Humerus morphology and histology of a new marine reptile (Diapsida) from the Muschelkalk-Keuper-Grenzbonebed (Middle Triassic, Ladinian) of Southwest Germany

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Abstract

A survey in the collection of the Muschelkalkmuseum Ingelfingen revealed a growth series of five humeri from the Grenzbonebed collected from localities in northeastern Baden-Württemberg (Southwest Germany). The Grenzbonebed is a tempestitic condensation horizon at the base of the Keuper that contains prefossilized vertebrate fossils reworked during a 100 ka minor sedimentary cycle. The humeri share a unique but simplified morphology due to adaptation to aquatic life. They are very robust and pachyostotic and have a dorsopreaxially elongated margin, a massive and ventrally protruding triangular proximal head as well as a preaxially slanted asymmetrical distal end. A detailed morphological comparison with humeri of other Triassic marine reptiles showed that they differ from humeri of all known taxa, including those of placodonts such as Paraplacodus, Placodus, Cyamodus, and Henodus. However, an analysis of the bone microstructure and histology revealed a close relationship with the humeri of Cyamodus, despite of distinct morphological differences. The five humeri and humeri of Cyamodus share a plexiform radiating fibro-lamellar bone tissue with moderate to high vascular density in the middle and outer cortex and a poorly developed medullary region, indicating osteosclerosis. Contrary to the pachyostotic humeri from the Grenzbonebed, Cyamodus humeri are not pachyostotic, thus suggesting different modes of locomotion in a similar shallow marine environment. The histological features of the pachyostotic humeri from the Grenzbonebed, which could point to placodont or pistosauroid affinities, respectively, are no reliable phylogenetic markers because convergent evolution of bone tissue is common among aquatic vertebrates sharing a similar environment and life style. Due to the unique humerus morphology the establishment of a new taxon, Horaffia kugleri gen. et sp. nov., is justified, although the remains are too poor to include them into a phylogenetic analysis or to assign them to a certain group.

K e y w o r d s : Germanic Basin, environment, bone histology, pachyosteosclerosis, radiating fibro-lamellar bone, high vascular density.

1. Introduction

Marine reptiles, especially Sauropterygia, were diverse and abundant faunal elements in the Middle Triassic of the western and eastern Tethys and in various epicontinental Peri-Tethys basins. Although the fossil sites have been intensively studied for more than 150 years in the Central European Basin and for some 50 years in South China (summarized in RIEPPEL 2000; LI 2006) the last decade has produced a number of new marine reptile taxa, which mainly originated from the Middle Triassic of the eastern Tethys (e.g., LI & RIEPPEL 2002; LI et al. 2011; LIU et al. 2011; JIANG et al. 2008a, b; ZHAO et al. 2008; SHANG et al. 2011; CHENG et al. 2012a, b; LI et al. 2013). However, also in the early Anisian Muschelkalk of Winterswijk (The Netherlands) three new taxa were recently discovered (KLEIN & SCHEYER 2013; NEENAN et al. 2013; KLEIN & SICHELSCHMIDT 2014), indicating that our knowledge of Triassic marine reptile diversity is still incomplete.

The black shale deposits of the Alpine and Chinese Triassic produced a high number of articulated skeletons, whereas the Germanic Basin yielded mostly isolated bones, many of them originating from condensation horizons, the classical Muschelkalk and Lower Keuper bone beds. Thus, alpha taxonomy of Middle Triassic Sauropterygia from the Germanic Basin is mostly based on skull morphology and postcranial material is reliably assigned only for a few taxa (summarized in RIEPPEL 2000a; KLEIN 2012). Taxonomic assignment is additionally hampered because many taxa (i.e., Eosauropterygia) have a similar postcranial morphology, because of morphological changes during ontogeny, and because of an assumed high intraspecific variability. However, if adequate samples are available, long bone histology can contribute to clarify the taxonomic status of sauropterygian postcranial material (e.g., KLEIN 2010, 2012; SANDER et al. 2013).

The Muschelkalkmuseum Ingelfingen (MHI) holds five humeri collected in quarries near Crailsheim and Vellberg along the Jagst and Bühler rivers (Baden-Württemberg, Southwest Germany) exposing the Muschelkalk-Keuper boundary bone bed ("Grenzbonebed"). The humeri exhibit a very characteristic morphology, which differs from all previously known taxa. It is the aim of the current paper to describe and compare their morphology and bone histology.

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2. Geological background: The Muschelkalk/Keuper Grenzbonebed

During late Anisian/early Ladinian times the sea level was high enough to flood wide areas of the Germanic Basin and to provide persistent marine conditions, which enabled diverse invertebrate and vertebrate palaeocommunities with high individual numbers to inhabit the Upper Muschelkalk Sea. Many fossil sites in natural and artificial outcrops of the Upper Muschelkalk limestones are thus quite productive and have yielded thousands of isolated marine reptile bones, mainly of Sauropterygia (placodonts, pachypleurosaurs, nothosaurs, pistosaurs) that accumulated within 200 years of collecting (HAGDORN 1988; HAGDORN & RIEPPEL 1998). During the early late Ladinian (early Longobardian), the Germanic Basin was influenced by changing sea levels and sedimentation rates that caused several minor sedimentary cycles with changing deltaic, limnic, and brackish conditions and short marine incursions (NITSCH 2005). During this interval, the Lower Keuper (Erfurt Formation, Lettenkeuper) marlstones, sandstones and dolomitic marls were deposited, which contain the famous vertebrate Lagerstätten of Gaildorf, Kupferzell, and Vellberg (SCHOCH 2002).

In Southwest Germany, the boundary between Muschelkalk and Keuper is defined by the base of the Fränkische Grenzschichten. This dark grev - or brownish in weathered condition - vertebrate sand (REIF 1971, 1982) is interpreted as a tempestitic condensation horizon unconformably overlying the 100 ka minor cycle of the Wimpfen Member of the Meißner Formation) (Fränkische Grenzschichten) (REIF 1971, 1982). In the Crailsheim and Rothenburg area the Grenzbonebed reaches a maximum thickness of up to 20 cm and replaces the entire Wimpfen Member. Towards the basin center, it becomes gradually thinner and the Wimpfen Member becomes thicker and eventually reaches its complete thickness of more than 3 m near Heilbronn (WAGNER 1913; REIF 1974; HAGDORN & SIMON 2005). The vertebrate and guartz sands of the Crailsheim Grenzbonebed were accumulated during a time span of 100 ka.

According to HAGDORN & REIF (1988), the 30 nominal taxa of the Crailsheim Grenzbonebed vertebrate fauna, which has also produced the here described pachyostotic

Table 1. Measurements (mm) and histological features of *Horaffia kugleri* an *Cyamodus* humeri (*). The percentage value of the medullary region was measured in diameter along the long axis of the sample in pre-postaxial direction. The maximum number of growth marks was counted postaxially in polarized light. Bc= bone compactness.

specimen number	length	prox. width prox. length	midshaft width midshaft length	distal width distal length	peri- meter	sampling location	size of the med. reg.	max. number of growth marks	bc (%)
MHI 2112/1	77.6	23.4/12.3	18.2/12.5	29/9.7	50	prox. to midshaft	10% 16.5%	5(?6) 5	87.2
MHI 2112/2	>111	31.4/29.2	21.9/16.7	~33.4/19.7	65	distal to midshaft	27.3% 38.6%	5(?6) 5 (inner one remodeled)	83.8
MHI 2112/3	134	36.5/39.5	28.8/21.8	50.4/27.1	82	photo of cross sec.	nm	?6	_
MHI 2112/5	146.5	43.7/49.7	34.8/25.4	53.3/29.9	98	micro CT scan	33.3%	?6	-
MHI 2112/4	152	42/37.8	32/20	55.2/20.1	92	prox. to midshaft	16.6%	5	82.7
*MHI 2112/6	~205	>38/>49.5	35.2/23.5	64.2/27.8	96	midshaft	~3.5%	5-7	84.7
*SMNS 54569	>129	61/38	35/23	nm/nm	92	prox. to midshaft	12%	6–7	87.1

	Length/ Distal width	Proximal width/ Distal width	Minimal width/ Distal width
*Nothosaurus	3.3–4.8	0.7–1.2	0.6-0.9
*Simosaurus	4.2-5.9	0.8–1.2	0.5-0.7
*Cyamodus/Placodus	2.7–3.5	0.6–1.0	0.4-0.6
Placodus (n=3)	2.9–3.6	0.58-0.88	0.48-0.59
Cyamodus (n=8)	2.2–3.57	0.67–0.94	0.42-0.68
Horaffia (n=5)	2.6-3.3	0.76-0.94	0.57-0.65

Table 2. Test of humerus proportions as established by RIEPPEL (1995: table 1). *Proportions of the humerus in *Cyamodus/Placodus* (n = 9), *Nothosaurus* (n = 35), *Simosaurus* (n = 9) copied from RIEPPEL (1995: table 1). Columns without an * were newly added. Because of the absence of specimen numbers in RIEPPEL's table 1 overlap of measured *Cyamodus/Placodus* specimen is possible.

humeri, are marine or limnic. Contrary to certain Lower Keuper bone beds, it does not contain terrestrial elements. The tetrapods are represented by abundant Eusauropterygia (Nothosaurus mirabilis, N. giganteus, Simosaurus), rare Pachypleurosauria, Placodontia (cyamodontoid tooth fragments), vertebrae of the enigmatic Blezingeria, and remains of Prolacertiformes (Tanystropheus) (HAGDORN & REIF 1988). Ichthyopterygia, Pistosaurus, and Placodus have not been found; according to HAGDORN & RIEPPEL (1998), they had already disappeared after the maximum flooding above the *postspinosus* biozone. So far, the Grenzbonebed has yielded neither diagnostic Cyamodus material nor armor fragments of the cyamodontoid Psephosaurus, which are frequently found in the upper Lettenkeuper (RIEPPEL 2000a; SCHEYER 2007). Among the temnospondyl amphibians, Plagiosternum is rather common while Mastodonsaurus and Plagiosuchus are rarer. Several upsection thin bone beds - e.g. the bone bed at the top of the marine Blaubank – contain a similar fauna.

3. Material and methods

The humeri stored in the collection of the Muschelkalkmuseum Ingelfingen (MHI) were recovered in quarries exposing the Grenzbonebed in the vicinity of Crailsheim: MHI 2112/1 Satteldorf-Barenhalden, abandoned Feldner quarry; MHI 2112/2 Vellberg-Eschenau, Schumann quarry; MHI 2112/3 Crailsheim-Tiefenbach, abandoned Härer guarry; MHI 2112/4 Obersontheim-Ummenhofen, Schneider quarry; MHI 2112/5 Obersontheim-Ummenhofen, Schneider quarry. For comparison, humeri of the placodonts Cyamodus and Placodus from the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Muschelkalkmuseum were measured and sampled. The morphological description follows the terminology of Rieppel (1994) and BICKELMANN & SANDER (2008). Measurements were taken with a digital calliper and are listed in Table 1. Bone proportions were compared according to RIEPPEL (1995: table 1) but revealed no significant results (Table 2). Histological samples were produced from MHI 2112/1, MHI 2112/2, MHI 2112/4 and from two Cyamodus humeri (SMNS 54569 and MHI 2112/6). If possible, bones were sampled exactly at midshaft by cutting an entire cross section. In some specimens, sampling location is proximal or distal to the midshaft on account of preservation at midshaft (Table 1). After cutting, the sampled bones were reassembled with plaster (Fig. 1). The samples were cut with a Buehler® Isomet3000 diamond rock saw. The thin sections were ground and polished to a thickness of about 60-80 µm using wet SiC grinding powders (SiC 600, 800). Thin sections were then studied with a Leica® DMLP compound polarizing microscope, equipped with a digital camera, a Leica® DFC 420C. Cross-sections were scanned with an Epson V740 PRO high-resolution scanner (Fig. 4a-c, f, g). The bone histological terminology follows FRANCILLON-VIEILLOT et al. (1990) [But see STEIN & PRONDVAI (2013) for the recently upcoming discussion on the nature of woven bone and its contribution to the fibro-lamellar complex]. MHI 2112/3 has an old fracture at midshaft; a photograph was taken from that region before gluing it again (Figs. 1c, 4d).

The midshaft of MHI 2112/5 was micro-CT scanned with a v|tome|x s by GE phoenix|x-ray at the Steinmann Institute of Geology, Mineralogy and Paleontology (StIPB) at a voxel size of 43.79 μ m. The micro-CT data were processed into image stacks using VGStudio MAX 2.0 software from Volume Graphics GmbH. After manipulating pictures from the image stack with Adobe Photoshop, gross microstructure such as vascular density and, to a restricted amount, vascular organization as well as growth marks could be identified (Fig. 4e). For further information on conventional (non-synchrotron) micro-CT scans and their direct comparison with thin sections from the same samples and sampling location see KONIETZKO-MEIER & SCHMITT (2013).

Bone compactness (bc) was analyzed with pixel counting computer program (©P. GÖDDERTZ, StIPB).



Fig. 1. Photographs of the pachyostotic humeri of *Horaffia kugleri* gen. et sp. nov. from the Grenzbonebed of northeastern Baden-Württemberg; **a**: Right humerus MHI 2112/4 Obersontheim-Ummenhofen (Schneider quarry); **b**: Left humerus MHI 2112/5 (holo-type) Obersontheim-Ummenhofen; **c**: Left humerus MHI 2112/3 Crailsheim-Tiefenbach (abandoned Härer quarry); **d**: Right humerus MHI 2112/2 Vellberg-Eschenau (Schumann quarry); **e**: Left humerus MHI 2112/1 Satteldorf-Barenhalden (abandoned Feldner quarry); **1**: Dorsal view; **2**: Ventral view; **3**: Postaxial view; **4**: Preaxial view. The white plaster band in a, d, and e marks the histological sampling location.

4. Systematic palaeontology

Diapsida Osborn, 1903

Horaffia kugleri gen. et sp. nov. Figs. 1–2, 4–6

Etymology: After the nickname "Horaffen" of the Crailsheim citizens that dates back to an episode in the "Städte-krieg" (War of the Cities) of 1449–1450.

Holotype: Left humerus MHI 2112/5, Muschelkalkmuseum Ingelfingen (Germany).

Referred material: Humeri MHI 2112/1, MHI 2112/2, MHI 2112/3, MHI 2112/4.

Ty pe locality: Obersontheim-Ummenhofen, Schneider quarry (County Schwäbisch Hall, Baden-Württemberg, Germany).

Type horizon: Muschelkalk-Keuper-Grenzbonebed, basal Erfurt Formation (Middle Triassic, early late Ladinian). D i a g n o s i s: Pachyosteosclerotic humerus with a simple morphology; proximal head dorsopreaxially elongated resulting in a triangular form; proximal head postaxially with a massive protrusion pointing ventrally (?deltopectoral crest); preaxially slanted asymmetrical distal end. Primary bone tissue is radiating fibrolamellar bone; bone compactness is between 82.7 and 86.8%.

Morphological description: The humeri of the new taxon, independent of their size, are massive bones with a rather simple pachyostotic morphology. Therefore their volume had increased and they have a swollen appearance (Figs. 1, 2). The bone surface is smooth except for the proximal and distal ends, which are both finely striated (Figs. 1, 2a1, b1). The midshaft area is constricted with a distinctly curved postaxial margin and a straight preaxial margin (Figs. 1, 2). The dorsal side is flat or slightly convex whereas the ventral side has proximally a distinct protruding ridge, which gives the ventral side a concave appearance (Figs. 1, 2c, d). The proximal width is always somewhat shorter when compared to



Fig. 2. Photograph and outline sketch of the holotype of *Horaffia kugleri* gen. et sp. nov. (left humerus, MHI 2112/5) from the Grenzbonebed of Obersontheim-Ummenhofen (Schneider quarry) with the main morphological features marked; **a1**, **a2**: Ventral view; **b1**, **b2**: Dorsal view; **c1**, **c2**: Postaxial view; **d1**, **d2**: Preaxial view. Note the dorsopreaxially elongated and pointed margin, which results in a triangular form of the proximal head (black arrow in c1). The proximal articulation facet spans from the dorsal to the ventral side (grey area in a2- d2) and is partially surrounded by a well set off margin (white arrows in b1 and c1). Note the distal articulation facet (Fig. 2b, c). The distal articulation facet is broadest at the preaxial bone side and is distinctly slanted (b). Abbreviations: dpc = deltopectoral crest; sldaf = slanted distal articulation facet.

the distal width but the proximal length is always much longer than the distal length (Table 1). The massive proximal head forms an acute triangle with an elongated and pointed dorsopreaxial margin (Fig. 2c1, black arrow). The proximal head has a distinct articulation facet spanning from the dorsal to the ventral side, which is best visible in postaxial view (Fig. 2c2, grey area). The articulation facet is well set off at the ventral and postaxial side of the bone by a distinct margin (Fig. 2b1, c1, white arrows). The rugose surface of the articulation facet gives evidence for a cartilage cap that was thick and strongly connected to the bone. The articulation facet is dorsopreaxially pointed (following the shape of the proximal head) and does not continue to the preaxial side (Fig. 2c). At the ventral side, the articulation facet is shorter but much broader than the preaxial side. In this region, the humerus is thickest and this area might represent the deltopectoral crest (Fig 2b-c, ?dpc). In preaxial and postaxial view, the proximal head appears angled and bends down ventrally (Fig. 2c, d). The proximal head has postaxially a rugose, striated, and well set off surface below the above described articulation facet, a possible insertion for muscles and tendons (Fig. 2c). The morphology of the asymmetrical distal end



Fig. 3. Photographs of humeri of the placodont taxa *?Cyamodus* and *?Placodus*; **a**: Left humerus of *?Cyamodus* (MHI 2112/6) from the Grenzbonebed of Satteldorf-Barenhalden (abandoned Feldner quarry); The proximal and distal ends are incomplete at the dorsopostaxial side (a3); **b**: Right humerus of *?Cyamodus* (SMNS 54583) from the Upper Muschelkalk of Hegnabrunn; **c**: Left humerus of *?Cyamodus* (SMNS 54581) from the Upper Muschelkalk of Unterrodach. Note the variability of the proximal and distal heads in SMNS 54583 and SMNS 54581. However, both share the proximal concavity at the postaxial side and the twisted proximal and distal ends; **d**: Left humerus of *?Cyamodus* (SMNS 54569) from the Upper Muschelkalk of Hegnabrunn in dorsal view; **e**: Left humerus of *?Placodus* (SMNS 59827) from the Upper Muschelkalk of Hegnabrunn; **1**: Dorsal view; **3**: Postaxial view; enf = Entepicondylar foramen; **4**: Preaxial view. Arrows indicate the postaxial depression at the proximal head. The plaster band marks the histological sampling location.





Fig. 4. Midshaft cross sections of humeri of *Horaffia kugleri* gen. et sp. nov. and of the placodont *?Cyamodus*; **a**: Thin section of MHI 2112/1; **b**: Thin section of MHI 2112/2; **c**: Thin section of MHI 2112/4; **d**: Photograph of cross section of MHI 2112/3 at midshaft fracture; **e**: picture of micro-CT scan of the midshaft region of MHI 2112/5 (holotype); **f**: Thin section of *?Cyamodus* humerus MHI 2112/6; **g**: Photograph of polished section of *?Cyamodus* humerus SMNS 54569. The white arrow marks the border of the medullary region; the black arrow indicates a large foramen.

is flat and broad. It is less massive (thick) than the proximal head. The distal end has an articulation facet spanning from the preaxial to the postaxial side, which is diametric to the proximal articulation facet (Fig. 2b, c). The rough bone surface indicates that the facet was most likely also capped by cartilage. The distal articulation facet is preaxially slanted (Fig. 2b). In MHI 2112/3 the distal margin has a protrusion which is centered and pointed in ventrodorsal view, whereas the distal end is simply semicircular in MHI 2112/5 and MHI 2112/1. The distal end is damaged in MHI 2112/4 and MHI 2112/2. None of the humeri has an entepicondylar foramen or any other morphological feature identified typical for the distal ends of sauropterygian humeri (e.g., RIEPPEL 1994), which were beside others used for comparison.

Morphological comparisons: Eosauropterygians known so far from the Upper Muschelkalk and/ or the Lower Keuper of Southwest Germany are: *Neusti*- cosaurus spp., Serpianosaurus, Nothosaurus mirabilis, N. giganteus, Simosaurus, and Pistosaurus. The pachyostotic Horaffia humeri differ from those of eosauropterygians in size (i.e., pachypleurosaurs), robustness, and morphology. Nothosaur humeri are distinctly flatter and more angled in their overall morphology. Additionally, they show well developed morphological features at their proximal and distal ends such as a distinct deltopectoral crest, a latissimus dorsi insertion, an ectepicondyle, an ectepicondylar groove, and an entepicondylar foramen (e.g., RIEPPEL 1994; BICKEL-MANN & SANDER 2008). Simosaurus has a slender humerus, which is well constricted at midshaft and not broadened distally. Pistosaur humeri exhibit an even more simple morphology when compared to Horaffia humeri. They are less curved, dorsoventrally flattened, and more slender with a small and short, proximal head that is not well set off.

The humerus of *Paraplacodus* from the Besano Formation (Grenzbitumenhorizont; Anisian/Ladinian boundary) of Monte San Giorgio (Alpine Triassic) shares with *Horaffia* humeri a massive appearance, a similar curvature of the midshaft, equally broad and massive proximal and distal ends, a slanted preaxial margin at the asymmetrical distal end, and the absence of an entepicondylar foramen (RIEPPEL 2000b: fig. 8A, C). The proximal head of *Paraplacodus* is more angled in relation to the midshaft and, contrary to the *Horaffia* humeri, the postaxial margin is longer in *Paraplacodus* than its preaxial margin. The proximal head of the right humerus of *Paraplacodus* figured in RIEPPEL (2000b: fig 8A) shows a comparable articulation facet, including a well set off margin.

In the Muschelkalk, so far no Placodus or Cyamodus skull were found together with a humerus. The humerus associated with the nearly complete Placodus skeleton described by DREVERMANN (1933) belongs to a nothosaur (RIEPPEL 1995). Humerus morphology of Placodus and Cyamodus was discussed by Vogt (1983) and RIEPPEL (1995). RIEPPEL (1995: 31) stated that the humeri of these two genera are very similar, and their identification is largely based on absolute size (Cyamodus tends to be larger) and stratigraphy (in the Upper Muschelkalk, above the spinosus biozone, Placodus is absent, whereas remains of Cyamodus still occur, however very rarely (HAGDORN 1993). Thus, isolated humeri were only tentatively assigned to both taxa. Humerus SMNS 59827 from the Upper Muschelkalk of Hegnabrunn near Kulmbach was figured by RIEPPEL (1995: fig. 3E) as a Placodus humerus. The morphology of this specimen is also herein used as representative for Placodus.

Humeri of *?Placodus* and *Horaffia* share the position of the deltopectoral crest (although the deltopectoral crest is much less pronounced in *?Placodus* than in *Horaffia*), a similar curvature of the midshaft and a broad distal end. They differ because the humerus of *?Placodus* is in general much more slender, narrower, and distally flatter. Its proximal head has a simple rectangular shape and is less massive and does neither show a dorsopreaxial elongation nor the ventrally protruding proximal part of the head. The nearly symmetrical distal end of the *?Placodus* humerus is divided into an entepicondyle, an ectepicondylar groove, and an ectepicondyle. These morphological characters were not identified in *Horaffia*. Additionally, a (broken off) entepicondylar foramen was identified in SMNS 59827 (Fig. 3d3, arrow/enf.). The humerus of *P. inexpectatus* from the Anisian of the Guizhou Province of China (JIANG et al. 2008a) differs by its simple small rectangular proximal head but shares the slanted preaxial distal margin with *Horaffia*.

Humeri assigned to Cyamodus by Vogt (1983) and RIEPPEL (1995) are SMNS 15937, SMNS 18057, and SMNS 17872 from the Upper Muschelkalk of the locality Heldenmühle near Crailsheim, SMNS 54581 (Fig. 3c) (formerly coll. WILD #1070) from the Upper Muschelkalk of Unterrodach (Franconia, Bavaria), and SMNS uncatalogued from the Upper Muschelkalk of Stuttgart-Zuffenhausen. Additionally, in the current study we assigned SMNS 54583 and SMNS 54569 (Fig. 3d) from the Upper Muschelkalk of Hegnabrunn (Franconia, Bavaria) (Fig. 3b) and MHI 2112/6 from the Grenzbonebed of Satteldorf, Barenhaldenmühle (Feldner quarry) (Fig. 3a) to ?Cyamodus. The latter is the first record of ?Cyamodus in the Grenzbonebed. Despite a certain variability, these humeri have the unique character of a distinct depression or concavity at the proximal ventropostaxial side (Fig. 3a-d, arrows).

?Cyamodus humeri share with the *Horaffia* humeri a massive proximal head and the curvature of the midshaft area. However, *?Cyamodus* humeri are more slender and their proximal head is generally more twisted in relation to the midshaft and has an elongated and protruding dorsal margin but not the distinct triangular shape of the *Horaffia* humeri. The distinct depression at the proximal ventropostaxial side typical for *?Cyamodus* is not developed in *Horaffia* or *?Placodus*. The distal end of *?Cyamodus* a distinct ectepicondylar groove, which is absent in *Horaffia*. *?Cyamodus* humeri show a capitellum and their entepicondyle is located more distally when compared to *?Placodus*, morphological details that are absent in *Horaffia*.

Humeri of the placodonts *Henodus* from the Middle Keuper (early Carnian) of Tübingen-Lustnau (Southwest Germany; v. HUENE 1936) and *Psephoderma alpinum* from the Rhaetian of the Alps (v. MEYER 1858) differ from *Horaffia* humeri in overall morphology, slenderness, and size range. *Psephosaurus suevicus* from the Lower Keuper of Ludwigsburg-Hoheneck and Kirchberg an der Jagst is only known from carapace fragments and attributed teeth and is thus not available for comparison.

The humerus of the diapsid marine reptile *Helvetico-saurus* from the Besano Formation (Grenzbitumenhorizont, Anisian-Ladinian boundary) of Monte San Giorgio





Fig. 5. Medullary regions of the humeri of *Horaffia kugleri* gen. et sp. nov. (**a**–**h**) and of the placodont ?*Cyamodus* (**i** – **l**). **a**: MHI 2112/1 in normal light; **b**: MHI 2112/1 in polarized light; **c**: MHI 2112/2 in normal light; **d**: MHI 2112/2 in polarized light; **e**: MHI 2112/2 (thin section distal to midshaft) in normal light; **f**: MHI 2112/2 (thin section distal to midshaft) in polarized light; **g**: MHI 2112/6 in normal light; **h**: MHI 2112/4 in polarized light; **i**: MHI 2112/6 in normal light; **j**: MHI 2112/6 in polarized light; **k**: SMNS 54569 in normal light; **l**: SMNS 54569 in polarized light. Note the sharp line that surrounds the medullary region and which is marked by white arrows.

(Alpine Triassic) shares with *Horaffia* humeri a similar overall shape with an asymmetrical broad and flat distal end (PEYER 1955: pl. 88, fig.18; RIEPPEL 1989: fig. 6). However, the proximal head of *Helveticosaurus* humeri are not as massive and differ in morphological details such as the lack of a protruded ventral portion or the dorsopreaxially elongated margin (triangular form).

Humeri of the thalattosaur *Askeptosaurus* from the Grenzbitumenhorizont of Monte San Giorgio differ from *Horaffia* humeri by their straight and from both sides constricted midshaft region (MÜLLER 2005).

Histological description: Bone microstructure and histology of *Horaffia* humeri are in accordance with that of the two sampled *?Cyamodus* humeri (SMNS 54569, MHI 2112/6) and are therefore described together.

The cross sections share a similar shape with a slightly convex dorsal margin and a straight ventral margin (Fig. 4). The margins of the cross sections of the small humeri MHI 2112/1 and MHI 2112/2 are smoother, forming an irregular oval with a preaxially pointed part (egg-shape). MHI 2112/4 has a distinct sharp edge at the dorsopostaxial



Fig. 6. Details of the plexiform to radiating fibro-lamellar bone tissue and vascular organization and density of humeri of *Horaffia kugleri* gen. et sp. nov. (**a**–**c**) and of the placodont ?*Cyamodus* (**d**–**f**). **a**: MHI 2112/1 in normal light; **b**: MHI 2112/2-1 in normal light; **c**: MHI 2112/4 in normal light; **d**: ?*Cyamodus* humerus MHI 2112/6 in normal light; **e**: SMNS 54569 in normal light; **f**: SMNS 54569 in polarized light. The polarized picture clearly shows the high vascular density, which is less obvious in normal light. Note the change in vascular canal organization in the outer cortex that is dominated by longitudinal vascular canals. Arrows indicate distinct growth marks.

margin, its postaxial margin is straight, and the narrower preaxial side is convex. MHI 2112/3 is preaxially pointed and postaxially convex. MHI 2112/5, MHI 2112/6, and SMNS 54569 are dorsopostaxially and ventro/mediopre-axially slightly pointed, whereas their counter edges are convex.

Humeri of Horaffia exhibit an oval or round medullary region (Table 1). Humeri of ?Cyamodus (MHI 2112/6, SMNS 54569) show a small free cavity or a medullary region. The medullary region in Horaffia as well as the area surrounding the free cavity in ?Cyamodus contains small and rare scattered pockets of calcified cartilage, secondary endosteal infillings of vascular canals, and secondary trabeculae. The medulla is in all samples always completely or partially surrounded by a well defined sharp line (Figs. 4b-c, e-f; 5; white arrows). Original cavities are now filled by calcite or other crystals and sediment. MHI 2112/2 differs from the other samples because its large medullary region contains a relatively large free cavity that is surrounded by a regular network of secondary trabecles. MHI 2112/2 is also the only sample that has a perimedullary region developed that consists of scattered large erosion cavities around the medullary region, reaching into the middle cortex (Fig. 4b).

Postaxially to the medullary region a large foramen (free cavity), which is lined by lamellar bone, is visible in MHI 2112/1 and in MHI 2112/4 (Fig. 4a, c; black arrows). No such foramina were identified in the *?Cyamodus* humeri (MHI 2112/6 and SMNS 54569).

The primary bone tissue consists of woven and parallel fibred bone (Fig. 6). Woven fibred bone dominates the inner to middle cortex whereas the amount of parallel fibred bone increases towards the outer cortex. In the larger samples (MHI 2112/4, MHI 2112/6, SMNS 54569), a general tendency towards a successive replacement of woven fibred bone by parallel-fibred bone is observed. All samples show a relatively constant amount of irregularly formed and sized osteocytes all over the cortex. Already in the smaller samples (MHI 2112/1, MHI 2112/2) the cortex is dominated by primary osteons well lined with lamellar bone (Fig. 6a, b). Primary osteons are very distinct and visible in normal light (Fig. 6). Vascular density is generally high when compared to eosauropterygian samples (KLEIN 2010; HUGI et al. 2011). It is moderate in the inner cortex but increases from the middle cortex towards the outer cortex, making the cortex here nearly spongeous (Fig. 4-6). Bone compactness is similar in Horaffia and ?Cyamodus (Table 1).

Nearly all vascular canals are primary osteons. They are longitudinal, radial and reticular (locally also circular) and mainly organized in radial rows (Fig. 6). The size of the vascular canals is smallest in the inner cortex, highest in the middle cortex, and moderate to high in the outer cortex. Vascular density and canal size is always greatest at the postaxial bone side. The vascular canals are often (but not always) aligned in rows (Fig. 6). The woven and parallel fibred bone together with the primary osteons form the 3D scaffolding of fibro-lamellar bone with the vascular canals arranged in a radiating to plexiform system. (FRANCILLON-VIEILLOT et al. 1990: fig. 14G; but see STEIN & PRONDVAI 2013 for the discussion on fibro-lamellar/woven bone).

The cortex is stratified by thin layers of avascular, highly organized parallel-fibred or lamellar bone (annuli) alternating with thick layers of highly vascularized, less organized parallel-fibred and woven bone (zones) as well as by changes in vascular organization (Fig. 6, arrows). The well separated medullary region is always surrounded by an inner ring of bone tissue, which is delimited to the middle cortex by a change in bone tissue and/or a thin layer of high organized parallel fibred bone, interpreted as a growth mark (Fig. 5, arrows). The middle and outer cortex is then irregularly stratified by thin layers of avascular highly organized parallel-fibred or lamellar bone, interpreted as growth marks, as well (Table 1; Fig. 6, arrows). These growth marks are often not traceable all around the cross section. At the preaxial side, where the cortex is thinner, the number of growth marks is always lower than at the postaxial side. Many growth marks and/or changes in bone tissue are visible in normal light but for a complete overview of the stratification the samples needed to be studied in polarized light.

5. Discussion

5.1. Bone histology and growth

The appearance of the medullary region is variable in the Horaffia humeri as well as in Cyamodus humeri. This is also the case in many other taxa and depends largely on the sampling location along the midshaft (KONIETZKO-MEIER & KLEIN 2013) but also reflects high individual variability. The development of the medullary region is generally poor, resulting in osteosclerosis (RICQLÈS & BUF-FRÉNIL 2001). As described above, the medullary region is well delimited from the primary cortex by a thin layer of lamellar bone, which is equivalent to the "sharp border" described by Hugi et al. (2011) for some pachypleurosaurs. Humerus histology of Horaffia and ?Cyamodus can be summarized as radiating to plexiform fibro-lamellar bone with a high vascular density in the middle and outer cortex. It largely resembles the bone tissue, the degree of vascular density, and the organization of vascular canals that is described for a Placodus humerus (see BUFFRÉNIL & MAZIN 1992: fig. 1; RICQLÈS & BUFFRÉNIL 2001: fig. 2B) and for a humerus and a femur of Placodontia indet. (KLEIN 2010: fig. 13A-E), including the poor development

of the medullary region. Pistosauroids also exhibit radiating fibro-lamellar bone tissue but with a much lower vascular density (bone compactness of 90% for humerus SMNS 84825) and a dominance of radial vascular canals (WIFFEN et al. 1995; KLEIN 2010; KRAHL et al. 2013) but lack high numbers of exceptionally large longitudinal, or generally reticular and circular oriented vascular canals (see figures in KRAHL et al. 2013).

The skeletochronological analysis of the current samples remains difficult due to the lack of undoubtedly and well traceable annual growth marks such as lines of arrested growth. The thin layers of highly organized parallel-fibred and/or lamellar bone, which irregularly stratify the cortices of the humeri are interpreted as growth marks, but it remains uncertain whether they represent annuli (in the meaning of annual phases of slow growth). It is also problematical that the humeri did not show much variation in the number of these growth marks, although they are interpreted as growth series due to their size ranges spanning from 77.6 mm to 152 mm (Table 1). So far we can only observe that the cortex of the humeri of Horaffia and ?Cyamodus is built of thick layers of very rapidly deposited bone tissue, which were irregularly interrupted by phases of slower growth. No growth stop or decrease in growth rate, for example reflecting sexual maturity, is indicated by a change to higher organized bone tissue or by an increase in the number of growth marks, is observed in the current sample.

The radiating to plexiform fibro-lamellar bone tissue with its high vascular density implies a fast growth rate and possibly an increased basal metabolic rate for Horaffia as well as for ?Cyamodus, as was discussed before for marine reptiles such as ichthyosaurs and plesiosaurs (BERNARD et al. 2010) and some Triassic Sauropterygia (KLEIN 2010; KRAHL et al. 2013), including Placodus (Buffrénil & Mazin 1992; Ricqlès & Buffrénil 2001). The relation between histological features, body size, swimming style, and metabolic rate in marine reptiles was recently reviewed by HOUSSAYE (2012). Interestingly, fibro-lamellar bone, which is unequivocally documented in the so far studied placodonts (BUFFRÉNIL & MAZIN 1992; RICQLÈS & BUFFRÉNIL 2001; KLEIN 2010; ?Cyamodus, current study), is among marine reptiles typical for pelagic, fast, active swimmers like ichthyosaurs and plesiosaurs. However, placodonts certainly inhabited shallow water close to coastal areas that provided benthic diet (SCHEYER et al. 2012).

5.2. Microanatomy and life style

The *Horaffia* humeri achieved an increase of bone mass by two different processes: (1) They are pachyostotic (Fig. 1), which is a morphological feature (increase in bone

volume) and the result of hyperplasy of periosteal bone (RICOLÈS & BUFFRÉNIL 2001; HOUSSAYE 2009). Pachyostosis seems to concentrate on particular bones such as vertebrae and ribs (HOUSSAYE 2009). Pachyostosis of humeri is among marine reptiles relatively uncommon and occurs in a lesser stage only in Placodus (BUFFRÉNIL & MAZIN 1992) and juvenile plesiosaurs (WIFFEN et al. 1995; FOSTOWICZ-FRELIK & GAZDZICKI 2001). (2) The Horaffia humeri show osteosclerosis, which is a histological feature and the result of an increase of inner bone compactness and/or the reduction of the medullary region (RICQLÈS & BUFFRÉNIL 2001; HOUSSAYE 2009). The Horaffia humeri are thus pachyosteosclerotic (RICQLÈS & BUFFRÉNIL 2001; HOUSSAYE 2009). High vascular density (number and size of vascular canals) increases towards the outer cortex leading to a reduction of primary bone density in the second half of the individual's life. This could be related to a change of locomotion or a general shift in life style during ontogeny. Both strategies (an increase and a decrease in body mass) were documented before in the ontogeny of aquatic vertebrates (RICQLÈS & BUFFRÉNIL 2001: 299). In many lineages of pelagic vertebrates (e.g., plesiosaurs) the bone microstructure shifts from a pachyosteosclerotic condition in juveniles to an osteoporotic-like condition in adults (RICQLÈS & BUFFRÉNIL 2001; BUFFRÉNIL et al. 2010), which is, however, in those taxa achieved by the resorption of primary bone.

Cyamodus humeri (MHI 2112/6, SMNS 54569) show osteosclerosis (poor development of the medullary region) but no pachyostosis (Fig. 3). Their vascular density is is comparable to that of *Horaffia* (Table 1). Additionally, both show resorption of primary osteons in their middle and outer cortex.

Increase in bone density and mass is typical for vertebrates secondarily adapted to an aquatic life in lagoonary or other shallow water environments. Bone mass increase contributes to passive buoyancy control, and mainly slow swimmers and/or bottom walkers benefit from this process (RICQLÈS & BUFFRÉNIL 2001; HOUSSAYE 2009). Bone mass increase enables tetrapods to dive for long times in shallow water and to adjust their position with minor energy cost (TAYLOR 2000). This is an advantage for animals feeding on slowly moving or stationary food.

Placodonts like *Cyamodus* are considered as axial subundulatory swimmers (BRAUN & REIF 1985; MASSARE & CALLAWAY 1990). Their body shape and general anatomy suggest that they were no fast swimmers but most likely bottom walkers (e.g., HOUSSAYE 2009) which fed on hardshelled diet as is obvious from their durophagous and very specialized dentition (CANOVILLE & LAURIN 2010; SCHEYER et al. 2012 and references therein). Bone microstructure of the humeri of the new taxon is typical of inhabitants of shallow aquatic environments but due to their pronounced pachyosteosclerosis there seemed to be a difference in locomotion and life style between *Horaffia* and ?*Cyamodus*. The study of long bone microanatomy is used to infer the general lifestyle of extinct taxa (see references in e.g., LAURIN et al. 2011 and HOUSSAYE 2012). Aquatic taxa tend to have smaller medullary cavities, a broad transition zone between the cortical compacta and the medulla, and have a higher compactness in the outermost cortex of the cross section. Interestingly, CANOVILLE & LAURIN (2010) inferred an amphibious but not aquatic lifestyle for *Placodus*. Bone compactness is 83.4% in *Placodus* and is thus reminiscent of aquatic taxa. However, the presence of a small but distinct medullary cavity and a narrow transition zone points to an amphibian lifestyle for *Placodus*.

The microanatomical characters of humeri of ?*Cyamodus* and *Horaffia* are ambiguous, too. Humeri of ?*Cyamodus* exhibit a small distinct medullary cavity as *Placodus* does, whereas humeri of *Horaffia* have a medullary region containing secondary trabecels etc. Nevertheless, the medulla is small in both taxa, which is typical for aquatic taxa and bone compactness values are within the aquatic range (Table 1), too. Additionally, humeri of *Horaffia* are highly pachyostotic, which is also an aquatic feature. The lack of a perimedullary region (transition zone between the cortical compacta and the medulla) and low compactness in the outermost cortex places both close to amphibious/terrestrial tetrapods.

6. Conclusions

The comparison and analysis of bone histology of the humeri described above (MHI 2112/1 - MHI 2112/5) from the Grenzbonebed of Southwest Germany revealed a unique morphology, different from any other taxon by their robustness or massiveness, their proximal head with a protruding preaxial margin, and their slanted preaxial margin of the distal end. The bone histology of the new taxon resembles that of placodonts. However, since convergent evolution of bone tissue is common among secondarily aquatic vertebrates (RICOLÈS & BUFFRÉNIL 2001; LAURIN et al. 2011; QUÉMENEUR et al. 2013), taxonomic assignment solely based on histology is sketchy. Thus, the humeri were herein assigned to the newly erected taxon Horaffia kugleri gen. et sp. nov. Problematic is the lack of any other bones from the Grenzbonebed that would fit morphologically and anatomically to these humeri.

The simple humerus morphology points to an advanced adaptation to a secondary aquatic life. Morphology and microanatomy document pachyosteosclerosis, which changes from the middle to the outer cortex to a more osteoporotic-like state. This is achieved by an increase in vascular density and vascular canal size via resorption of primary bone (osteoporosis). However, some microanatomical features contradict a fully aquatic life style when compared to modern aquatic vertebrates. *Horaffia kugleri* and the placodont *?Cyamodus* share a radiating to plexiform fibro-lamellar bone tissue with high vascular density, and large radial, longitudinal, and reticular vascular canals, the lack of secondary osteons, and the presence of a poorly developed medullary region (osteosclerosis). Additional histological similarities with *?Placodus* could point to a placodont affinity of *Horaffia kugleri*. The presence of another placodont is not unlikely due to a relative high diversity of placodont taxa during the Middle and Late Triassic (e.g., RIEPPEL 2000a). Another possibility is an affiliation to the placodont *Psephosaurus*. However, this poorly known genus occurring in the uppermost Erfurt Formation (Lower Keuper) of Southwest Germany has not yet been identified in the Grenzbonebed by diagnostic osteoderms.

General simplification of humerus morphology, pachyostosis of the humerus, and the change from osteosclerosis to a more osteoporotic-like stage could also point to pistosauroid affinities of Horaffia kugleri. However, humerus morphology, microstructure, and histology of Pistosaurus, which is well known from the Upper Muschelkalk of southern Germany, differ in many characters from that of Horaffia (KRAHL et al. 2013). The phylogenetic relationships of the large eusauropterygian Bobosaurus from the early Carnian of Italy (DALLA VECCHIA 2006) remain unresolved, but according to DALLA VECCHIA (2006) it shows some plesiosaur features. Bone histology of Bobosaurus is not known. When compared to Horaffia kugleri, plesiosaurs have a comparable fibro-lamellar bone tissue but with a much lower vascular density and differences in vascular canal organization. For plesiosaurs an ontogenetic change from osteosclerosis to osteoporosis is documented (WIFFEN et al. 1995; FOSTOWICZ-FRELIK & GAZDZICKI 2001) that is achieved by the resorption of primary bone and not by an increase in vascularity. However, plesiosaurs do not appear before the Rhaetian (Late Triassic) or Hettangian (Early Jurassic) (BENSON et al. 2012), making plesiosaur relationships of Horaffia kugleri very unlikely.

An originally by one of us (H. HAGDORN) hypothesized assignment of the *Horaffia* humeri to *Blezingeria*, a poorly known marine reptile from the Grenzbonebed, cannot be unequivocally excluded but is unlikely due to distinct differences in size and massiveness of humeri when compared to vertebrae.

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