly opening up the natural gap between the main carapace and the pelvic shield. This condition is in accordance with previous assessments that fossils of the Monte San Giorgio locality can show signs of disturbance either by light bioturbation, wave action, synsedimentary slumpings or diagenetic pressure compaction of the sediment (Tintori 1992; Röhl et al. 2001; Rieppel 2002).

Pectoral and Pelvic Girdles

In contrast to the interpretative drawing in Pinna (1992, figure 1), more elements pertaining to the vertebral column in PIMUZ T58 could be identified associated with the pelvic shield, whereas elements previously identified as belonging to the pelvic and pectoral girdles are either not observable or have been misidentified (Figures 6-8). In PIMUZ T58, only the scapulae are well recognisable, whereas armour plates of the marginal series of the carapace have been misidentified as coracoids. The position and the size and shape of the bones both argue against the presence of coracoids in this matter. Other elements of the pectoral girdle might be present as well, but they are too poorly preserved to be identified with confidence.

Although often fragmentary, the ilia and ischia are preserved, but no pubic bone could be identified. It is not clear why the pubes and coracoids, both thin, large flat bones in *C. hildegardis* (e.g., Pinna 1980), are not identified in PIMUZ T58. Hypothetically, because of the flattened shape and ventral position in the animal, these bones could have been more easily disturbed and dislocated than other girdle elements, and thus, might not be preserved on the slab with the rest of the skeleton. Alternatively, due to their thin nature, the bones could be present but are too severely crushed and obscured by overlying or underlying postcranial elements or fragments of armour. Based on the PIMUZ specimens, shape and size of the pubic bones and the coracoids thus cannot be inferred, and Pinna’s (1980) reconstruction of the pelvic and pectoral girdles in the juvenile specimen MSNM V458 has to be consulted instead.

Tail Armour

Pinna (1992) and Rieppel (2002) agree that the dorsal part of the tail is covered by a median row and two lateral rows of armour plates. However, Rieppel interpreted the elements of the lateral series to be enlarged, whereas Pinna identifies only smaller elements whose positions are not exactly known as belonging to the lateral series. Here Rieppel’s (2002) identification of larger plates in the lateral series is confirmed and Pinna’s interpretation is attributed to a misidentification of caudal vertebral centra as lateral armour plates in the proximal part of the tail (Pinna 1992, figure 21: v10-v16).

Following Pinna (1992) the ventral series of the tail was also covered by a row of armour plates, whereas the presence of chevron bones in the holotype PIMUZ T4763 commented upon by Peyer (1931) could not be confirmed. Chevron bones, if present, would be rather slender elements situated below the posterior edge of the vertebral centra; however, the only bones lying ventral to the caudal centra are the massive posteriorly tapering elements identified as dermal tail armour herein. These plates are positioned below the anterior edges of the vertebral centra, respectively. If hemapophyses are present in the more proximal part of the tail, they are completely obscured by the large overlying armour plates.

Novel Interpretation of the Postcranial Skeleton and Associated Armour

Based on the data and discussion presented herein, a new hypothetical association between the reconstructed skeleton and the dermal armour of *C. hildegardis* is proposed (Figure 10.1). According to this new interpretation, the round to ovoid main shield covers the main trunk of the animal from about the first to the 1n dorsal. If the posterior mar-

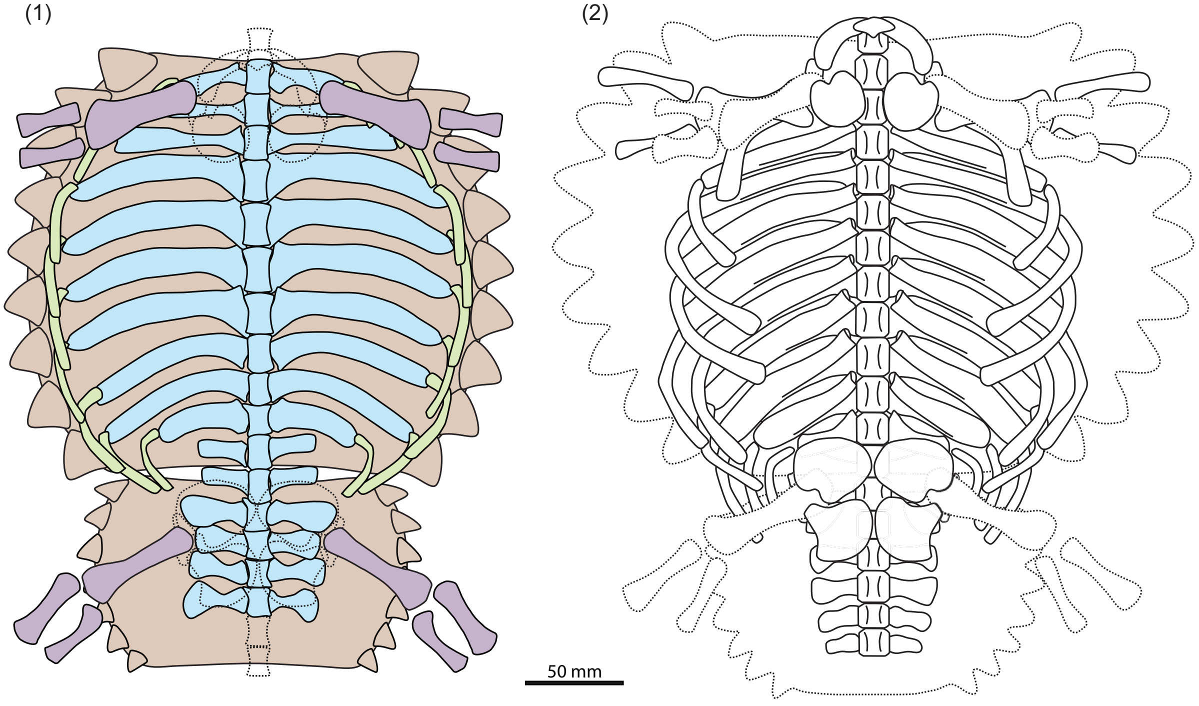

FIGURE 10. Comparison of the novel (1) vs. previous (2) interpretations of the postcranial skeleton and associated armour of *Cyamodus hildegardis*. (1) In the novel interpretation, the shape of the round main carapace shield is interpreted to be roughly mirrored by the transverse processes and associated ribs. Note that the shapes of these skeletal elements were adapted from PIMUZ T58, thus they are not shown in a strictly ventral view. Dorsal 11 and 12 are reconstructed without ribs, thus the total number of ribs shown mirrors the numbers shown in Pinna (1980, figure 1). The pelvic shield covers the complete sacral region and the base of the tail roughly up to caudal 3. The gap between the armour shields lies at the level of dorsal 12. The positions of the pectoral and pelvic girdles (adapted from Pinna 1980, figure 1), as well as a cervical and two caudal centra are indicated by dotted lines. (2) Previous reconstructions of the postcranial skeleton (adapted from Pinna 1980, figure 1; solid lines) and overall armour shape (adapted from Pinna 1992, figure 19; dotted lines). The interpretative sketch of the skeleton based on the juvenile specimen MSNM V458 has been simply superimposed and scaled to the same size (based on humerus proportions) as the armour shape based on the older specimens. Following these sketches, the main carapace would cover the trunk region from dorsal 1 to sacral 1, whereas the pelvic shield covers the area from sacral 3 to at least caudal 6. Otherwise, the main carapace is too wide to show a closer association with the underlying endoskeletal elements. Note the differences in the proportions of the zeugopodial elements. For colour coding of elements see Figures 6-9. (A greyscale version of this figure is also available).

gin of the main carapace would be reconstructed with a convex margin instead of a straight or slightly concave one, the main armour might also span onto the 12th dorsal. The width of the main carapace is basically reflected by the length of the transverse processes plus ribs. Measuring the length of the transverse processes plus associated ribs at dorsal 6, the carapace has a maximum width of approximately 215 mm. As mentioned before, the length of the main carapace is more difficult to assess. A first approximation, however, can be given by taking the length of the dorsal vertebral centra associated with the carapace as a proxy. Those centra of PIMUZ T58 preserved in ventral view (dorsals 2-4, 8-9?; sacrals 1-3?, caudal 1?) range between 15 and 22 mm (average 18.5) in length indicating a carapace length (for eleven dorsals) of approximately 205 mm. Although these numbers should be regarded with caution, they overall fit the measurements taken directly at the specimen, leading to similar length-width ratios in both approaches (see Table 1). The pelvic shield is interpreted to cover partly dorsal 12, the complete sacrum and the base of the tail roughly to caudal 3 (Figure 10.1).

A similar comparison (Figure 10.2) of previous interpretative reconstructions of *C. hildegardis* based on Pinna (1980, figure 1: skeletal reconstruction based on the juvenile specimen MSNM V458; 1992, figure 19: schematic reconstruction of overall body shape), yielded no close association between dermal armour and the underlying skeletal elements. By simply overlaying and scaling the drawings to the same size (based on humerus length), however, it became apparent that Pinna (1992) most probably meant the sacral 2 and not caudal 2 when identifying the position of the gap between the main carapace and pelvic shield. Apart from this, the sketches of the zeugopodial elements were found to be disproportionally large in the skeletal drawing based on the juvenile specimen. It could be that the zeugopodial elements have been misidentified in MSNM V458 by Pinna (1990), leading to skeletal reconstructions of these elements which are only marginally shorter than the humerus. This observation is further strengthened by the fact that the larger (and heavier) humerus has been dislocated significantly to the posterior trunk region, whereas the supposed (lighter) zeugopodial elements remained close to their natural position in the anterior trunk region.

CONCLUSIONS

The new interpretation of the relationship between endoskeletal postcranial elements and associated dermal armour and the resulting life reconstruction of *C. hildegardis* will serve to better understand and explain future findings of cyamodontoid placodonts. It is hypothesised that these new data will have implications for future comparative biomechanical, i.e., on locomotion, and systematic studies of placodonts, especially in comparison to the well preserved cyamodontoids from China.

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REFERENCES

Diedrich, C. 2009. The vertebrates of the Anisian/Ladinian boundary (Middle Triassic) from Bissendorf (NW Germany) and their contribution to the anatomy, palaeoecology, and palaeobiogeography of the Germanic Basin reptiles. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 273:1-16.

Furrer, H. 2003. Der Monte San Giorgio im Südtessin - Vom Berg der Saurier zur Fossil-Lagerstätte internationaler Bedeutung. *Neujahrsblatt, Naturforschende Gesellschaft in Zürich,* 206:1-64.

Gregory, W.K. 1946. Pareiasaurs versus placodonts as near ancestors to the turtles. *Bulletin of the American Museum of Natural History,* 86:275-326.

Jaekel, O. 1907. Placochelys placodonta aus der Obertrias des Bakony. *Resultate der Wissenschaftlichen Erforschung des Balatonsees, 1. Band. 1. Teil. Paläontologischer Anhang III. Band* (7):1-91.

Jaekel, O. 1907. *Placochelys placodonta* aus der Obertrias des Bakony. *Resultate der Wissenschaftlichen Erforschung des Balatonsees, 1. Band. 1. Teil. Paläontologischer Anhang III. Band (8):*1-91.

Kuhn-Schnyder, E. 1964. Die Wirbeltierfauna der Tessiner Kalkalpen. *Geologische Rundschau,* 53:393-412.

Kuhn-Schnyder, E. 1979. *Die Fossilien des Monte San Giorgio. Führer zum Paläontologischen Museum Meride (Kt. Tessin)*.

Li, C. 2000. Placodont (Reptilia: Placodontia) from Upper Triassic of Guizhou, Southwest China. *Vertebrata PalAsiatica,* 38:314-317. (in Chinese with English summary)

Li, C. and Rieppel, O. 2002a. A new cyamodontoid placodont from Triassic of Guizhou, China. *Chinese Science Bulletin,* 47:156-159. (in Chinese)

Li, C. and Rieppel, O. 2002b. A new cyamodontoid placodont from Triassic of Guizhou, China. *Chinese Science Bulletin,* 47:403-407.

Münster, G. 1839. *Beiträge zur Petrefaktenkunde, mit XVIII nach der Natur gezeichneten Tafeln der Herren Hermann v. Meyer und Professor Rudolph Wagner.* Buchner'sche Buchhandlung, Bayreuth.

Naish, D. 2004. Fossils explained 48 - Placodonts. *Geology Today,* 20:153-158.

Nosotti, S., and Pinna, G. 1993. *Cyamodus kuhn-schnyderi* n. sp., nouvelle espèce de Cyamodontidae (Reptilia, Placodontia) du Muschelkalk supérieur allemand. *Comptes Rendus de l'Academie des Sciences Paris Série II,* 317:847-850.

Nosotti, S. and Pinna, G. 1996. Osteology of the skull of *Cyamodus kuhnschnyderi* Nosotti & Pinna 1993 (Reptilia, Placodontia). *Paleontologia Lombarda, Nuova serie,* 6:3-42.

Nosotti, S., and Teruzzi, G. 2008. I rettili di Besano-Monte San Giorgio. *Natura,* 98(2):1-99.

Peyer, B. 1931. Die Triasfauna der Tessiner Kalkalpen III. Placodontia. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft,* 51:1-25.

Peyer, B. 1944. *Die Reptilien vom Monte San Giorgio*. Naturforschende Gesellschaft in Zürich, Neujahrsblatt, Gebr. Fretz AG, Zürich.

Peyer, B. and Kuhn-Schnyder, E. 1955. Placodontia, p. 459-486. In Piveteau, J. (ed.), *Traité de Paléontologie*. Masson et Cie, Paris.

Pinna, G. 1980. Lo scheletro postcraniale di *Cyamodus hildegardis* Peyer, 1931 descritto su un esemplare del Triassico Medio Lombardo (Reptilia Placodontia). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 121:275-306.

Pinna, G. 1990. *Protenodontosaurus italicus* n.g., n.sp., un nuovo placodonte del Carnico italiano. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 131:5-12.

Pinna, G. 1992. *Cyamodus hildegardis* Peyer, 1931 (Reptilia, Placodontia). *Memoire della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 26:1-21.

Pinna, G. 1999. *Placodontia (Reptilia Triadica). Fossilium Catalogus Animalia, Pars. 136*. Backhuys Publishing, Leiden.

Pinna, G. and Nosotti, S. 1989. Anatomia, morfologia funzionale e paleoecologia del rettile placodonte *Psephoderma alpinum* Meyer, 1858. *Memoire della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 25:17-50.

Renesto, S. and Tintori, A. 1995. Functional morphology and mode of life of the Late Triassic placodont *Psephoderma alpinum* Meyer from the Calcare di Zorino (Lombardy, N Italy). *Rivista Italiana di Paleontologia e Stratigrafia,* 101(1):37-48.

Rieppel, O. 2000. Sauropterygia I - Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. *Handbuch der Paläoherpetologie / Handbook of Paleoherpetology,* 12A:1-134.

Rieppel, O. 2001. The cranial anatomy of *Placochelys placodonta* Jaekel, 1902, and a review of the Cyamodontoidea (Reptilia, Placodonta). *Fieldiana: Geology, New Series,* 45(1514):1-104.

Rieppel, O. 2002. The dermal armor of the cyamodontoid placodonts (Reptilia, Sauropterygia): morphology and systematic value. *Fieldiana: Geology, New Series,* 46(1517):1-41.

Röhl, H.-J., Schmid-Röhl, A., Furrer, H., Frimmel, A., Oschmann, W., and Schwark, L. 2001. Microfacies, geochemistry and palaeoecology of the Middle Triassic Grenzbitumenzone from Monte San Giorgio (Canton Ticino, Switzerland). *Geologia Insubrica,* 6:1-13.

Tintori, A. 1992. Fish taphonomy and Triassic anoxic basins from the Alps: a case history. *Rivista Italiana Paleontologia e Stratigrafia,* 97(3-4):393-408.

von Huene, F. 1936. Henodus chelyops, ein neuer Placodontier. *Palaeontographica, Abt. A,* 84:99-148.

von Huene, F. 1938. Der dritte *Henodus*. Ergänzungen zur Kenntnis des Placodontiers *Henodus chelyops* Huene. *Palaeontographica, Abt. A,* 89:105-114.

von Meyer, H. 1858. *Psephoderma alpinum* aus dem Dachsteinkalke der Alpen. *Palaeontographica,* 6:246-252.

Westphal, F. 1975. Bauprinzipien im Panzer der Placodonten (Reptilia triadica) - Principles of structure and growth in the dermal armor of placodonts (Reptilia triadica). *Paläontologische Zeitschrift,* 49(1/2):97-125.

Westphal, F. 1976. The dermal armour of some Triassic placodont reptiles, p. 31-41. In Bellairs, A.d.A. and Cox, C.B. (eds.), *Linnean Society Symposium Series No. 3. Morphology and Biology of Reptiles.* Academic Press, London.

Yin, G., Zhou, X., Cao, Z., Yu, Y., and Luo, Y. 2000. A preliminary study on the early Late Triassic marine reptiles from Guanling, Guizhou, China. *Geology-Geochemistry,* 28(3):1-23. (in Chinese with English summary)

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

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