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## Long bone histology and microanatomy of Placodontia (Diapsida: Sauropterygia)

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**Key words:** bone mass increase, bone tissue types, extinct marine reptiles, high growth rates, PCA, swimming capabilities, Triassic

### Abstract

Placodontia, an enigmatic group of durophagous and in part heavily armoured animals, were members of Sauropterygia, the most diverse and successful group of Mesozoic marine reptiles. Microanatomy and histology of long bones of several armoured and non-armoured Placodontia were studied, covering most of their taxonomic breadth, to elucidate the paleoecology, physiology, and lifestyle of its members. Results reveal an unexpected and not phylogenetically or stratigraphically related disparity of microanatomical and histological features for the group. The non-armoured *Paraplocodus* and the heavily armoured *Psephoderma* grew with lamellar-zonal bone tissue type, which is typical for modern sauropsids. In the former, the tissue is nearly avascular surrounding a compacted medullary region, whereas in the latter, the lamellar-zonal bone tissue is vascularized framing a large open medullary cavity and a perimedullary region. Armoured *Henodus* and Placodontia indet. aff. *Cyamodus* as well as non-armoured *Placodus* exhibit a reduced medullary cavity and grew with highly vascularized plexiform to radiating fibro-lamellar bone. Several long bones of Placodontia indet. show circumferential fibro-lamellar bone and can be distinguished into two groups on the basis of microanatomical features. In addition, all bones that grew with fibro-lamellar bone show locally primary spongy-like architecture and had secondarily widened primary osteons throughout the cortex, resulting in a secondarily spongy tissue. The highly vascularized fibro-lamellar bone of these Placodontia indicates growth rates comparable to that of open marine ichthyosaurs. Differences in microanatomy and bone histology as expressed by a principal component analysis, thus clearly indicate different paleoecologies, including differences in lifestyle and swimming modes and capabilities in Placodontia. This would have reduced competition in the shallow marine environments of the Tethys and might be a key to their success and diversity. A certain developmental plasticity among the studied placodonts is interpreted as response to different environmental conditions as is obvious from inter- and intraspecific histological variation. Most striking is the difference in life history strategy in armoured *Psephoderma* and non-armoured *Paraplocodus* when compared to armoured

*Henodus*, Placodontia indet. aff. *Cyamodus*, non-armoured *Placodus*, and Placodontia indet. Bone tissue of *Psephoderma* and *Paraplocodus* indicates low growth rates and a low basal metabolic rate, as many modern sauropsids have such as the marine iguana, whereas the others grew with extremely fast growth rates, more typical for birds and mammals, indicating an increased basal metabolic rate.

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### Introduction

Placodontia were part of the Sauropterygia, a diverse group of diapsid marine reptiles that ranged from the late Lower Triassic until the end of the Cretaceous (Rieppel, 2000a; Motani, 2009). The Triassic radiation included predominately shallow marine forms such as

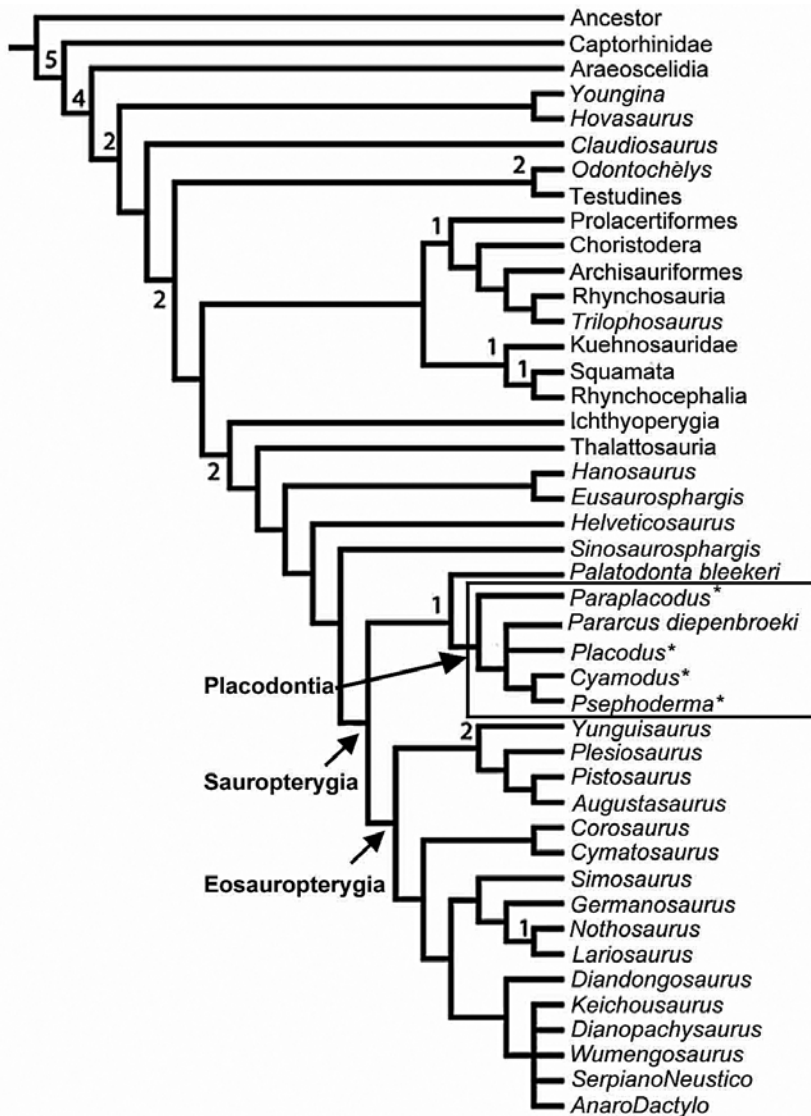


Fig. 1. Phylogenetic relationships within Diapsida, including Sauropterygia and Placodontia. The asterisks mark the histologically studied members of Placodontia. Cladogram modified from Neenan *et al.* (2013) and Klein and Scheyer (2014).

Placodontia, Pachypleurosauria, Nothosauria, and Pistosauria; conversely, the Jurassic and Cretaceous seas were ruled by the open marine Plesiosauria. The latter had a global distribution, whereas most Triassic representatives were largely restricted to epicontinental seas of the Tethys Ocean. Triassic Sauropterygia are notable for having a large variety of ecologies, life histories and feeding strategies, which enabled them to live contemporaneously in the same habitats.

Placodonts were the sister group of Eosauropterygia (Pachypleurosauria, Nothosauria, Pistosauria; Rieppel, 1994) (Rieppel, 2000a; Neenan *et al.*, 2013) (Fig. 1), and they first appeared in the fossil record in the early Anisian (Lower Muschelkalk) of the Germanic Basin

(Hagdorn and Rieppel, 1999; Neenan *et al.*, 2013). Beyond the Germanic Basin they occurred along the epicontinental coasts of the western Tethys (Rieppel, 2000a: circummediterranean Muschelkalk localities in Spain, Tunisia, Israel, and Saudi Arabia) and can also be found in the Anisian, Ladinian, and Carnian of China (Li, 2000; Li and Rieppel, 2002; Jiang *et al.*, 2008; Zhao *et al.*, 2008). Placodontia vanished from the fossil record of the Germanic Basin in the Lower Carnian, but survived in the Alpine Triassic realm until the end of the Late Triassic (Furrer *et al.*, 1992; Renesto *et al.*, 1995; Hagdorn and Rieppel, 1999).

The phylogenetic relationships within Placodontia have repeatedly been tested in recent years, and is

currently considered to be divided into a non-armoured placodontoid grade and a heavily armoured monophyletic Cyamodontoidea (Rieppel, 2000a, b, 2001; Jiang *et al.*, 2008; Neenan *et al.*, 2013). The placodontoid grade contains at least three taxa (Rieppel, 2000a; Jiang *et al.*, 2008; Klein and Scheyer, 2014). Cyamodontoidea were more diverse, with at least nine genera (*e.g.* Rieppel, 2000a, b, 2001; Zhao *et al.*, 2008).

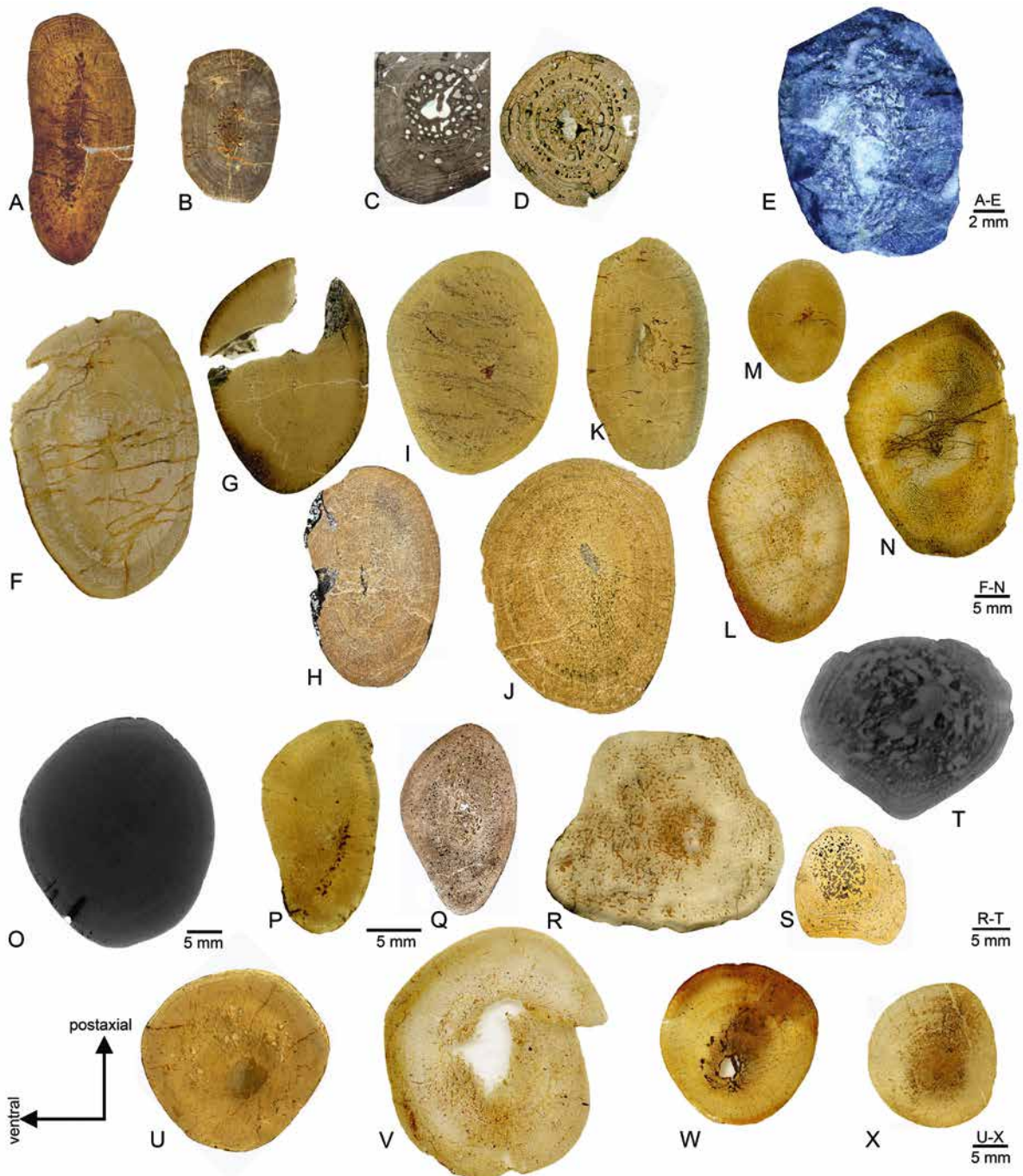
Placodonts shared some unique morphological features such as a massive, akinetic skull, and a reduced but specialized dentition, enabling a durophagous diet (summarized in Scheyer *et al.*, 2012; Neenan *et al.*, 2014). According to Hagdorn and Rieppel (1999), all placodonts with the exception of *Henodus* Huene, 1936 are exclusively found in marine sediments, and their occurrence was strongly related to the availability of shelly prey items. Most Cyamodontoidea showed numerous armour plates (osteoderms) fused into one or two dorsal shields, and in some cases, an additional ventral armour shield (Rieppel, 2002; Scheyer, 2007, 2010). Conversely, the placodontoid *Paraplacodus* Peyer, 1931 lacked any kind of armour and *Placodus* Agassiz, 1833 showed only a single row of osteoderms along its vertebral column (Rieppel, 1995, 2000a, b; Jiang *et al.*, 2008). While the postcranial anatomy of *Paraplacodus* and *Placodus* is reasonably well known (*e.g.* Drevermann, 1933; Rieppel, 1995, 2000a, b, 2002; Jiang *et al.*, 2008), the postcranial morphology of many cyamodontoids is only partly understood due to obscuring dermal armour, and the fact that they are commonly embedded in large slabs of rock matrix.

*Placodus* is the best-known placodontoid so far. Due to its cylindrical, sea cow-like body shape, *Placodus* has always been interpreted as a slow bottom walker that needed a heavy skeleton to act as ballast, allowing it to walk/stay on the seafloor when feeding (*e.g.* Vogt, 1983; Westphal, 1988; Rieppel, 1995; Scheyer *et al.*, 2012). Despite its occurrence in solely marine sediments (Hagdorn and Rieppel, 1999) some authors consider the lifestyle of *Placodus* as not being fully marine (aquatic) but as amphibious, similar to that of the extant marine iguana *Amblyrhynchus cristatus* Bell, 1825 from the Galapagos Islands (Westphal, 1988) that only enters the sea for feeding. The main reason for this is the lack of gross morphological specialization for an aquatic life in the *Placodus* skeleton (Carroll, 1988; Westphal, 1988). *Placodus* limbs are not specially adapted for swimming and it is assumed that *Placodus* was still able to walk on land (Vogt, 1983; Carroll, 1988). Rieppel (1995: 38) stated that ‘the skeletal structure of *Placodus* clearly indicates a durophagous in-

habitant of coastal stretches and shallow seas’. An amphibian lifestyle for *Placodus* was also hypothesized based on the analysis of humerus microstructure by Canoville and Laurin (2010; please note that the sample they used is not undoubtedly assignable to a certain placodont taxon). However, the streamlined body, stiff vertebral column as shown by hyposphen and hypantrum processes, as well as the long and laterally flattened tail of *Placodus* clearly indicates certain swimming capabilities (Vogt, 1983; Westphal, 1988; Rieppel, 1995). Additionally, Neenan and Scheyer (2012) concluded that the alert head position of *Placodus* was ideally suited for feeding in an aquatic environment. Vogt (1983) and Westphal (1988) considered *Placodus* to be an axial swimmer whereas Braun and Reif (1985) identified *Placodus* as a subcarangiform swimmer. Despite divergences concerning its mode of locomotion, there is a consensus that *Placodus* was in any case a slow and not very active swimmer. Based on morphology, Westphal (1988) concluded long diving capabilities for *Placodus* due to movable ribs and a large ribcage volume. This was later confirmed by other authors who studied bone histology and microanatomy in a placodont humerus; documenting that bone mass increase would have counteracted an increased oxygen store (*e.g.* Buffrénil and Mazin, 1992; Taylor, 1994; Houssaye, 2009).

The heavily armoured cyamodontoids have a dorsoventrally flattened and laterally extended body, reminiscent of the shape and morphology of flat aquatic turtles, such as snapping turtles (Chelydridae) or the mata mata (*Chelus fimbriatus*). Another hypothesis states that they buried themselves in sand or gravel on the seafloor, like rays (Mazin and Pinna, 1993; Renesto and Tintori, 1995) or soft shelled turtles (Ernst and Barbour, 1989). The cyamodontoid armour and the turtle shell evolved convergently and are only superficially similar (Scheyer, 2010), because the armour of placodonts is not connected to the underlying postcranial skeleton. In *Cyamodus hildegardis* Peyer, 1931 for example, the armour can be divided into a main carapace, a pelvic shield, and tail armour (Scheyer, 2010).

The study of bone tissues of extinct vertebrates reveals insights into growth rates and thus into their metabolism and physiology (*e.g.* Bakker, 1980; Ricqlès, 1983, 1992; Padian and Horner, 2004; Padian *et al.*, 2004; Montes *et al.*, 2007). From the preserved growth record, growth patterns and life history strategies can be deduced (*e.g.* Castanet *et al.*, 1993; Buffrénil and Castanet, 2000; Sander and Klein, 2005; Sanchez *et al.*, 2010; Hugi and Sánchez-Villagra, 2011; Köhler *et al.*,



**Fig. 2.** Photographs of cross sections of sampled bones. A, Cross section of humerus and B, Femur of *Paraplocodus broilii* (PIMUZ T5845). C, Cross section of humerus (PIMUZ A/III 1476) and D, Femur (PIMUZ A/III 0735) of *Psephoderma alpinum*. E, Photograph of a breakage at midshaft of *Henodus* (GPIT/RE/7289). F-M, Cross sections of Placodontia indet. aff. *Cyamodus* sp. humeri. F, SMNS 59831. G, MHI 2112-6. H SMNS 15891. I, SMNS 54569. J, SMNS 15937. K, SMNS 54582. L, MHI 697. M, MHI 1096. N, Cross section of a humerus of the marine reptile *Horaffia kugleri* (MHI 2112-4). O, Micro-CT image of the cross section of a humerus (SMNS 59827) assigned to *Placodus gigas* (Vogt, 1983; Rieppel, 1995). P-X Cross sections of humeri and femora of Placodontia indet. P, humerus MB.R. 454. Q, humerus IGWH 9. R, femur SMNS 84545. S, femur IGWH 23. T, Micro-CT image of the cross section of placodont femur MB.R. 965. U, femur MB.R. 961. V, femur MB.R. 814.2. W, femur MB.R. 812. X, femur SMNS 54578. For locality information and stratigraphic age see Table 1.

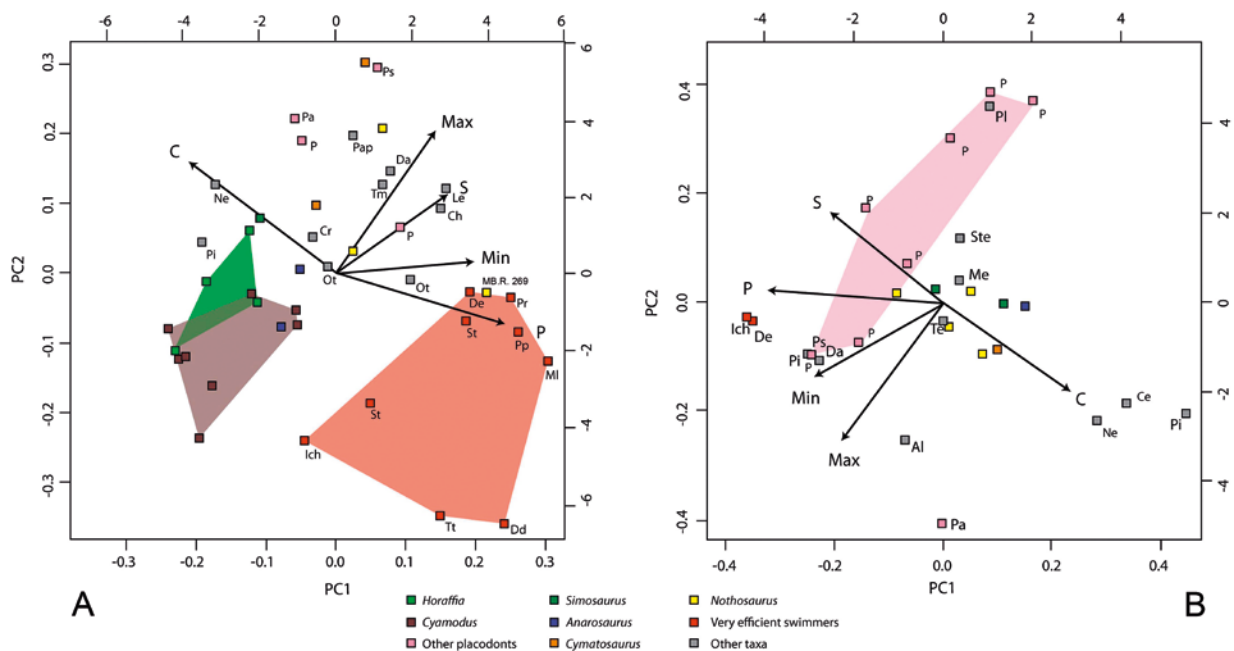


Fig. 3. Microanatomical clusters obtained by Principal Component Analysis (PCA). Graphs showing the distribution of the variance in the humerus and femur sections of modern and extinct aquatic taxa for which bone profiler values were obtained (see S3). The comparative taxa are included to observe, in addition to the placodont diversity, the distribution of Placodontia within aquatic taxa. A, based on humeri. B, based on femora. Abbreviations for the taxa in the PCA graphs as in (S3).

2012; Chinsamy Turan, 2012; Griebeler *et al.*, 2013). The two main trends in life history strategies in extant vertebrates can be summarized—though largely simplified—as lamellar-zonal bone tissue vs. fibro-lamellar bone tissue. Both tissue types seem to be linked to a certain metabolism (poikilotherms vs. homoeotherms; see *e.g.* Houssaye, 2012). Bone microstructure (*i.e.*, bone compactness, occurrence and size of the medullary cavity, presence of perimedullary region, spongy- or trabecular-like organization, vascularity, etc.) has shown to reflect lifestyle (*e.g.* Canoville and Laurin, 2010; Houssaye *et al.*, 2010, 2014; Dumont *et al.*, 2013; Quemeneur *et al.*, 2013) and can indicate ecological preferences (*e.g.* Buffrénil *et al.*, 1987, 1990; Laurin *et al.*, 2004, 2007, 2011; Germain and Laurin, 2005; Hayashi *et al.*, 2013; Houssaye *et al.*, 2013).

It is the aim of the current paper to describe and compare long bone histology and microanatomy of armoured and non-armoured placodont taxa and to address and compare their lifestyles in a phylogenetic framework. The following questions will be addressed: since our placodont sample spans most of the stratigraphical range of the group, can evolutionary stasis or changes/trends be identified? As the samples originate from various localities of the Germanic Basin (shallow

marine environments) and of the Alpine Triassic (shallow to open sea environments), can histology be linked to habitat preferences? Can histological characteristics of isolated long bones be used for taxonomic assignment to a group? If so, this would increase the morphological knowledge of placodonts as was done before for other Sauropterygia (*e.g.* Klein, 2010, 2012; Sander *et al.*, 2013).

*Previous works on long bone histology and microanatomy of placodonts*

Placodont long bone tissue has been previously studied by Buffrénil and Mazin (1992). The humerus sampled and described therein was assigned to *Placodus*, although this assignment cannot be verified. The humerus that was figured by Drevermann (1933) in his description of *Placodus gigas* was later identified to belong to a nothosaur (Rieppel, 1995). The skeleton of the complete *P. inexpectatus* is still embedded in sediment, which makes it difficult to address and compare all morphological features of both humeri of that individual (Jiang *et al.*, 2008; NK, pers. obs.). Thus, an unequivocal taxonomical assignment to a certain placodont taxon of the humerus thin sectioned by Buffrénil

Table 1. List of material, measurements (in mm), localities, and stratigraphical information of sampled placodont bones and *Horaffia kugleri*. Abbreviations: dw/dl = distal width/distal length; mw/ml = midshaft width/midshaft length; nm = not measured; pw/pl = proximal width/proximal length; pm = perimeter.

taxon/specimen number/bone	length	pw/ pl	mw/ ml	dw/ dl	pm	stratigraphic age	locality	limb bones
<i>Henodus</i> (armoured)								
GPIT/RE/7289 humerus	nm	nm	nm	nm	~55	Carnian	Tübingen-Lustnau (B-Württemberg, Germany)	reduced
<i>Psephoderma</i> (armoured)								
PIMUZ A/III 1476 humerus	55.4	14.6 nm	6.0 6.2	nm nm	20	Rhaetian	Tinzenhorn, Fil da Stidier, Filisur (Grissons, Switzerland)	reduced
PIMUZ A/III 0735 femur	85.6	25.1 10.1	9.3 8.5	19.0 nm	30	Rhaetian	Chrachenhorn, Monstein (Grissons, Switzerland)	reduced
Placodontia indet. aff. <i>Cyamodus</i> (armoured)								
SMNS 59831 humerus	> 120	nm	39.1 26.05	95 38.9	110	Ladinian (Upper Muschelkalk)	Weiblingen (B-Württemberg, Germany)	massive
SMNS 15937 humerus	222	52.4 29	35.6 29.2	65 ~30	105	Ladinian (Upper Muschelkalk)	Crailsheim/Tiefenbach (B-Württemberg, Germany)	massive
MHI 2112/6 humerus	~205	> 38 > 49.5	35.2 23.5	64.2 27.8	96	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Satteldorf-Barenhalden (B-Württemberg, Germany)	massive
SMNS 54569 humerus	> 129	61 38	35 23	nm nm	92	Ladinian (Upper Muschelkalk)	Hegnabrunn (Bavaria, Germany)	massive
SMNS 54582 humerus	> 85	nm	29.5	68	~79	Ladinian (Muschelkalk/Keuper)	Obernbreit (Bavaria, Germany)	massive
SMNS 15891 humerus	175	45.5 22	28 17	~54 24	76	Ladinian (Upper Muschelkalk)	Crailsheim/Tiefenbach (B-Württemberg, Germany)	massive
MHI 697 humerus	> 111	nm	28.9 18.2	59.2 20.2	82	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Satteldorf-Barenhalden (B-Württemberg, Germany)	massive
MHI 1096 humerus	> 67	> 24.7 20.2	18.5 13.2	nm nm	54	Ladinian (Upper Muschelkalk)	Ummenhofen (B-Württemberg, Germany)	massive
aff. <i>Placodus</i> (non-armoured)								
SMNS 59827 humerus	148	28.4 35	24 20	49 17.5	75	Ladinian (Upper Muschelkalk)	Hegnabrunn (Bavaria, Germany)	massive
<i>Paraplacodus</i> (non-armoured)								
PIMUZ T5845 humerus	104.5	24.5 ~12	~16 ~6	~35 nm	~39	Anisian/Ladinian (Besano Formation, Middle Grenzbitumenzone)	Monte San Giorgio, Meride (Ticino, Switzerland)	reduced

PIMUZ T5845 femur	89.1	nm	9.8	nm	~25	Anisian/Ladinian (Besano Formation, Middle Grenzbitumenzone)	Monte San Giorgio, Meride (Ticino, Switzerland)	reduced
MB.R. 454 humerus	120	20.8	18.5	34	53	Anisian (Lower Muschelkalk)	Ohrdruf (Górný Śląsk, Poland)	massive
IGWH 9 humerus	68	29 13 15	9.9 14.5 9	17 20 9.5	~36.5	Anisian (Lower to Middle Muschelkalk)	Freyburg, River Unstrut valley (East-Germany)	massive
SMNS 84545 femur	>160	58	32	nm	~105	Ladinian (Muschelkalk/Keuper)	Hegnabrunn (Bavaria, Germany)	massive
IGWH 23 femur	>57	27 28	15.5 14.5	nm nm	~55.3	Anisian (Lower to Middle Muschelkalk)	Freyburg, River Unstrut valley (East-Germany)	massive
MB.R. 814.2 femur	>100	nm	38	nm	~127	Anisian (Lower Muschelkalk)	Górný Śląsk, Poland	massive
MB.R. 961 femur	>145	nm >47 >41	33 28.6 27.4	nm >34 >28	~89	Ladinian (Upper Muschelkalk)	Bayreuth	massive
SMNS 54578 femur	>122	30	20	22.5	72	Ladinian (Upper Muschelkalk)	Hegnabrunn (Bavaria, Germany)	massive
MB.R. 812 femur	>120	34 >35	21.5 25.5	30.4 >31	~70.6	Anisian (Lower Muschelkalk)	Opatowitz (Górný Śląsk, Poland)	massive
MB.R. 965 femur	146	25 30.5 36	24 15.4 15.5	>28 35 19	56	Anisian (Lower Muschelkalk)	Górný Śląsk, (Poland)	massive
<i>Horaffia kugleri</i>								
SMNS 84816 humerus	~83.5	22.3 13.7	15.3 10.5	32.85 10	43	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Crailsheim (B-Württemberg, Germany)	massive
MHI 2112/1 humerus	77.6	23.4/ 12.3	18.2/ 12.5	29 9.7	50	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Satteldorf-Barenhalden (B-Württemberg, Germany)	pachyostotic
MHI 2112/2 humerus	>111	31.4 29.2	21.9 16.7	~33.4 19.7	65	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Vellberg-Eschenau (B-Württemberg, Germany)	pachyostotic
MHI 2112/3 humerus	134	36.5 39.5	28.8 21.8	50.4 27.1	82	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Crailsheim/Tiefenbach (B-Württemberg, Germany)	pachyostotic
MHI 2112/4 humerus	152	42 37.8	32 20	55.2 20.1	92	Ladinian (Muschelkalk/Keuper Grenzbonebed)	Obersontheim-Ummenhofen (B-Württemberg, Germany)	pachyostotic



Table 2. Bone histological and microanatomical characteristics of sampled placodont long bones and *Horaffia kugleri* humeri. Abbreviations: C = bone compactness; cc = calcified cartilage in medullary region; FLB = fibro-lamellar bone tissue; LZB = lamellar zonal bone tissue; nm = not measurable; smr = size of medullary region measured along the long axis of the sample in pre-postaxial direction.

specimen number	sampling location	medulla	smr	cc	bone tissue	dom. vascular system	C
<i>Henodus</i>							
GPII/RE/7289	photo of midshaft cross section	?	nm	?	?FLB	?plexiform to radiating	nm
<i>Psephoderma</i>							
PIMUZ A/III 1476 humerus	midshaft	med. region/perimed.	15.5%	no	LZB	longitudinal	91.2
PIMUZ A/III 0735 femur	midshaft	med. region/perimed.	22.6%	no	LZB	circumferential	78.2
<i>Placodontia</i> indet. aff. <i>Cyamodus</i>							
SMNS 59831 humerus	midshaft	free med. cav.	7.2%	no	FLB	plexiform to radiating	82.3
SMNS 15937 humerus	midshaft	free med. cav.	13.1%	no	FLB	plexiform to radiating	79.9
SMNS 54569 humerus	midshaft to prox.	med. region	12%	yes	FLB	plexiform to radiating	87.1
MHI 21126 humerus	midshaft	free med. cav.	~3.5%	no	FLB	plexiform to radiating	84.7
SMNS 54582 humerus	midshaft	free med. cav.	18.3%	yes	FLB	plexiform to radiating	84.7
SMNS 15891 humerus	midshaft	free med. cav.	13.5%	no	FLB	plexiform to radiating	85.9
MHI 697 humerus	midshaft	med. region	18%	yes	FLB	plexiform to radiating	81.8
MHI 1096 humerus	midshaft	free med. cav.	12.7%	no	FLB	plexiform to radiating	78.5
aff. <i>Placodus</i>							
SMNS 59827 humerus	micro-CT-scan	med. region	nm	?	?FLB	?plexiform to radiating	nm
<i>Paraplacodus</i>							
PIMUZ T 5845 humerus	midshaft	med. region	45%	yes	LZB	reticular to radiating	94.7
PIMUZ T 5845 femur	midshaft	med. region	35.3%	yes	LZB	reticular to radiating	97.9
<i>Placodontia</i> indet.							
IGWH 9 humerus	midshaft	med. region	33%	yes	FLB	circumferential to reticular	82.7
MB.R. 454 humerus	midshaft	med. region	61% (41%)	no	FLB	circumferential to reticular	82.4
SMNS 84545 femur	midshaft	med. region/peri.	23.4%	no	FLB/LZB	circumferential to reticular	77.5
IGWH 23 femur	midshaft	med. region/peri.	60%	no	FLB	circumferential to reticular	83.5
MB.R. 814.2 femur	midshaft	free med. cav./perimed.	32.6%	no	FLB	circumferential to reticular	75.1
MB.R. 961 femur	midshaft	free med. cav.	19.7%	no	FLB	circumferential to reticular	79.3
MB.R. 812 femur	midshaft	free med. cav.	16.6%	no	FLB	circumferential to reticular	75.7
SMNS 54578 femur	midshaft to distal	med. region/peri.	42.3% (26.4%)	no	FLB	circumferential to reticular	72.8
MB.R. 965 femur	micro-CT-scan	med. region	?	?	?FLB	?circumferential to reticular	nm
<i>Horaffia kugleri</i>							
SMNS 84816	midshaft	free med. cav.	7.7%	yes	FLB	plexiform to radiating	86.3
MHI 2112/1 humerus	midshaft	med. region	10% (16.5%)	yes	FLB	plexiform to radiating	87.2
MHI 2112/2 humerus	midshaft	free med. cav./perimed.	27.3% (38.6%)	yes	FLB	plexiform to radiating	83.8
MHI 2112/4 humerus	midshaft	med. region	16.6%	no	FLB	plexiform to radiating	82.7

and Mazin (1992) is not possible. Buffrénil and Mazin (1992) characterized the bone tissue as highly vascularized fibro-lamellar bone with a mainly plexiform and reticular vascularization that is in some parts essentially radial. According to Buffrénil and Mazin (1992) inner resorption is very limited. Ricqlès and Buffrénil (2001: 292) also referred to the placodont sample of Buffrénil and Mazin (1992) and characterized the bone as having a ‘pachyostotic-like condition [resulting] from an absence, or a very poor development of the marrow cavity, instead of a true hyperplasy of periosteal cortices’. Among a sample of various Triassic Sauropterygia Klein (2010) studied two bones assigned to Placodontia indet. that are also included into the current study (IGWH 9, IGWH 23; Table 1) and found that these two bones have the highest growth rates within Sauropterygia. In their quantitative study of humeral microanatomy and lifestyle in amniotes Canoville and Laurin (2010) included the placodont sample of Buffrénil and Mazin (1992) and postulated that this specimen had an amphibious lifestyle. However, they admitted that their inference required to be interpreted with caution, because of an ‘apparent contradiction in the various signals’ (Canoville and Laurin, 2010: 401). Houssaye (2012), in a review on bone histology of aquatic reptiles with inferences on secondary adaptations to an aquatic life, concluded that the sampled placodont bone from the study of Buffrénil and Mazin (1992), together with some ichthyosaurs and plesiosaurs, showed the highest growth rates within aquatic reptiles.

Klein and Hagdorn (2014) described a new marine reptile taxon, *Horaffia kugleri*, from the Ladinian of southwest Germany. Its bone histology is described and compared to that of cf. *Cyamodus* (herein assigned to Placodontia indet. aff. *Cyamodus*) humeri from the same horizon. Humeri of *Horaffia kugleri* are pachyostotic whereas those of cf. *Cyamodus* are not. Humerus histology is essentially similar in both taxa and can be summarized as highly vascularized, plexiform to radiating fibro-lamellar bone tissue with a poorly developed medullary cavity or region, resulting in osteosclerosis. The samples of *Horaffia kugleri* and cf. *Cyamodus* described by Klein and Hagdorn (2014) are included in the PCA of the current study.

## Material and methods

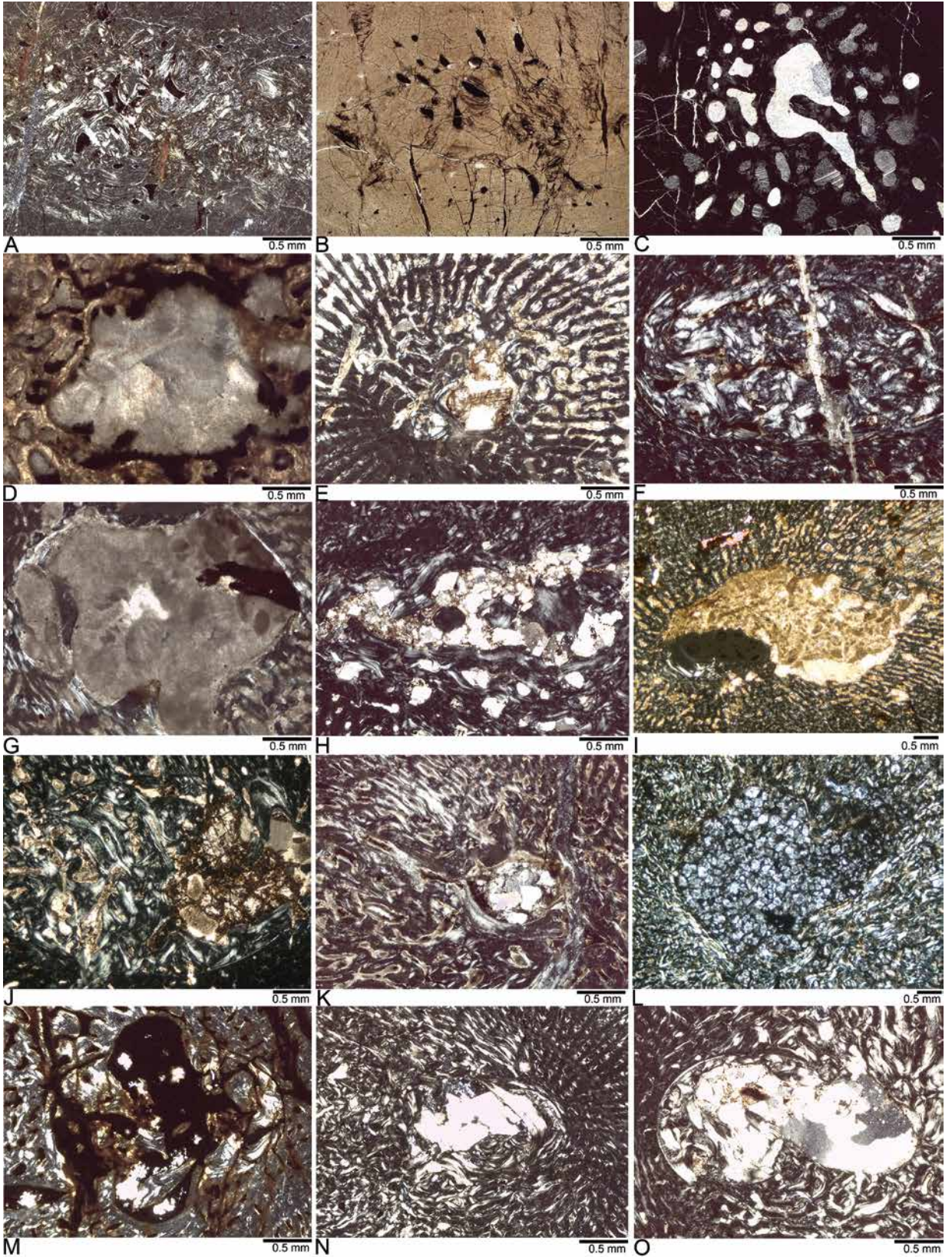
For the current study humeri and femora of placodonts were sampled (Fig. 2). These bones usually have most of the primary periosteal bone tissue preserved (e.g. Klein

and Sander, 2007) and yield the strongest ecological signal (Canoville and Laurin, 2010). A morphological description for each bone is given in the supplementary information (S1). The material includes armoured and non-armoured Placodontia and spans most of the stratigraphical range of the group from the early Anisian (Middle Triassic) to the Rhaetian (Late Triassic) (Table 1). Paleogeographically, the sample focuses on the western Tethys *i.e.*, on localities from the Germanic Basin and the Alpine Triassic. For further information on localities, as well as the paleogeographical and stratigraphical ranges of placodont taxa, please see Rieppel and Hagdorn (1997), and Hagdorn and Rieppel (1999). A complete list of the bones sampled in this study, with associated measurements, is given in Table 1.

The humeri and femora were photographed, measured, and described using traditional paleontological methods (Table 1; S1-2). When possible, bones were sampled exactly at midshaft by cutting an entire cross section. The importance of exact midshaft samples for comparability was pointed out before (e.g. Konietzko-Meier and Klein, 2013). However, in some specimens, sampling location is slightly proximal or distal to the midshaft on account of bone preservation (see Table 2). The thin sections were produced following standard petrographic methods (Klein and Sander, 2007). Thin sections were then studied and photographed with a Leica® DMLP compound polarizing microscope, equipped with a digital camera (Leica® DFC 420C) and a Leica® DM 750P compound polarizing microscope equipped with a digital Leica® ICC50HD camera. Cross-sections were scanned with an Epson V740 PRO high-resolution scanner (Fig. 2). The bone histological terminology follows Francillon-Vieillot *et al.* (1990). The size of the medullary cavity/region was measured along the pre-postaxial width of the bones (Table 2).

Some samples were micro-CT scanned with a vltomelxs by GE phoenixlx-ray at the Steinmann Institute of Geology, Mineralogy and Paleontology (StIPB) (Table 2). Image visualization was performed using VGStudio MAX 2.0 software (Volume Graphics GmbH) and Adobe Photoshop. CT slices were used to trace vascularity and bone tissue type. However, contrast between bone and the infilling sediment, and resolution were not always sufficient to precisely determine these features.

Scanned pictures of thin sections were transformed into black (vascular spaces) and white (bone) pictures (S4) that were analyzed with the program Bone Profiler (Girondot and Laurin, 2003) (Table 2; Fig. 3; S3). We



examined five parameters provided by this software to characterize the bone density distribution: C, P, S, Min and Max. C is the global bone compactness for the whole sectional area. P, is the relative distance from the center of the section to the point where the most abrupt change in compactness is observed, which is proportional to the size of the medullary cavity. S, is the reciprocal of the slope at the inflection point, generally reflects the width of the transition zone between the cortical bone and the perimedullary region. Min and Max are, respectively, the minimum and maximum asymptotes and thus represent the minimum and maximum bone compactness values in a section. A Principal Component Analysis (PCA) was performed on the Bone Profiler parameters cited above using the statistic software R (R Development Core Team, 2008) in order to explore the distribution of the different taxa in morphospace while optimizing the variance. Various extant and fossil aquatic amniotes (S3) were added to our sample in the PCA.

#### Abbreviations

IGWH	Institute of Geosciences of the Martin-Luther-University Halle-Wittenberg, Germany
MfN (MB.R.)	Museum of Natural History, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Germany
MHI	Muschelkalkmuseum Ingelfingen, Germany
PIMUZ	Paleontological Institute and Museum of the University of Zurich, Switzerland
SMNS	Stuttgart State Museum of Natural History, Germany

## Results

### Microanatomical description

The humerus and femur of *Psephoderma alpinum* both have a central free medullary cavity that is surrounded by scattered large erosion cavities (in a perimedullary region), which reach far into the cortex (Table 1; Figs 2C, D; 3C, D). The erosion cavities are mainly roundish to oval shaped. In the humerus, they are randomly organized whereas those in the femur are arranged in circumferential rows. Vascular density is low (Table 2, 3).

The photograph of the midshaft cross section of the *Henodus* humerus indicates a relatively large medullary region consisting of large cavities and randomly organized trabecles (Table 1; Fig. 2E) surrounding a rather small medullary cavity. The vascular system is dominated by a radial organization and contains longitudinal and radial canals as far as observable. In general, microstructure of *Henodus* seems to be comparable to that of Placodontia indet. aff. *Cyamodus humeri* (see below).

Midshaft samples of humeri of Placodontia indet. aff. *Cyamodus* usually show a small free medullary cavity (Figs 2F-M; 4E-L) that is lined by a thin layer of endosteal bone, those that were not taken exactly at midshaft have a medullary region consisting of small cavities, endosteal bone deposits, and scattered pockets of calcified cartilage (Figs 4F, J). The medullary region is then surrounded by a sharp line, which consists of a very thin layer of endosteal bone. Vascular density in the humeri is poor in the innermost cortex but always high in the middle and outer cortex (Table 2; Figs 2F-M; 4E-L). Contrary to the condition in other vertebrates vascular density increases towards the outer cortex in Placodontia indet. aff. *Cyamodus humeri*. Long and thick, mainly radial vascular canals forming a primary trabecle-like architecture dominate locally the inner to middle cortex of the pre- and postaxial bone sides. The entire cortex of humeri MHI 1096, SMNS 15937, and SMNS 59831 is spongy-like in organization: al-

- ◀ Fig. 4. Details of medulla and inner cortex of Placodontia long bones. A, Humerus in polarized light and B, Femur in normal light of *Paraplagcodus broilii* (PIMUZ T5845). The medullary region consists of endosteal deposits with pockets of calcified cartilage in between. In the femur large erosion cavities occur in the centre of the section. C, Humerus (PIMUZ A/III 1476) and D, Femur (PIMUZ A/III 0735) of *Psephoderma alpinum* both in polarized light. Note that the medullary cavities are surrounded by a distinct perimedullary region. E-L, Placodontia indet. aff. *Cyamodus humeri* all in polarized light. Except for SMNS 54569 (Fig. 3), which represents a more proximal sample and MHI 697 all midshaft samples exhibit a small free cavity. SMNS 54569 (Fig. 3) and MHI 697 (Fig. 3F) show a medullary region infilled by secondary trabecels, sediment filled cavities, and pockets of calcified cartilage. E, MHI 1096. F, MHI 697. G, SMNS 59831. H, SMNS 15891. I, SMNS 54582. J, SMNS 54569. K, MHI 2112/6. L, SMNS 15937. M-O, Humeri of the marine reptile *Horaffia kugleri*. *Horaffia kugleri* has a small free cavity surrounded by a medullary region at midshaft. M, MHI 2112/4. N, SMNS 84816. O, MHI 2112-1.

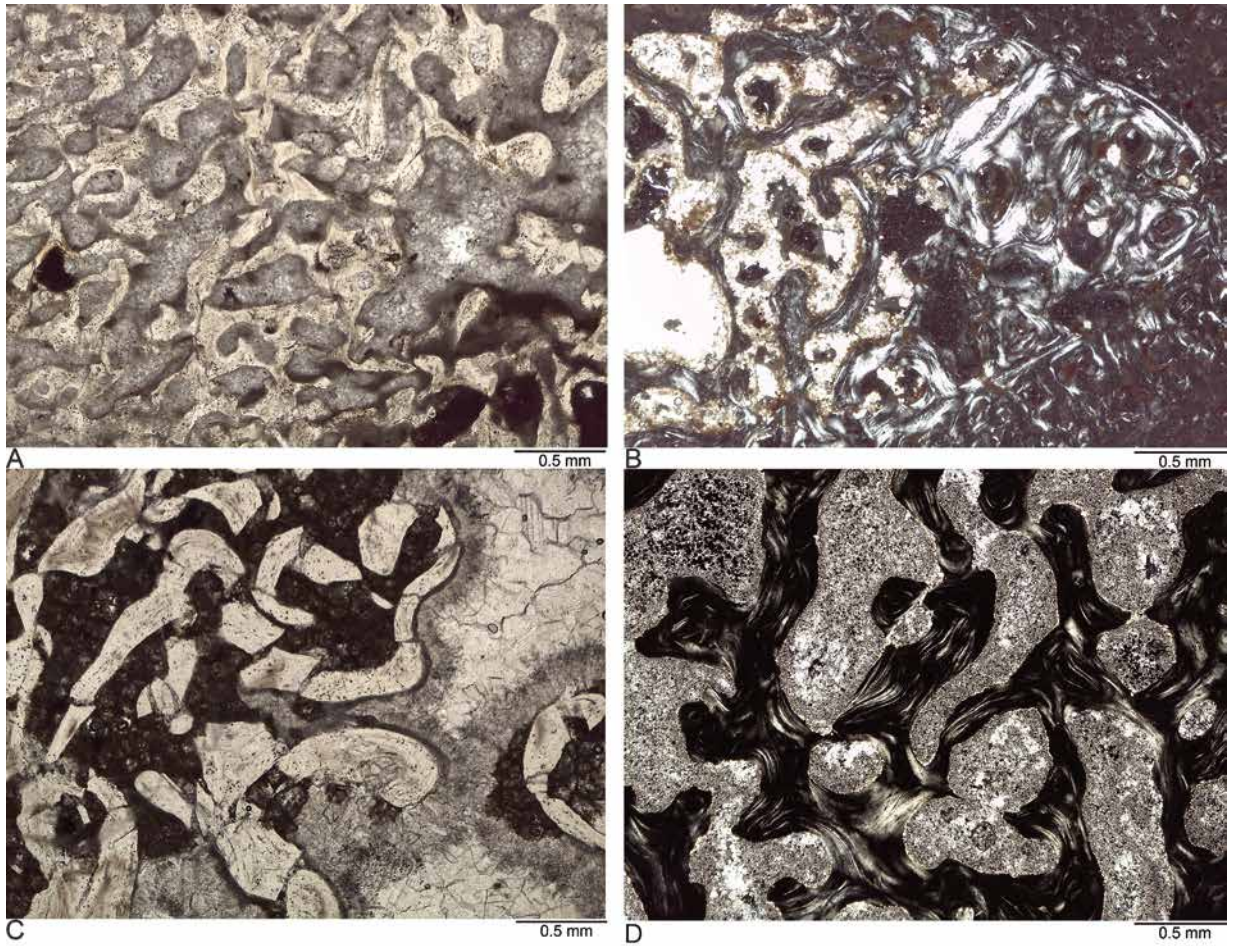


Fig. 5. Details of medulla and inner cortex of Placodontia indet. humeri and femora. All bones have a large medulla consisting of secondary trabecles and large cavities. A, Medulla of humerus MB.R. 454 in normal light. B, Medulla of humerus IGWH 9 in polarized light. C, Medulla of femur SMNS 84545 in normal light. D, Medulla of femur IGWH 23 in polarized light.

though the surface occupied by bony tissues represents much more than 50% of the cortex surface, the high amount of primary osteons with large vascular spaces confers to the cortex a spongy aspect (Table 2, 3; Figs 2, 7). In the other samples, the inner cortex can be locally spongy-like and/or trabecular-like. All samples share a spongy-like organization of the outer cortex (Fig. 7). The spongy-like organization is the result of locally primary spongy and trabecular bone and secondarily widened primary osteons.

The midshaft of a humerus (SMNS 59827), which is thought to represent aff. *Placodus* (Vogt 1983; Rieppel 1995) was micro-CT-scanned. The resolution of the resulting pictures is poor, which is however often the case for Muschelkalk samples (NK,

pers. obsv.). A medullary cavity in the center of the cross section cannot be identified and the organization seems to be rather loose, most likely indicating a medullary region (Fig. 2O). The vascular system resembles that of humeri of Placodontia indet. aff. *Cyamodus*. The outer cortex clearly shows large vascular canals (Fig. 2O).

The humerus and femur of *Paraplacodus broilii* both have a medullary region that is densely packed with endosteal deposits and pockets of calcified cartilage (Figs 2A, B; 4A, B). The bone tissue is nearly avascular (Table 2; Figs 6C, D).

The medullary region of humerus MB.R. 454 (Placodontia indet.) is very large (Figs 2P, 5A). The area consists of thin secondary trabecles surrounding intertrabecular spaces. Humerus IGWH 9 (Placodontia

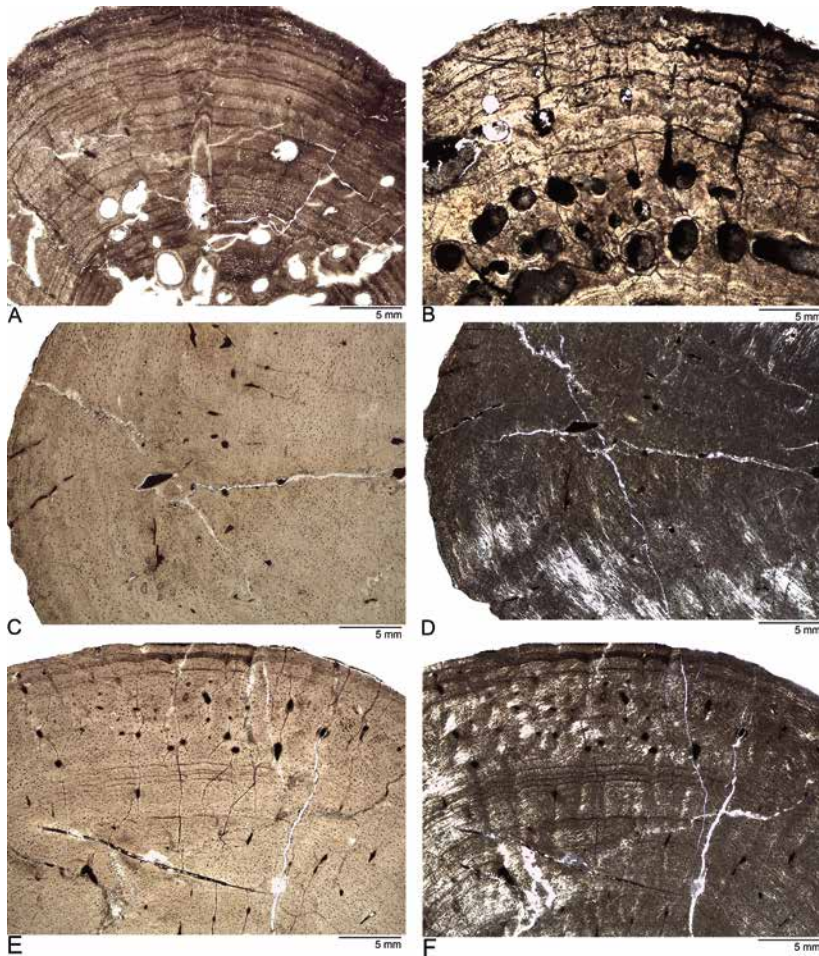


Fig. 6. Histological details of armoured *Psephoderma* and non-armoured *Paraplacodus*. A, Detail of lamellar-zonal bone tissue of *Psephoderma* humerus (PIMUZ A/III 1476) and B, femur (PIMUZ A/III) in normal light. Note the large erosion cavities of the perimedullary region in both bones. C, Detail of lamellar-zonal bone tissue of *Paraplacodus* humerus (PIMUZ T5845) in normal light and D, in polarized light. E, Detail of lamellar-zonal bone tissue of *Paraplacodus* femur (PIMUZ T5845), normal light and F, in polarized light.

indet.) also shows a large medullary region and a trabecle-like architecture at the postaxial bone side (Figs 2Q, 5B). The medullary region is filled by endosteal deposits. Vascular density is moderate (MB.R. 454) or high (IGWH 9) (Table 2). Bone compactness increases towards the outer cortex in both samples.

Femora IGWH 23 and SMNS 84545 (both *Placodontia* indet.) both have a large medullary region that consists of several generations of secondary trabecles (Fig. 5C, D). Please note that the cortex is incomplete in IGWH 23 at the dorsal and preaxial bone sides due to preservation (Fig. 25). Ventrally, large irregularly shaped cavities are aligned in circumferential rows. The cortex is in both scattered with randomly shaped and oriented large cavities, resulting in a spongy-like tissue (Fig. 2R, S).

Midshaft sections of placodont femora MB.R. 814.2, MB.R. 961, and MB.R. 812 (Figs 2U, V, X)

have an off-centered free medullary cavity, which corresponds to a medullary region in the more distal section SMNS 54578 (Fig. 2W). The medullary region in non-midshaft sample SMNS 54578 consists of secondary trabecles. Vascular density in all specimens is high (Table 2). The vascular canals have undergone resorption resulting in the formation of large cavities. All samples show locally (mainly at the dorso-postaxial bone sides) a radial or irregularly formed trabecle-like architecture and locally spongy-like tissue. Vascular density decreases towards the outer cortex. One placodont femur (MB.R. 965) was micro-CT-scanned. The quality of the resulting pictures documents a similar microstructure as was described for the femora above: most of the cross section shows a large medullary region followed by spongy-like tissue in the inner cortex (Fig. 2T). Locally a trabecle-like architecture is visible. Only the outer cortex region is compact.

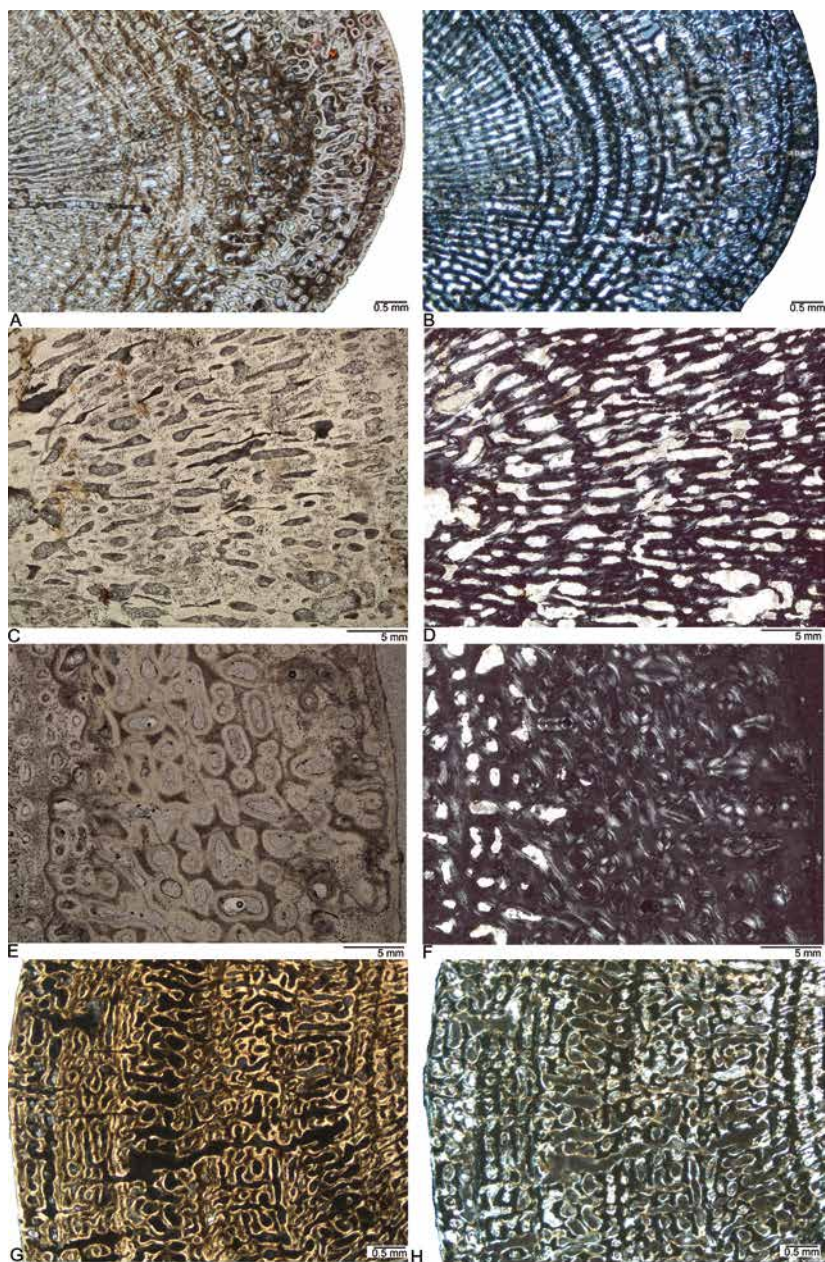


Fig. 7. Histological details of humeri of Placodontia indet. aff. *Cyamodus*. A, Detail of the postaxial bone side of humerus MHI 1096 in normal light and B, in polarized light. The inner cortex shows a spongy tissue and a radial trabecle-like structure. In the middle cortex vascular canal organization changes to longitudinal and mainly irregular vascular spaces. The spongy tissue continues until the outermost cortex. Note the fibro-lamellar bone tissue between the radial trabecular spaces. C, Detail of spongy inner cortex with radial, longitudinal, and irregularly formed vascular canals of humerus SMNS 54582 in normal light and D, in polarized light. E, Detail of outer cortex with secondarily widened longitudinal primary osteons of humerus SMNS 54569 in normal light and F, in polarized light. G, Detail of humerus SMNS 15937 in normal light and H, in polarized light. The middle to outer cortex shows a trabecle-like structure with radial, circumferential, reticular, and irregular vascular canals. Vascular canals are connected by anastomosis. The entire cortex contains secondarily widened vascular canals.

### Histological description

The bone tissue of the humerus and femur of *Psephoderma alpinum* is altered by diagenesis in both samples and its nature is obscured under cross-polarized light. Scattered erosion cavities, which are thinly lined by lamellar bone, indicate remodelling. Primary bone tissue seems to consist solely of lamellar bone and did not show any osteocyte lacunae. Both bones show only a

few longitudinal vascular canals in their outer cortex that are thinly lined by lamellar bone, and so correspond to primary osteons (Fig. 6A). In the humerus they occur at the postaxial side and in the femur at the ventral side (Fig. 6B). The cortex is divided by growth marks (Klein *et al.*, unpubl. data). The bone tissue type can be summarized as lamellar-zonal bone.

The cortex of *Henodus* shows mainly longitudinal and radial vascular canals that are arranged in a plexi-

form to radiating system (Table 2), resembling that of Placodontia indet. aff. *Cyamodus* humeri. Details of bone tissue cannot be established due to the poor resolution of the micro-CT-scan.

The bone tissue type of Placodontia indet. aff. *Cyamodus* can be summarized as radiating to plexiform fibro-lamellar bone. Woven bone is typically comprised by lamellar bone. However, the core of woven bone can correspond to parallel-fibred bone based on the extinction pattern under polarized light that is made of coarse and thick fibers, which overlay each other. However, the large, round, and numerous osteocyte lacunae resemble the chaotic arrangement seen in typical woven bone. In the outer cortex of SMNS 59831 osteocyte lacunae are almost flat, and thus more in accordance with typical parallel-fibred bone. All kinds of vascular canals are present: radial, longitudinal, reticular, and circumferential ones. Vascular canals often show a tendency to anastomose. Radial vascular canals in the outer cortex are often connected to the bone surface. Longitudinal vascular canals tend to be lined up in rows whereas radial canals can cross growth marks. Onset of remodelling processes is indicated by local cross cutting and cementing lines are sometimes visible (Fig. 7). In two samples (SMNS 54582, MHI 2112-6) infilled (mature) secondary osteons (sensu Currey, 2002) can occur in the innermost cortex. In the inner cortex, vascular canals are often not or only incompletely lined by lamellar bone representing neither simple vascular canals nor fully developed primary osteons (Fig. 7, S5A-C), which we identify as immature primary osteons (Klein, 2010). The number of fully lined primary osteons increases generally towards the outer cortex. The primary osteons are throughout the entire cortex secondarily widened by successive resorption processes. A thick layer of lamellar bone surrounds the widened primary osteons then, which are however, far away from being infilled, resulting in incomplete or immature secondary osteons (S5, 6). The development of these osteons can impede the observation of the nature of the collagenous wave of the surrounding bone (Figs 7E-H). Bone tissue can locally be obscured by diagenesis (*i.e.* bacteria and/or fungal growth) or by a dark permineralization of the bone. Placodontia indet. aff. *Cyamodus* humeri show an alternation of broad, highly vascularized layers of fibro-lamellar bone (zones) and thin, avascular layers made of highly organized parallel-fibred bone or lamellar bone (annuli) (Klein *et al.*, unpubl. data). No clear increase in bone tissue organization from the inner to the outer cortex is visible except in the medium sized humerus SMNS 54582 (that has in general a

higher organized and less vacularized bone tissue) and SMNS 59831, which is the largest sampled bone and the only one that shows lamellar bone in the outermost cortex.

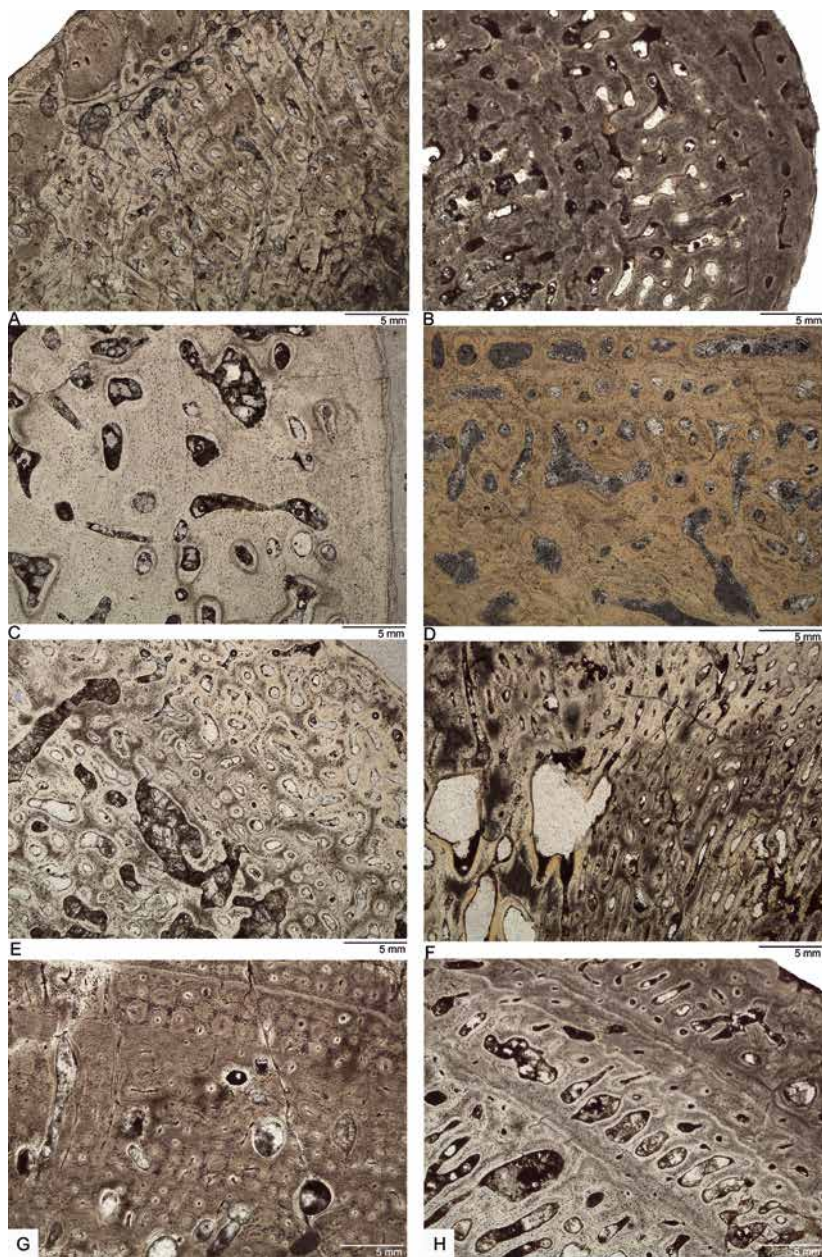
Details of bone tissue of the humerus assigned to Placodontia indet. aff. *Placodus* (SMNS 59827) cannot be addressed due to the poor resolution of the micro CT-scan. Growth marks are visible in the outer cortex.

The primary bone tissue of the humerus and femur assigned to *Paraplacodus broilii* is in the inner cortex highly organized parallel-fibred bone that, towards the outer cortex, grades into lamellar bone (Figs 6C, D). Simple longitudinal and radial vascular canals dominate the tissue but immature primary osteons also occur. The entire bone tissue is interspersed by regularly sized, small but round osteocyte lacunae. The cortex is divided by growth marks (Klein *et al.*, unpubl. data). The bone tissue type can be summarized as lamellar-zonal bone.

The bone tissue of humeri MB.R. 454 and IGWH 9 (both Placodontia indet.) consists of coarse parallel-fibred bone, intermixed with woven bone. Primary osteons are surrounded by lamellar bone, resulting in fibro-lamellar bone tissue (Figs 8A, B). Numerous thick osteocyte lacunae are accumulated in the areas of woven and coarse parallel-fibred bone. Both samples share an increase in organization towards the outermost cortex. Vascular canals are radial, longitudinal, and reticular. They are arranged in a mainly plexiform system and canals are locally lined up in rows. The inner cortex is dominated by immature primary osteons, the outer cortex by fully developed primary osteons. The cortex of MB.R. 454 and IGWH 9 is divided by growth marks (Klein *et al.*, unpubl. data).

In femora IGWH 23 and SMNS 84545 (both Placodontia indet.) the bone tissue consists of fibro-lamellar bone with coarse parallel-fibred and woven bone (Figs 8C, D). The organization of the bone tissue increases towards the outer cortex. In SMNS 84545, tissue organization is generally higher and the outer cortex is solely made of avascular lamellar bone, except for a few, mainly radial canals that open into the surface. Osteocyte lacunae are small but numerous and accumulated in the areas of woven and coarse parallel-fibred bone. In both, the vascular canals are mainly irregularly/reticularly formed. Some represent immature, others mature primary osteons. In SMNS 84545 vascular canals are largely eroded into irregularly formed cavities. The cortex is in both samples divided by growth marks. Infilled (mature) secondary osteons are rare but can occur in the inner cortex.





*Fig. 8.* Histological details of Placodontia indet. humeri and femora. All samples are in normal light. A, Detail of cortex of humerus MB.R. 454. B, Detail of cortex of humerus IGWH 9. C, Detail of cortex of femur SMNS 84545. D, Detail of cortex of femur IGWH 23. The cortex is spread with irregularly formed large vascular canals. E, Detail of cortex of femur SMNS 54578. F, Detail of cortex of femur MB.R. 812. G, Detail of cortex of femur MB.R. 961. H, Detail of cortex of femur MB.R. 814.2. All samples have secondarily widened primary osteons.

The bone tissue in the Placodont indet. femora (MB. R. 814.2, MB.R. 961, MB.R. 812, SMNS 54578) is fibro-lamellar with woven bone or coarse parallel-fibered bone and primary osteons surrounded by lamellar bone (Figs 8E-H). The organization of the bone tissue increases towards the outer cortex as the number of vascular canals decreases. In the two largest sampled femora, MB.R. 814.2 and MB.R. 961, the outer cortex is made of lamellar bone. All kind of

vascular canals occur (longitudinal, radial, circumferential, and reticular) but longitudinal and radial ones dominate. Locally, vascular canals are lined up in circumferential rows. Most of the vascular canals have been developed into primary osteons but immature primary osteons also occur. Details of the bone tissue of femur MB.R. 965 are not visible in micro-CT-pictures. All samples show growth marks throughout the cortex (Klein *et al.*, unpubl. data). All Placo-

dontia indet. bones show locally primary spongy and trabecular bone and a secondary widening of osteons (Fig. 8; S5, 6).

#### Results of the Principal Components Analysis

The PCA of the humeri (see Fig. 3A) shows that the two main axes explain 66.7% of the variance (46.1 and 20.9% respectively). C is the only parameter that negatively contributes to the first axis. Taxa on the first axis essentially discriminate based on C and P (projections values of -0.21 and 0.24, respectively). On the second axis, they essentially discriminate based on Max and C (projections of 0.20 and 0.16, respectively). Only P negatively contributes to the second axis. The graph shows that very efficient swimmers (orange rectangle in Fig. 3A including cetaceans, ichthyosaurs, *Prognathodon* [Mosasauridae], *Dermochelys* [leatherback turtle], and the elephant seal *Mirounga*), together with the nothosaur humerus MB.R. 269, group together notably as a result of their relatively lower compactness. All specimens of Placodontia indet. aff. *Cyamodus* and *Horaffia* show a restricted distribution that highlights the strong ‘intraspecific’ similarity and, moreover, group together, close to the pachypleurosaur *Anarosaurus* and the *Pistosaurus* specimens. These taxa clearly distinguish from other less efficient swimmers, notably based on the relatively lower compactness of the cortex and the sharp transition between the compacta and the medullary cavity (with almost no spongy transition zone). *Paraplagodus* and *Psephoderma* are among the taxa showing the highest compactness. Together with the two Placodontia indet. humeri MB R 454 and IGWH 9, they group with the taxa showing a wider transition zone.

The PCA of the femora (see Fig. 3B) results in two main axes jointly explaining 72.4% of the variance (49.2 and 23.2%, respectively). Only the parameter C positively contributes to the first axis. On this axis, taxa essentially discriminate based on P (projection of -0.28) and, to a lesser extent, C and Min (projections of +/-0.24). Both S and P positively contribute to the second axis. On the second axis, taxa essentially discriminate based on Max (projection of 0.264) whereas P does almost not contribute to this axis. Because of its high compactness and absence of medullary cavity, *Paraplagodus* is isolated from the other taxa sampled. The other placodonts generally display an open medullary cavity or highly spongy medullary region and a rather large transition zone. Despite variation in the values of the corresponding parameters, the placodonts

sampled (among which no Placodontia indet. aff. *Cyamodus*) display a rather restricted distribution distinct from the other taxa except *Plesiosaurus*.

It must be specified that, as Bone Profiler was originally conceived for tubular structures, some peculiar microanatomical organizations obtain aberrant values in the program. It was the case for *Paraplagodus* bones, notably because compactness was higher in the core than in the outer surface of the bone, so that there was no sigmoid adapted to describe the structure. This was corrected based on an estimate for the analysis. As a result, *Paraplagodus* should have been much further away from the other taxa in the analysis (Fig. 3).

## Discussion

### Microanatomical tendencies

Within our placodont sample, five main distinct types of microanatomical organization are observed: 1) extremely compact humerus (CI=94.7%) and femur (CI=97.9%) with no medullary cavity in *Paraplagodus*; 2) strongly compact humeri (78.5% <CI<87.1%; mean value=83.1%) with a small open medullary cavity in Placodontia indet. aff. *Cyamodus* (no femur was available); 3) strongly compact humerus (CI=91.2%) with a small medullary cavity surrounded by a spongiosa and a compact outer cortex, and a rather compact femur (CI=78.2%) with a reduced medullary cavity surrounded by a thick spongiosa, with almost no outer compact cortex, in *Psephoderma*; and 4) humeri and femora with a large medullary region but no open medullary cavity and 5) femora with an open medullary cavity surrounded by a rather large spongiosa.

The extremely compact bones of *Paraplagodus* show strong osteosclerosis. Remodelling occurs in the core of the sections and is characterized by abundant endosteal bone deposits so that the medullary area is compacted. The humeri of Placodontia indet. aff. *Cyamodus* show a strong inhibition of primary bone resorption and remodelling process is initiated although only incompletely. They are similar to those of the diapsid *Horaffia kugleri*. However, if the latter are characterized by pachyosteosclerosis (Klein and Hagdorn, 2014), those of Placodontia indet. aff. *Cyamodus*, with no morphologically observable thickening, only display osteosclerosis (S2). As a result of the PCA Placodontia indet. aff. *Cyamodus* and the diapsid *Horaffia kugleri* along with *Pistosaurus* and the pachypleurosaur *Anarosaurus* are

well separated from both the remaining placodonts on the one hand and sustained swimmers on the other (Fig. 3).

The *Psephoderma* femur is characterized by periosteal bone resorption in form of a perimedullary region containing large erosion cavities. This is to a lesser degree also visible in the much smaller and more gracile humerus. Periosteal remodelling is initiated by the deposition of a thin layer of lamellar bone around the large erosion cavities. The femur organization of *Psephoderma* rather resembles that of the femur, humerus and rib of the diapsid *Claudiosaurus* (Buffrénil and Mazin, 1989) that was an anguilliform swimmer (Houssaye, 2012). Some humeri and femora from our sample, referred to as Placodontia indet. have a large medullary region consisting of secondary trabecles. The occurrence of open medullary cavities in other femora of Placodontia indet. suggests different functional requirements (swimming styles) and slow swimming skills.

#### *Ecological inferences and possible swimming styles*

According to Ricqlès and Buffrénil (2001), increase in skeletal density and mass is a clear advantage for poorly active aquatic tetrapods because the resulting additional ballast allows a hydrostatic (passive) control of body trim in water and counteracts lung buoyancy. As a result it facilitates diving and extended underwater stays and improves stability in rough water (Taylor, 1994). Conversely, this skeletal specialization increases the inertia of the body and induces limitations of the swimming speed and capabilities to perform rapid maneuvers (Ricqlès and Buffrénil, 2001). A different pattern is a spongy general organization as a result of the combined absence of medullary cavity with an increase in cortical porosity due to the development of erosion bays, which are not entirely filled up by secondary bone (Ricqlès and Buffrénil, 2001). In general one could say that taxa that lived in shallow water display an increase in bone compactness (Laurin et al., 2004), whereas species that lived in open marine habitats tend to have spongy bone (Ricqlès, 1977), as is obvious in e.g. several ichthyosaurs (Buffrénil and Mazin, 1990; Talevi and Fernandez, 2012; Houssaye et al., 2014).

All placodonts sampled share a thick cortex and clearly display bone mass increase (BMI) via osteosclerosis. However, the processes involved are disparate, as are the same global swimming mode. All placodonts are known from marine sediment except for *Henodus* that was found in lagoonal or lake sediments.

Thus, based on sediments and microanatomy an aquatic lifestyle in shallow marine habitats can be inferred for all. Due to their specialized durophagous dentition all placodonts have fed predominately on hard shelled mollusks that moved only slowly or were sessile. Thus, there was no need for placodonts to be fast swimmers. However, the discussion of swimming styles and capabilities remains difficult, because among modern aquatic vertebrates only sirenians display BMI, which makes interpretation of the placodont data difficult. Additionally, morphological, histological, and microanatomical inferences contradict each other in some taxa.

BMI is most intense in *Paraplacodus*. Importantly this taxon lacks any kind of armour, which could otherwise also serve as a source of body mass increase (e.g. Scheyer, 2007). If it was an inefficient swimmer, achieving long dives close to the bottom, a high increase in bone mass would have been advantageous to control buoyancy. BMI is generally concentrated in the anterior portion of the body when it is also involved in body trim control (Houssaye, 2009). The occurrence of strong BMI in *Paraplacodus* humeri and femora would be in accordance with a bottom-walker rather than shallow-swimmer ecology for this taxon.

*Psephoderma alpinum* also shows high bone compactness among the sample in spite of resorption processes in the cortex. *Psephoderma* was armoured with a dorsal shield consisting of a main carapace and a pelvic shield, which increases body mass, too. Its overall habitus and largely inflexible body axis would suggest a comparable swimming style to modern freshwater turtles that is a combination of bottom-walk and rowing with the limbs. However, *Psephoderma* has slender and short (reduced) limb bones making rowing with effective strokes unlikely. Microanatomy is similar to *Claudiosaurus* that was an anguilliform swimmer. However, an anguilliform swimming mode for *Psephoderma* is unlikely due to a largely inflexible body axis (dorsal armour). Although in modern interpretations the dorsal armour is divided at the pelvic region anguilliform movements are still restricted. The best interpretation is so far that *Psephoderma* has had a passive lifestyle sitting most of the time on the bottom/ground (or was maybe buried in analogy to some flat turtles). For feeding it slowly walked the ground. Certain propulsion by wriggling movements of the pelvic and tail region is conceivable. Higher resorption in the femur than in the humerus further indicates more active movements of the limbs and thus might support more active swimming when compared

to *Paraplacodus* (that has a similar high BMI).

Humeri of Placodontia indet. aff. *Cyamodus* also show BMI although to a lesser extent when compared to *Paraplacodus* and *Psephoderma*. The humerus assigned to aff. *Placodus*, the humerus of *Henodus*, and the humeri of the diapsid *Horaffia* all share a similar microanatomy and histology. Thus, similar compactness values are assumed for aff. *Placodus* and *Henodus* (although they are both not tested in the PCA due to the lack of a thin section). The lower BMI indicates more efficient swimming in these taxa when compared to *Paraplacodus* and *Psephoderma*, because less BMI suggests more maneuverability.

*Cyamodus hildegardis* was armoured with a dorsal shield consisting of a main carapace and a pelvic shield (Rieppel, 2002; Scheyer, 2010). Other *Cyamodus* species most likely carried armour as well (as evidenced in *C. kuhnschnyderi*; see Nosotti and Pinna, 1996) but their exact configuration on the body is not known. In addition, *Cyamodus hildegardis* also carried a heavily armoured tail (Scheyer, 2010). *Henodus* was heavily armoured as well, with a closed dorsal and ventral shield (Huene, 1936). Thus, body mass was increased by armour in both taxa. *Cyamodus* has long and massive humeri, *Henodus* humeri are tiny (reduced). Based on its morphology, lifestyle and swimming capabilities of *Henodus* are interpreted as similar to those described above for *Psephoderma*, making *Henodus* mainly a bottom walker. No propulsion by wriggling seems possible due to its entirely enclosed body.

Humeri of Placodontia indet. aff. *Cyamodus* are long and massive (as it is the case in all *Cyamodus* spp.), allowing strong strokes and making a swimming style by rowing with the limbs possible. [Please note that it is unknown if the feet of any placodont were webbed.] Additionally, the divided dorsal shield would have allowed some (minimal) propulsion by wriggling with the rear and tail.

*Placodus* has only one single row of osteoderms along its vertebral column that has not much contributed to body mass. It was classified as a subcarangiform swimmer (Braun and Reif, 1985), which is supported by its laterally compressed tail (Drevermann, 1933) and the supposed BMI.

We did not know if armour was present or not for the taxa represented by humeri and femora assigned to Placodontia indet. All bones show a high compactness and have a large spongy medullary area of a comparable size to that of some otariids (but combined with a much higher compactness in Placodontia indet.). In addition, some femora show an open

**Table 3.** Summary of morphological, histological, and microanatomical results. Abbreviations: lm = large and massive, lp = large and pachyostotic, ss, short and slender/reduced, B, armour present: y = yes, n = no, C, coarse parallel-fibred bone, present. y = yes, n = no, D, bone tissue type: lamellar-zonal bone tissue (LZB), circumferential fibro-lamellar bone (cFBL), p/rFBL plexiform to radiating fibro-lamellar bone, E, secondarily widened vascular canals present. y = yes, n = no, F, calcified cartilage at midshaft: n = not present, y = present, G, trabecle-like architecture in the cortex present. y = yes, n = no, H, ostcl. = osteosclerosis; paosteo. = pachyosteosclerosis, I, endosteal remodelling present. y = yes, n = no, J, swimming style: bw = bottom walker, acsw = more active swimming, slsw = slow swimming, Placodontia indet. group A refers to humeri IGWH 9 and MB.R. 454 and femora IGWH 23 and SMNS 84545, Placodontia indet. group B refers to femora MB.R. 961, MB.R. 812, MB.R. 814.2, and SMNS 54578.

Taxon	A	B	C	D	E	F	G	H	I	J	environment
<i>Henodus</i>	ss	y	?	r/p FBL	?	?	y	?ostcl.	?n	bw	lake/lagoonal deposits
<i>Psephoderma</i>	ss	y	n	LZB	y	n	n	ostcl.	y	bw/slsw	shallow marine (Alpine Triassic)
Placodontia indet. aff. <i>Cyamodus</i>	lm	y	y	r/p FBL	y	y/n	y	ostcl.	n/y	acsw	shallow marine (Germanic Basin)
aff. <i>Placodus</i>	lm	n	?	r/p FBL	?	?	y	?ostcl.	?n	acsw	shallow marine (Germanic Basin)
<i>Paraplacodus</i>	ss	n	n	LZB	n	y	n	ostcl.	y	bw	shallow marine (Germanic Basin)
Placodontia indet. (group A)	lm	?	y	cFBL	y	n	y	ostcl.	y	slsw	shallow marine (Germanic Basin)
Placodontia indet. (group B)	lm	?	y	cFBL	y	n	y/n	ostcl.	y	slsw	shallow marine (Germanic Basin)
<i>Horaffia kugleri</i>	lp	?	y	cFBL	y	y	y	paosteo.	n	bw/slsw	shallow marine (Germanic Basin)

medullary cavity. Thus, microanatomy indicates certain, but not very fast, swimming capabilities.

It is also unknown whether the diapsid *Horaffia* was armoured. Its humeri were large and pachyostotic (Klein and Hagdorn, 2014). Microanatomy clearly documents osteosclerosis (Klein and Hagdorn, 2014; current study). Both identify this taxon as a shallow marine inhabitant most likely a bottom walker or slow swimmer but due to the lack of a complete skeleton this remains rather speculative.

### *Histological characteristics*

Placodonts share several histological features. Numerous primary osteons occur in all bones that grew with fibro-lamellar bone. Primary osteons are not developed in *Psephoderma alpinum* and they are rare in *Paraplacodus broilii*, which both grew with lamellar-zonal bone. All placodonts share immature (*i.e.* incompletely lined) primary osteons that predominately occur in the inner cortices. Incompletely lined primary osteons are also described for other Sauropertygia such as a pachypleurosaurs and a pistosauroid (Klein, 2010), and for young *Alligator mississippiensis* (Woodward *et al.*, 2014). There thus might be a correlation between aquatic lifestyle (and an inferred increased growth rate when compared to terrestrial forms; see White, 2011) and incompletely lined primary osteons.

Resorption occurs in all placodont samples. *Psephoderma* humerus and femur exhibit a perimedullary region in which periosteal bone is resorbed and partially replaced (remodelled). The entire medullary region of *Paraplacodus* is made of secondary (endosteal) bone, resulting in a very compact centre. Some Placodontia indet. show an extended medullary region filled by secondary trabecels. In fact, the Placodontia indet. sample can be divided into two groups based on the presence of a medullary cavity in some femora (MB.R. 961; MB.R. 812; MB.R. 814.2; SMNS 54578) and the presence of a large medullary region, respectively (IGWH 9, 23; SMNS 54585; MB.R. 454). The presence of a free cavity in some Placodontia indet. aff. *Cyamodus* and Placodontia indet. is not typical for aquatic tetrapods (*e.g.* Quemeneur *et al.*, 2013; Hayashi *et al.*, 2013).

In those samples that grew with fibro-lamellar bone remodelling is always only initiated, which means that secondarily widened (eroded) vascular canals or primary osteons are surrounded by a layer of circumferentially deposited lamellar bone but stay widely open and are not infilled. Mature secondary osteons are very rare and are restricted to the inner cortex of few samples.

The absence of large amounts of mature secondary osteons (Francillon-Vieillot *et al.*, 1990; Currey, 2002) in the placodont samples expressing fibro-lamellar bone is atypical. Ricqlès (1976) hypothesized a possible relation between fibro-lamellar bone and remodelling (*i.e.*, the presence and number of secondary osteons), which is true for many extant and extinct vertebrates such as large herbivorous mammals, large birds, dinosaurs, and ichthyosaurs (*e.g.* Klein and Sander, 2008; Houssaye *et al.*, 2014).

All placodonts, thanks to an inhibition of bone remodelling, have a good and fairly complete growth record preserved, which is the subject of another study (Klein *et al.*, unpubl. data).

*Paraplacodus*, one humerus of Placodontia indet. aff. *Cyamodus*, and some humeri of *Horaffia* show pockets of calcified cartilage at midshaft. Retention of calcified cartilage at midshaft is often coupled with osteosclerosis and is recognized in many secondarily aquatic vertebrates, *e.g.* in pachypleurosaurs and plesiosaurs (Buffrénil *et al.*, 1990; Ricqlès and Buffrénil, 2001; Hugi *et al.*, 2011; Krahl *et al.*, 2013). It is also described in some armour plates of placodonts (Scheyer, 2007).

Two major histological groups can be distinguished among placodonts, which do not follow the classical phylogenetic distinction into armoured vs. non-armoured Placodontia. The armoured *Psephoderma* and the non-armoured *Paraplacodus* both grew with compact, low vascularized or avascular lamellar-zonal bone, indicating a slow growth rate and rather low basal metabolic rate comparable to that of modern amphibians and reptiles. The armoured *Henodus*, non-armoured aff. *Placodus*, and the armoured Placodontia indet. aff. *Cyamodus* grew with plexiform to radiating fibro-lamellar bone tissue, indicating high growth rates and a high basal metabolic rate. For Placodontia indet. and for *Horaffia* it is unknown if the individuals had carried an armour or not, also grew with fibro-lamellar bone tissue but here the organization is more circumferential, indicating somewhat lower growth rates (Margerie *et al.*, 2004). Fibro-lamellar bone tissue is known from modern birds, dinosaurs, most synapsids, and from other extinct marine reptiles such as ichthyosaurs and plesiosaurs (*e.g.* Chinsamy-Turan 2005, 2011; Houssaye *et al.*, 2014; Wiffen *et al.*, 1995). Thus, fibro-lamellar bone tissue clearly originated several times within different vertebrate lineages.

The fibro-lamellar bone of placodonts has the typical scaffolding of woven bone surrounded by lamellar bone. However, sometimes the woven bone component is re-

placed or grades into parallel-fibred bone with specially thick and coarse fibers. Both always contain a high amount of thick and numerous osteocyte lacunae. A replacement or modification of the woven bone component by parallel-fibred bone in the fibro-lamellar tissue was described before for archosaurs (Ricqlés *et al.*, 2003), the ornithomimid dinosaur *Gasparinisaura* (Cerda and Chinsamy, 2012), and the titanosaur dinosaur *Ampelosaurus* (Klein *et al.*, 2012). An atypical parallel-fibred bone was mentioned for mosasaurs (Houssaye *et al.*, 2013) and for the temnospondyl *Plagiosaurus* (Konietzko-Meier and Schmitt, 2013), which both did not grow with fibro-lamellar bone. It also occurs within the fibro-lamellar bone of ichthyosaurs (Houssaye *et al.*, 2014).

Locally, a high amount of radial vascular canals occurs within the fibro-lamellar bone of some placodonts. Radial bone tissue reveals according to Margerie *et al.*, (2004:869) in the king penguin chick the highest growth rates. In ichthyosaurs, a radial arrangement of vascular canals was interpreted as a consequence of the insertion of Sharpey's fibers and thus linked to mechanical reasons (Houssaye *et al.*, 2014). The local radial trabecle-like architecture in the inner cortex of some placodont samples may also indicate mechanical properties in addition to high overall growth rates. The fibro-lamellar bone tissue in combination with the plexiform to radiating organization indicates for Placodontia indet. aff. *Cyamodus* the highest growth rates among placodonts but also among other Triassic Sauropterygia and is comparable to that of ichthyosaurs (Buffrénil and Mazin, 1990; Houssaye *et al.*, 2014).

In all placodonts that grew with fibro-lamellar bone, primary tissue is in general highly vascularized. Locally it is even spongy-like or trabecular-like. Primary osteons are secondarily widened by successive resorption processes, resulting in an overall secondary spongy tissue, which is similar to some ichthyosaurs (Houssaye *et al.*, 2014).

In spite of certain inter- and intraspecific variability within the placodont sample that grew with fibro-lamellar bone, the primary bone tissue is in general very similar to that of ichthyosaurs. Differences include the lack of a medullary cavity, high endosteal and periosteal remodelling, and an overall more spongy organization, in ichthyosaurs (Houssaye *et al.*, 2014). The similarities are notable, because ichthyosaurs were efficient and sustained swimmers that lived in the open marine sea with a comparable body shape and lifestyle to dolphins or tunas. Placodonts have a cylindrical, sea cow-like body shape (non-armoured forms) or resemble the shape and morphology of flat aquatic turtles (armoured forms).

Long bone histology allows the identification and assignment of isolated bone fragments to Placodontia. Neither the combination of the avascular to low vascularized lamellar-zonal bone tissue of *Psephoderma* and *Paraplacodus* nor the special plexiform to radiating fibro-lamellar bone tissue of aff. *Placodus*, Placodontia indet. aff. *Cyamodus*, and *Henodus* or circumferential fibro-lamellar bone of Placodontia indet. has so far been reported in the here described combinations in any long bone of any other marine reptile (e.g. Sander, 1990; Wiffen *et al.*, 1995; Pellegrini 2007; Klein, 2010; Hugi, 2011; Hugi *et al.*, 2011; Krahl *et al.*, 2013; Houssaye *et al.*, 2014).

#### *Different bone tissue types and growth strategies*

As summarized in Table 3, long bone histology indicates two major groups, which do not follow the classical phylogenetic distinction into armoured vs. non-armoured Placodontia (Fig. 1). The armoured *Psephoderma* and the non-armoured *Paraplacodus* both grew with lamellar-zonal bone tissue indicating slow growth rates and a low basal metabolic rate, comparable to modern reptiles. *Henodus*, aff. *Placodus*, Placodontia indet. aff. *Cyamodus*, and Placodontia indet. grew with fibro-lamellar bone tissue combined with a high, though extremely variable, vascular density, indicating high growth rates and an increased (sustained high) basal metabolic rate. Both tissue types represent two completely different growth strategies in these closely related taxa. Differences in growth rate and basal metabolic rate as well as the somewhat lower BMI in *Henodus*, Placodontia indet. aff. *Cyamodus*, aff. *Placodus*, and Placodontia indet. could point to a more active lifestyle when compared to *Psephoderma* and *Paraplacodus*. Perhaps a more active lifestyle also includes sustained swimming (?migration) over long distances for aff. *Placodus*, Placodontia indet. aff. *Cyamodus*, and Placodontia indet. but not for *Henodus*.

That the two different growth strategies are the result of gross differences in habitat/environment or climate can be excluded. All bones exhibiting fibro-lamellar bone originate from localities within the Germanic Basin, whereas *Psephoderma* and *Paraplacodus* samples originate from localities settled in the Alpine Triassic realm. All localities were interpreted to represent shallow marine environments. During the Middle Triassic, climate was subtropical warm with alternating dry and wet seasons (megamonsoonal intervals) (Parish *et al.*, 1982; Röhl *et al.*, 2001). Accordingly, water temperatures of the Muschelkalk Sea and the Alpine

Triassic lagoonal settings have been correspondingly high and less metabolic effort was needed for marine reptiles to sustain a high growth- and basal metabolic rate in both realms. Thus, strong differences in paleoclimate can be excluded as explanation why some placodonts grew with fibro-lamellar bone whereas others grew with lamellar-zonal bone.

High predatory pressure that makes faster growth necessary, although conceivable as a trigger for the presence of fibro-lamellar bone in those placodonts from the Germanic Basin, appears very unlikely since predators also occurred in the environments of the Alpine Triassic. Predatory pressure might even be higher in environments of the Alpine Triassic due to the presence of a higher number of possible predators such as ichthyosaurs, large nothosaurs, and thalattosaurs.

So far we can only observe that *Henodus*, Placodontia indet. aff. *Cyamodus*, aff. *Placodus*, and Placodontia indet. followed a different life history strategy when compared to *Psephoderma* and *Paraplacodus* the exact reasons for this have yet to be fully understood.

### Concluding remarks

The study of the morphology, long bone microanatomy, and histology of Placodontia clearly shows that extinct taxa are not ‘simply similar’ to modern taxa but that they could have had a variety of features, which are in certain combinations sometimes without a modern analogy so that the possibilities for interpretation are limited.

Clear evolutionary trends within Placodontia regarding microanatomical and histological features are not observable but identification might be hampered due to still limited sample size. Fibro-lamellar bone tissue already occurs in placodonts from the late early Anisian and persists until the early Carnian with *Henodus*. The lamellar-zonal bone type is so far only documented in stratigraphically younger placodonts from the Anisian-Ladinian boundary and the Rhaetian. A similar distribution of lamellar-zonal bone and fibro-lamellar bone is documented in pachypleurosaurs (Sauropterygia). *Neusticosaurus* ssp. from the Anisian-Ladinian boundary of the Alpine Triassic show lamellar-zonal bone (Sander, 1990; Hugi et al., 2011) whereas the stratigraphically older *Anarosaurus heterodontus* from the Lower Muschelkalk of Winterswijk (Germanic Basin) grow with incipient fibro-lamellar bone (Klein, 2010). This could indicate that the fibro-lamellar bone tissue was inherited from the unknown terrestrial ancestor of Sauropterygia and was later abandoned in some taxa.

In conclusion, all placodonts sampled followed an essentially or probably exclusive aquatic lifestyle. However, we observe distinct differences in histology and microanatomy that lead to different growth strategies and life (swimming) styles in Placodontia independent from phylogenetic relationships, ontogenetic stages or the presence or absence of armour. The differences imply a high inter- as well as intraspecific variability, most likely depending on the environment each individual lived in (developmental plasticity), and diverse lifestyles among the group.

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**Online supplementary material**

S1. Morphological description of sampled humeri and femora

S2. Photographs of sampled bones.

S3. Table with Bone Profiler values.

S4. Cross sections of bones transformed into black and white pictures.

S5. Histological details of Placodontia.

S6. Histological details of Placodontia.