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Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods

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Abstract

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The microstructure of dorsal osteoderms referred to the chroniosuchid taxa *Chroniosuchus*, *Chroniosaurus*, *Madygenerpeton* and cf. *Uralerpeton* is compared to existing data on the bystrowianid chroniosuchian *Bystrowiella* and further tetrapods. Chroniosuchid osteoderms are marked by thin internal and relatively thick external cortices that consist of lowly vascularised parallel-fibred bone. They are structured by growth marks and, in case of *Madygenerpeton*, by lines of arrested growth. The cancellous middle region is marked by a high degree of remodelling and a primary bone matrix of parallel-fibred bone that may include domains of interwoven structural fibres. Whereas the convergence of *Bystrowiella* and chroniosuchid osteoderms is not confirmed by our observations, the internal cortex of the latter displays a significant peculiarity: It contains distinct bundles of shallowly dipping Sharpey's fibres with a cranio- or caudoventral orientation. We interpret this feature as indicative for the attachment of epaxial muscles which spanned several vertebral segments between the medioventral surface of the osteoderms and the transversal processes of the thoracic vertebrae. This finding endorses the hypothesis that the chroniosuchid osteoderm series was part of a crocodylian-like trunk bracing system that supported terrestrial locomotion. According to the measured range of osteoderm bone compactness, some chroniosuchian species may have had a more aquatic lifestyle than others.

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Introduction

Chroniosuchians are a group of anamniote tetrapods whose fossils have been discovered within Permian and Triassic continental successions of Europe and Asia. They constituted an abundant faunal element in the tetrapod assemblages of Eastern Europe throughout the Late Permian and survived there up to the Middle Triassic (Sennikov 1996; Golubev 2000; Novikov *et al.* 2000). Isolated occurrences from the Middle and the Late Permian of China (Young 1979; Li and Cheng 1999), from the Middle Triassic of south-west Germany (Witzmann *et al.* 2008), and from the Middle to early Late Triassic of Kyrgyzstan, Middle Asia (Schoch *et al.* 2010), indicate a wider geographical distribution despite the limited variety of the group (12 valid Russian species, see Novikov *et al.* 2000; four more non-Russian species).

On the basis of their vertebral structure and skull morphology, chroniosuchians have been classified either as seymouriamorphs (Tatarinov 1972) or as embolomere relatives (Ivakhnenko and Tverdokhlebova 1980; most following works) prior to their consideration in cladistic analyses. Recent cladistic approaches confirmed their belonging to the amniote stem-group (*sensu* Ruta *et al.* 2003), whereas their close relationship with embolomeres or another reptiliomorph group is still under discussion (Clack and Klembara 2009; Klembara *et al.* 2010; Schoch *et al.* 2010; Fig. 1A,B). According to the lepospondyl hypothesis of lissamphibian ancestry, seymouriamorphs, embolomeres and further related

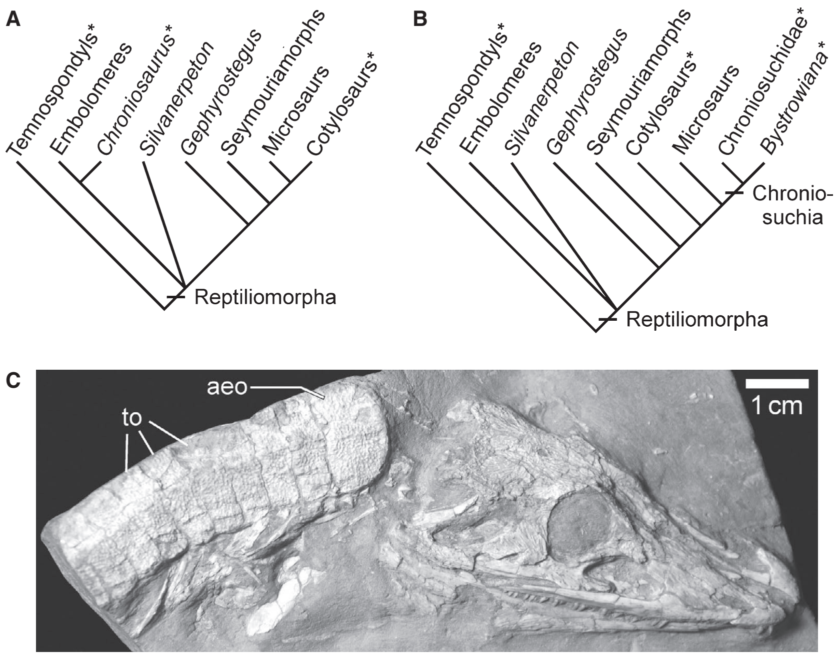

Fig. 1—Relationships and appearance of the Chroniosuchia. —**A**, **B.** Cladograms for the crown-group Tetrapoda according to recent phylogenetic hypotheses considering chroniosuchians. —**A.** Relationships simplified after the tree of Klembara *et al.* (2010). —**B.** Simplified after Schoch *et al.* (2010). The occurrence of a dorsal osteoderm system in some or all members of a group is denoted with an asterisk. —**C.** Anterior skeleton of the chroniosuchid *Chroniosaurus dongusensis* (specimen PIN 3585/124), displaying the anterior part of the osteoderm shield.

groups–chroniosuchians probably included–would not be part of the amniote stem but lie outside the tetrapod crown-group (Laurin and Reisz 1997; Vallin and Laurin 2004). Two major subtaxa of the Chroniosuchia have been defined, mainly on the basis of their distinct osteoderm morphologies (see Golubev 1998; Novikov and Shishkin 2000): 'Chroniosuchidae' and 'Bystrowianidae' were erected by V'yushkov (1957*a,b)* as two families of batrachosaurs which he did not regard as closely related. Later, Ivakhnenko and Tverdokhlebova (1980) joined the two groups within the Chroniosuchia (=Chroniosuchida, Tatarinov 1972). Including *Bystrowiana permira* (V'yushkov 1957*b*) as the only better known bystrowianid and four chroniosuchid taxa, the analysis of Schoch *et al.* (2010) recovered Chroniosuchia as a monophyletic group comprising *Bystrowiana* and Chroniosuchidae as sister taxa.

This approach is dedicated to a key feature of chroniosuchians – a single dorsal series of highly characteristic osteoderms, beginning with an axially elongated anterior-end osteoderm in contact with the skull, which is followed by numerous shorter osteoderms along the animal's back (Fig. 1C). As in the osteoderm series of the plagiosaurid temnospondyl *Plagiosuchus pustuliferus* (Fraas 1896), the ventral side of each chroniosuchian osteoderm bears a medial keel, the *processus ventralis*, which formed the connection to one corresponding vertebra (as reconstructed by Ivakhnenko and Tverdokhlebova 1980; fig. 12). Unlike the condition in *P. pustuliferus* (see Witzmann and Soler-Gijón 2010), however, the chroniosuchian *processus ventralis* was not accommodated by an incision of the neural arch. Instead, it was either co-ossified with the neural spine via a horizontal suture (in bystrowianids) or forming a deep indentation enclosing the neural spine (in chroniosuchids; Golubev 1998*a*).

A peculiarity of the chroniosuchian osteoderm series with relevance for the functional interpretation of their histological properties is the articulation of each two neighbouring plates. Unlike the very slight overlap of successive dorsal osteoderms in *P. pustuliferus* (Witzmann and Soler-Gijón 2010) and the more considerable overlap in the osteoderm double row of some dissorophid temnospondyls (Dilkes and Brown 2007; Dilkes 2009), the articulation in chroniosuchians is marked by a multifold overlap of complexly interlocking osteoderm processes. In chroniosuchids, it involves the axially elongated ventral process (*processus ventralis*), a pair of anterior wings (*alae anteriores/processus articulares anteriores*) and a corresponding pair of posteroventral wing facets (*facies alares*), a pair of posterior processes (*processus articulares posteriores*) and a corresponding anteroventral depression (*depressio ventralis*) on the central body, and the corresponding posterodorsal and anteroventral facets on the lateral osteoderm wings (*alae scutulumi*) (Golubev 1998; Novikov and Shishkin 2000; overlapping parts are grey-shaded in Fig. 2A). The osteoderm articulation in bystrowianid chroniosuchians is defined by enlarged anterior wings and wing facets, and an often shelf-like posterior articular plate (*lamina articularis*) which is accommodated by an anteroventral depression (*depressio ventralis*), but it lacks the lateral osteoderm wings (*alae scutulumi*).

Apart from the interpretation that the osteoderms supported thermoregulation (Hartmann-Weinberg 1935), the function of the osteoderm system was not explicitly addressed in early approaches on chroniosuchians, but the term 'armour' and the hypothesis that a trilobite-like curling of the animal was possible (Ivakhnenko and Tverdokhlebova 1980, p. 25) imply that the broad osteoderm systems of chroniosuchids were regarded as protection carapaces. Recently, the

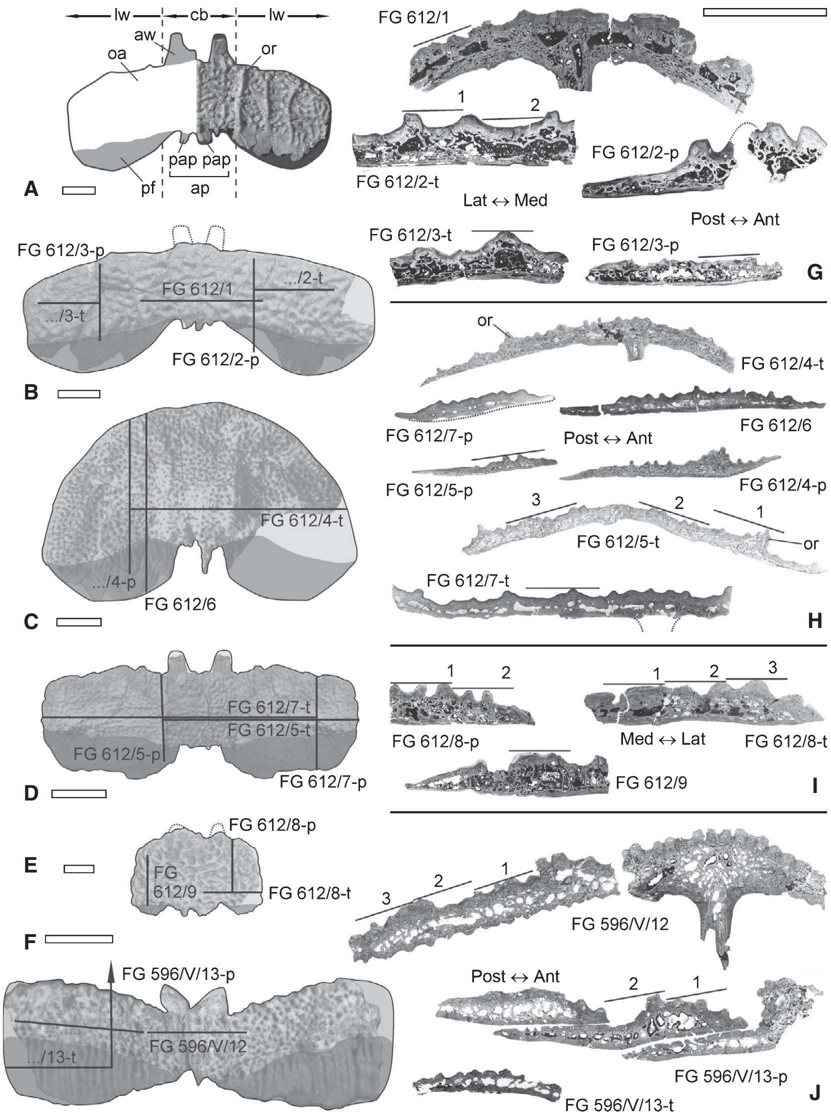

Fig. 2—Chroniosuchian osteoderm morphology, position and overview images for all considered thin sections. —**A.** Terminology of chroniosuchid osteoderm features for the exemplary specimen PIN 523/20 (after Golubev 1998; Novikov and Shishkin 2000). Overlap areas are grey-shaded. —**B–F**. Exemplary chroniosuchid osteoderms in dorsal view, belonging to the species *Chroniosuchus paradoxus* (SGU 104B/646, B), *Chroniosaurus dongusensis* (PIN 3713/39 in C; PIN 3585/119 in D), *Uralerpeton tverdochlebovae* (PIN 1100/8, E), and *Madygenerpeton pustulatus* (FG 596/V/5, F). The posterodorsal facets are marked in dark grey. —**G–J.** Overview images of osteoderm thin sections marked in B–F, sorted according to taxa. —**G**. *Chroniosuchus licharevi*. —**H**. *Chroniosaurus dongusensis*. —**I**. cf. *Uralerpeton tverdochlebovae*. —**J**. *Madygenerpeton pustulatus*. Suffixes '-p' and '-t' refer to parasagittal and transversal sections, respectively. Thin black bars and numbers 1–3 mark the positions of sections considered for compactness analysis. Dotted lines designate outlines of fragmented osteoderms. All scale bars equal 1 cm.

elaborateness of articulation led to the hypothesis that the osteoderm series functioned as a support device for the axial skeleton and musculature – in agreement with a lifestyle that included some terrestrial locomotion (Clack and Klembara 2009; Buchwitz and Voigt 2010; Witzmann and Soler-Gijón 2010). Whereas the lack of articulated hand and foot skeletons is a hindering factor for the interpretation of chroniosuchian locomotion, lifestyle and the role of their osteoderm systems, another indication was provided by studies on the long bone histology of basal tetrapods which found the bone compactness profile of the chroniosuchian *Chroniosaurus dongusensis* (Tverdokhlebova 1972) to be that of a terrestrial or semi-terrestrial animal (Laurin *et al.* 2004, 2006; Kriloff *et al.* 2008).

Seventy years earlier, Hartmann-Weinberg (1935) published the first histological study on chroniosuchid osteoderms, which were falsely referred to the seymouriamorph *Kotlassia prima* (Amalitzky 1921) by that time. However, as pointed out by Bystrow (1940), she misinterpreted some part of the osteoderm bone as dentine layers similar to those of crossopterygian cosmoid scales, leading her to wrong conclusions regarding lifestyle, palaeoenvironment and homology with skeletal elements of other tetrapods. Only one other study provides further histological data on the osteoderms: Witzmann and Soler-Gijón (2010) include a sample of the bystrowianid *Bystrowiella schumanni* (Witzmann *et al.* 2008). They found that its limited similarity with the osteoderm types of different temnospondyl taxa allows no simple functional or ecological conclusions by analogy.

Given the lack of recent histological data on chroniosuchid osteoderms, this approach focuses on a detailed description of the osteoderm bone tissues occurring in the Chroniosuchidae. We are comparing four chroniosuchid taxa, each on the basis of several osteoderms, to address the following issues: (1)

indications for the homology of chroniosuchid and *Bystrowiella* osteoderms; (2) the mode of skeletogenesis; (3) palaeobiological implications from osteoderm development; (4) the structure of adjacent soft tissues and osteoderm-osteoderm joints and how they might have constrained the mechanics of the osteoderm system; and (5) palaeoecological inference from the analysis of bone compactness.

Institutional abbreviations

FG, Geological Institute of the TU Bergakademie, Freiberg, Germany; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, MA, USA; PIN, Borissyak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SGU, Saratov State University, Saratov, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; THU, Teikyo Heisei University, Ichihara City, Chiba Prefecture, Japan.

Anatomical abbreviations

aeo, anterior-end osteoderm; ant, anterior; ap, articular plate; aw, anterior wings; cb, central body; cl, cancellous layer; cpfb, coarse parallel-fibred bone; ec, external cortex; ic, internal cortex; ice, intercentrum; isf, interwoven structural fibres; lat, lateral; lb, lamellar bone; lw, lateral wings; med, medial; na, neural arch; oa, ornamented dorsal area; or, ornamentation ridge; pap, posterior articulation process; pce, pleurocentrum; pf, posterodorsal facet; pfb, (homogenous) parallel-fibred bone; post, posterior; shf, Sharpey's fibres; to, trunk osteoderm; tp, transversal process; vp, ventral process.

Materials

Our histological description involves the following chroniosuchid taxa and specimens (Table 1, Fig. 2B–J; see also list in Golubev 2000, p. 7–8, for the Russian localities):

1. *Chroniosuchus licharevi* (Riabinin and Shishkin 1962): FG 612/1 to 3, three fragments of trunk osteoderms from the Lopingian (Tatarian Series, Upper Vyatkian Substage, *Chroniosuchus paradoxus* Tetrapod Zone) of Gorokhovets, a locality in the Vladimir Region, European part of Russia. These form a part of a larger assemblage of tetrapod remains (Sennikov *et al.* 2003) including cranial and postcranial material of the chroniosuchid *Chroniosuchus licharevi* which has not yet been described in detail.
2. *Chroniosaurus dongusensis*: FG 612/4 to 7, two osteoderms from each of two classical chroniosuchid localities of the Lopingian (Tatarian Series, Upper Severodvinian Substage, *Chroniosaurus dongusensis* Tetrapod Zone): (1) Dongus-6, Orenburg Region, and (2) Poteryakha-2, Vologda Region, both in the European part of Russia. Only for *C. dongusensis*, we obtained samples of the half-moon-shaped anterior-end osteoderms (Fig. 2C), whose ornamentation is similar to that of the trunk osteoderm series.
3. cf. *Uralerpeton tverdochlebovae* (Golubev 1998): FG 612/8 and 9, two osteoderm fragments from the Lopingian strata (Tatarian Series, Upper Vyatkian Substage, *Archosaurus rossicus* Tetrapod Zone) of Vyazniki-1, a locality in the Vladimir Region, European part of Russia. The same locality also yielded material of another chroniosuchian, *Bystrowiana permira*, and we conditionally assign FG 612/8 and FG 612/9 to *Uralerpeton tverdochlebovae* and not to *Bystrowiana permira* because of (1) a diagonal ventral ridge in FG 612/9, which is reminiscent of an osteoderm crest only occurring in chroniosuchids (*crista scutulumi ventralis externa*, see Golubev 1998) and (2) the meddled appearance of the dorsal ornament which is unlike the more regular polygonal pattern in *Bystrowiana* (see Golubev 2000 for examples of both species).
4. *Madygenerpeton pustulatus* (Schoch *et al.* 2010): FG 596/V/12, an isolated fragmentary osteoderm, and FG 596/V/13, a series of three adjacent osteoderms, from the

Table 1 Taxonomic assignment, inventory number, locality, stratigraphy, and relevant morphological data of specimens described in this study

Taxon	Specimen	Locality/Stratigraphy	Osteoderm morphology
Chroniosuchus licharevi	FG 612/1 FG 612/2 FG 612/3	Gorokhovets, European Russia/Upper Vyatkian Substage, Tatarian Series, Lopingian	Width/axial length >2.5, pitted dorsal ornamentation
Chroniosaurus dongusensis	FG 612/4* FG 612/5	Dongus-6, European Russia; Upper Severodvinian Substage, Tatarian Series, Lopingian	Width/axial length >2.5, pustular dorsal ornamentation
	FG 612/6* FG 612/7	Poteryakha-2, (same data as for locality Dongus-6)	
cf. *Uralerpeton tverdochlebovae*	FG 612/8 FG 612/9	Vyazniki-2, European Russia, Upper Vyatkian Substage, Tatarian Series, Lopingian	Width/axial length <2.5, pitted dorsal ornamentation, small posterodorsal facets
Madygenerpeton pustulatus	FG 596/V/12 FG 596/V/13	Madygen, SW Kyrgyzstan, Madygen Fm, Middle- Late Triassic	Width/axial length >4, pustular dorsal ornamentation, enlarged posterodorsal facets with concentric grooves/ridges

The asterisk signifies specimens of half-moon shaped anterior-end oseteoderms.

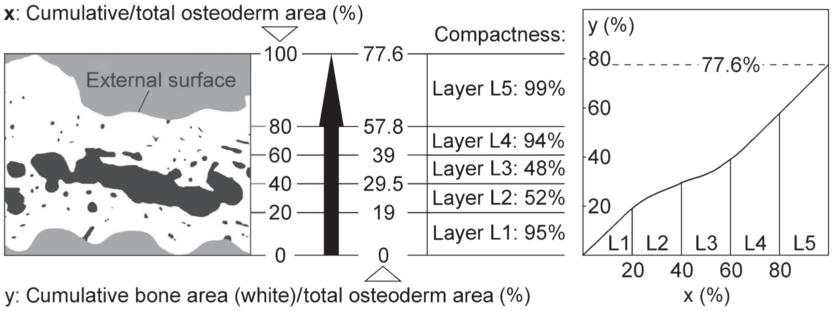

Fig. 3—Digitalisation image of a 5-mm-wide measurement section of *Madygenerpeton pustulatus* osteoderm FG 596/V/12 and the procedure of deriving compactness parameters (L1 to L5, total compactness) and a cumulative compactness curve (on the right). Colours: white, bone area; black, internal space; grey, area outside osteoderm.

south-west outcrop area (environs of the village Madygen) of the late Middle or early Late Triassic Madygen Formation, Batken Region, south-west Kyrgyzstan, Central Asia.

For the comparison of bone compactness profiles, we include further osteoderm thin sections from the material of Witzmann and Soler-Gijón (2010): of the bystrowianid chroniosuchian *Bystrowiella schumanni* the osteoderm specimen SMNS 91226 (sectioned transversally and parasagittally) from the upper Middle Triassic (Ladinian, Upper Lower Keuper) of Vellberg-Eschenau in southern Germany; of the dissorophid temnospondyl *Aspidosaurus* sp. one osteoderm (sectioned parasagittally) belonging to the MCZ 1477 material from the Lower Permian of Texas, Rattlesnake Canyon locality, Nocona Formation, USA; and of the plagiosaurid temnospondyl *P. pustuliferus* the osteoderm specimen SMNS 91227 (sectioned transversally) from the Erfurt Formation, Middle Triassic (Ladinian) of Thuringia, Germany. Furthermore, a transversal thin section of SMNS 91330, a dorsal osteoderm of the plagiosaurid *Gerrothorax* sp. from the upper Middle Triassic (Untere Graue Mergel, Ladinian) of Kupferzell-Bauersbach in southern Germany, was included.

Methods

The dermal bone fragments were embedded in synthetic resin. To cover differences within the histology of the morphologically complex osteoderms the samples were cut either parasagittally (with varying distances from the midline), transversally, or in both directions (see Fig. 2B–F). Polished thin sections with a thickness between 40 and 50 μm were prepared. We were using Leica DC 300 and Zeiss Axiolab A polarisation microscopes for the examination of the thin sections. Besides individual photomicrographs of important details, overview images of the complete sections with a 63- to 80-fold magnification have been generated as mosaics of micrographs (see Fig. 2G–J) by means of a Zeiss Discovery V12 stereomicroscope and an AxioCamMRC5 digital camera system. The latter performs an automatic scan of the thin section in a raster predefined via the device-controlling software AxioVision (module 'MosaiX').

To assess the amount of internal space of the fossil osteoderm bone, which is usually filled with fine sediment, carbonatic, silicic or iron oxide cements, and its distribution over the osteoderm thickness, 5-mm-wide dorsoventral sections of well-preserved osteoderm parts have been demarcated in the overview images. Thereby, posterodorsal facet regions and the close vicinity of the *processus ventralis* have not been considered. Employing a vector graphics software (e.g. CorelDraw), the areas not belonging to the osteoderm and all non-diagenetic internal spaces within the dorsoventrally oriented rectangular demarcation areas have been digitalised as polygons (Fig. 3). In the next step, the demarcation rectangles with (1) osteoderm/outside-osteoderm areas and (2) bone/-non-bone areas marked as black polygons/white background have been transferred to raster images (e.g. TIFF bitmap files). The raster images allow us a simple counting of black and white pixels per line of the raster. Thus, each line of pixels perpendicular to the dorsoventral trend can be assigned a ratio of bone area to overall osteoderm area, i.e. a compactness value. We are parting the dorsoventral sections in one per cent area increments and define the compactness for each increment on the basis of the black-and-white raster data (Supporting information).

Averaging the incremental compactness values over the length of the dorsoventral transect total values of compactness have been derived for each of the 31 measured 5-mm wide dorsoventral sections. Spatial variation of compactness is illustrated by plots of the cumulative percentage of bone area against the cumulative percentage of osteoderm area and by average compactness values for layers of 20 area per cent (L1 to L5 in Fig. 3). These data have been used as a comparison criterion.

Description

We describe the bone histology employing the terminology of Francillon-Vieillot *et al.* (1990). As in the approaches of Scheyer and Anquetin (2008) on turtle shell bone histology and Witzmann and Soler-Gijón (2010) on temnospondyl scutes, we are using the term 'external' for the outer osteoderm section and for the osteoderm surface oriented towards the body surface and 'internal' for the inner section and for the osteoderm surface oriented towards the visceral surface of the body. As our sample only includes dorsal osteoderms, 'external' and 'dorsal' as well as 'internal' and 'ventral' are mostly corresponding. Chroniosuchian osteoderms display a diploë structure, i.e. they comprise compact external and internal cortices with a cancellous region in the middle, which is referred to as the 'interior' here. Following Witzmann and Soler-Gijón (2010), the tubercles and ridges of the external ornament that are cut in the thin sections have been designated as 'saddles' while the grooves and pits between them are referred to as 'valleys'.

External cortex

In most of the specimens, the external cortex consists of homogenous parallel-fibred primary bone and is sparsely vascularised (Fig. 4A,B,E,F), comprising primary vascular channels in low density and more rarely isolated secondary osteons. Osteoderms of cf. *Uralerpeton* have an external cortex made up of less well ordered parallel-fibred bone with a coarse appearance (*sensu* Scheyer and Anquetin 2008) and an inhomogeneous patchy or bundle-wise extinction under cross-polarised light (Fig. 4C). The external cortex is mostly thicker than the internal cortex but not as thick as the cancellous middle region. Often, the thickness varies because of the high relief of the dorsal ornamentation which includes particularly pronounced parasagittal ridges in *Chroniosaurus* and *Madygenerpeton* (see Fig. 2A,H). Exposing the channels and cavities of the middle layer below, a few large and deep incisions occur in the otherwise thick external cortex of the cf. *Uralerpeton* specimens FG 612/8 and 9.

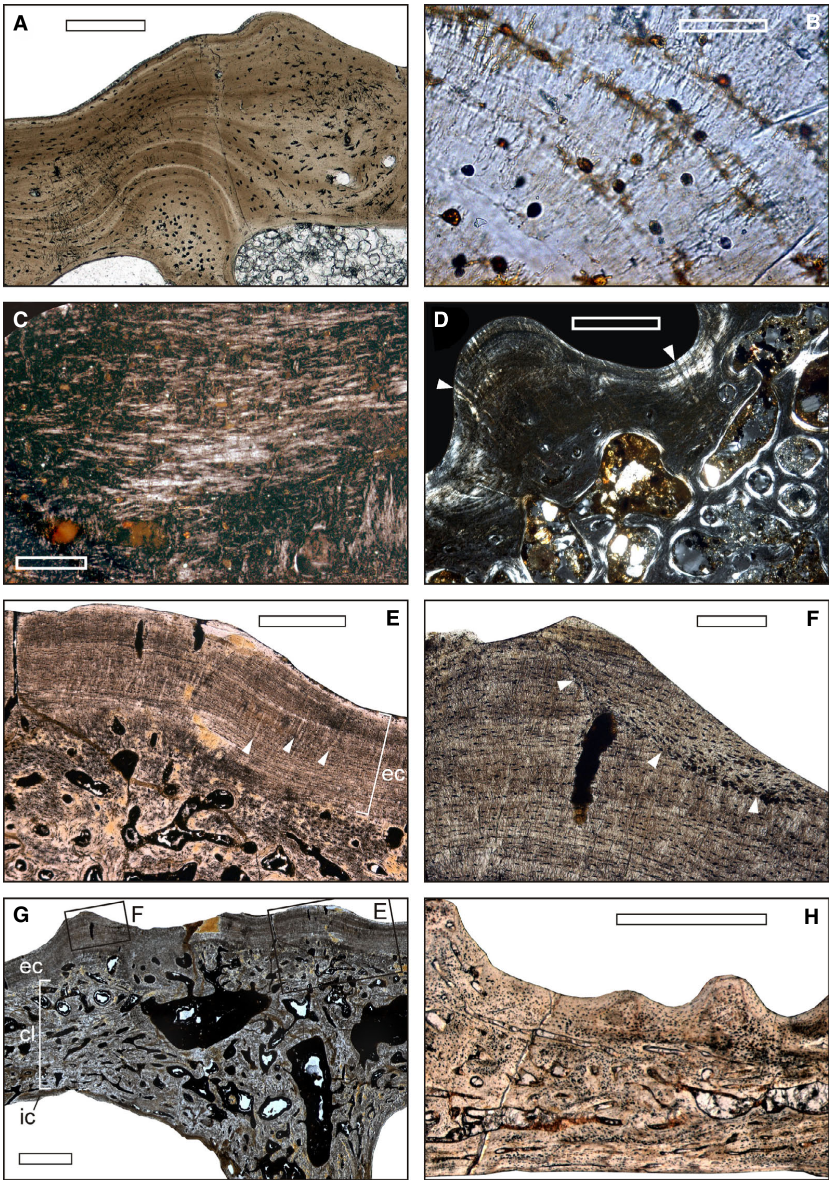

Fig. 4—Chroniosuchid osteoderms: structure of the external cortex (**A**–**F**) and cancellous middle region (**D, E, G, H**). —**A**. *Chroniosaurus dongusensis* specimen FG 612/6, growth zonation and bone cell distribution. —**B**. *Madygenerpeton pustulatus*, specimen FG 596/V/12, growth marks and cell lacunae with long and branched canaliculi. —**C, D**. cf. *Uralerpeton tverdochlebovae*, specimen FG 612/8 in cross-polarised light. Arrows in C mark Sharpey's fibres below sculptural saddles and valleys. Coarse parallel-fibred cortical bone brings about the patchy extinction in **D**. —**E**–**G**. *Chroniosuchus licharevi*, specimen FG 612/1. In E, arrows mark the trend of Sharpey's fibres; in **F**, secondary bone fills the relief of an abraded sculptural saddle (arrows). Large polygonal and smaller shred-like cavities structure the cancellous layer in **G**. —**H**. *Chroniosaurus dongusensis*, transversal section through specimen FG 612/4 with secondary osteons and larger erosion cavities in the middle region. Scale bars: A, F, 0.2 mm; B, 0.05 mm; C, 0.1 mm; D, E, 0.5 mm; G, H, 1 mm.

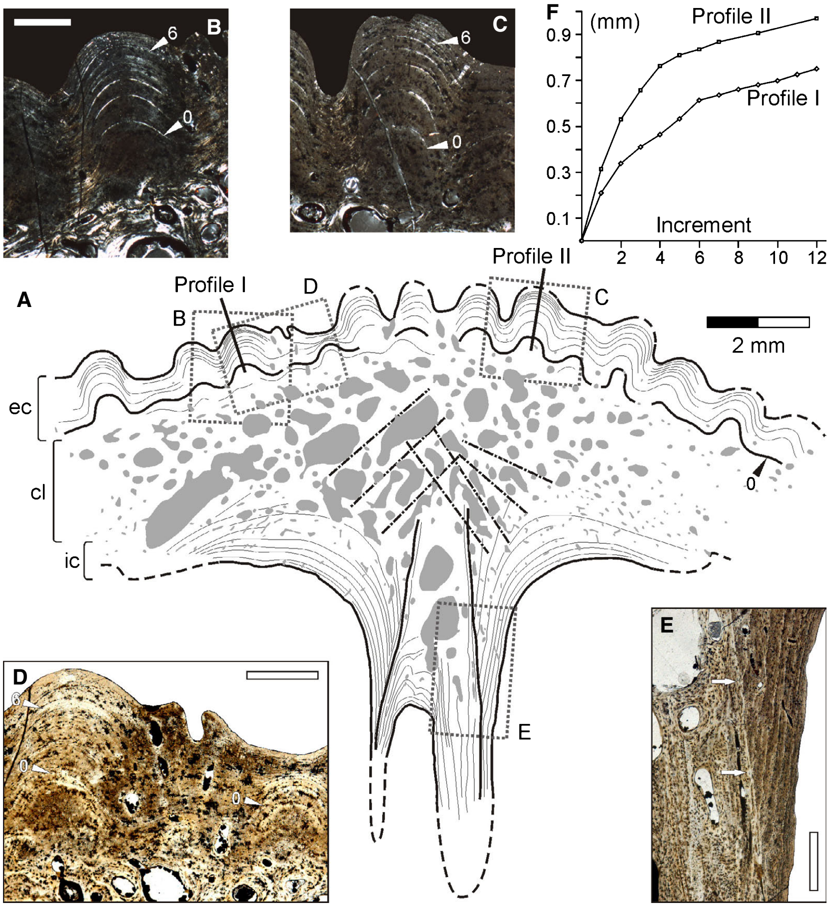

Fig. 5—*Madygenerpeton pustulatus,* specimen FG 696/V/12: Growth zonation, lines of arrested growth and structure of the cancellous layer in the medial part of the osteoderm. —**A**. Schematic drawing of a transversally orientated thin section. Black lines in the external cortex represent resting lines; in the internal cortex they represent growth marks (including resting lines). The dash-dotted lines exemplarily trace the oblique trend of bone trabeculae. Dotted frames indicate the position of detail photomicrographs B–E. —**B, C**. Detail photomicrographs of the external cortex in cross-polarised light. —**D, E.** Detail photomicrographs in normal light. —**F**. Growth profiles for two transects through the external cortex with relatively complete preservation of LAGs. Arrows with number in A–D mark lines of arrested growth (numbering consistent with diagram in F); arrows in E point to the tapering of younger resting lines at an older resting line. Unlabelled scale bars: 0.5 mm.

The external cortex of chroniosuchids is marked by a high density of cell lacunae which have long and branched canaliculi in *Chroniosuchus*, cf. *Uralerpeton* and *Madygenerpeton* (Fig. 4B) In *Chroniosuchus* and *Madygenerpeton*, shape and arrangement of the lacunae and canaliculi are often following the direction of bone fibres and bone growth marks. No regular variation in the orientation of lacunae and canaliculi occurs in cf. *Uralerpeton*, and in the *Chroniosaurus* sample the external cortices are marked by lacunae in irregular arrangement with short or no canaliculi.

The studied chroniosuchid specimens feature growth marks in the external cortex that are often well visible under normal light (Figs 4A,B,E,F and 6C). They reflect modifications of the sculptural relief during the preserved growth phase of the cortex. Especially in osteoderms with pustular ornamentation, relief compensation and buried saddles occur frequently (Figs 4A, 5A and 6C), whereas in *Chroniosuchus licharevi*, the position of sculptural maxima appears to be relatively constant over time. Both of the sectioned *Madygenerpeton* specimens display a dense growth zonation and some of the bone growth marks, that are also visible in cross-polarised light as thin and light horizons within the otherwise homogenous parallel-fibred bone, apparently represent lines of arrested growth (LAGs, resting lines *sensu* Francillon-Vieillot *et al.* 1990), (Fig. 5). In some of the sculptural saddles that are only moderately overprinted with iron oxide cements, the presumable lines of arrested growth are preserved in a complete profile, documenting variation in growth increment width (Fig. 5F, Supporting information). Apart from bone growth marks, the primary bone of external cortex in cf. *Uralerpeton* is structured by undulating cementing lines that may represent lines of bone resorption. Sculptural saddles in *Chroniosuchus* specimen FG 612/1 display a marked concave boundary line between primary parallel-fibred bone and equally compact secondary bone filling the relief (Fig. 4F), indicating bone re-growth after either resorption or abrasion through an injury.

Sharpey's fibres, i.e. mineralised ingrowing fibrillary processes from adjacent soft tissues (Francillon-Vieillot *et al.* 1990, p. 504), occur in the external cortices of all osteoderm samples and are sometimes also visible in normal light (Fig. 4E). In *Chroniosuchus* and cf. *Uralerpeton*, they appear to be more abundant below the saddles of the dorsal sculpture than below the valleys (Fig. 4D). Sometimes they reach their highest density along the saddle flanks and not at the top (see Fig. 7A). In the external cortices of the sculptured osteoderm parts of *Chroniosaurus* and *Madygenerpeton*, Sharpey's fibres are notably less abundant than in the external cortex of

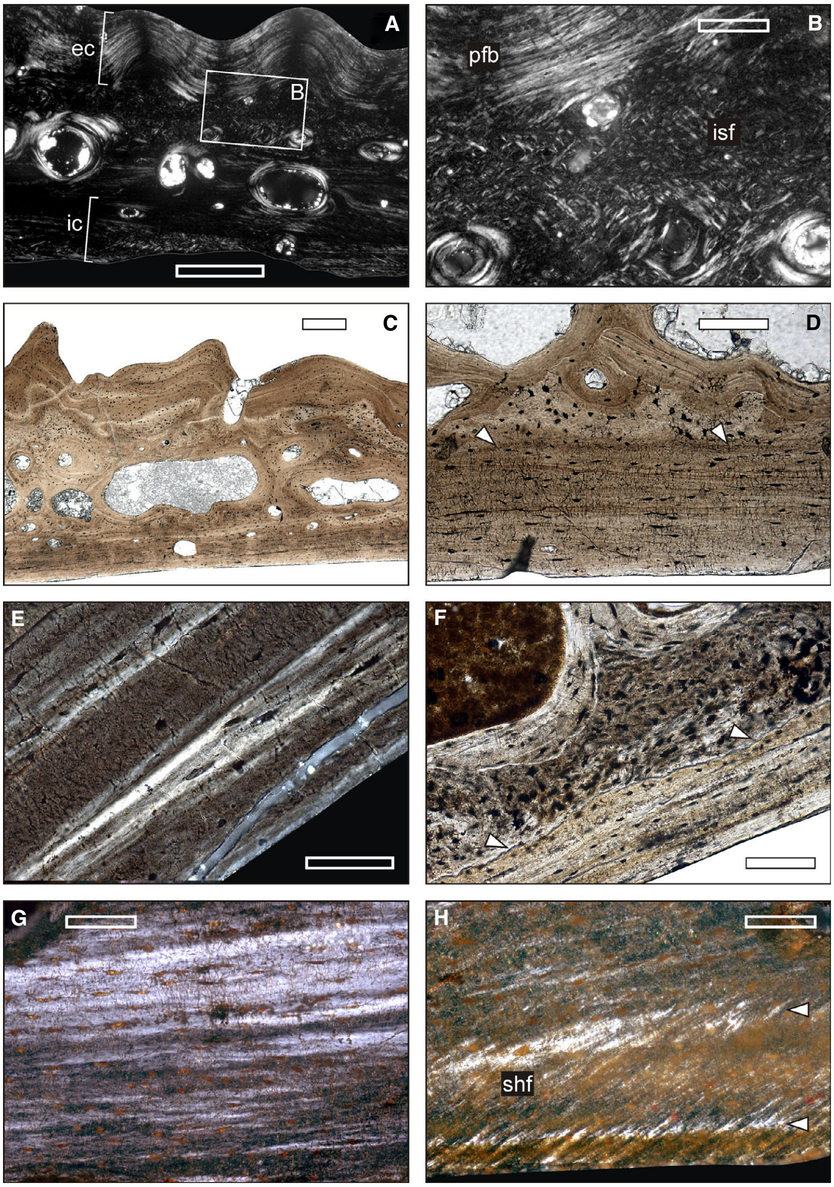

Fig. 6—Chroniosuchid osteoderms: structure of the middle layer (A–C) and internal cortex (D–H). —**A, B**. *Chroniosaurus dongusensis*, specimen FG 612/7 in cross-polarised light. —**C–E**. *Chroniosaurus dongusensis*, specimen FG 612/6. Arrows in D mark the boundary between the middle region and more orderly zonal bone of the internal cortex. In cross-polarised light (E) domains of contrasting extinction indicate the transition of parallel-fibred to lamellar cortical bone. —**F**. cf. *Uralerpeton tverdochlebovae*, specimen FG 612/8. Arrows mark the undulating boundary between osteoderm middle region and internal cortex. —**G, H**. *Chroniosuchus licharevi*, specimen FG 612/2 in cross-polarised light. The parallel-fibred primary bone in G is marked by local transitions to lamellar bone. Sharpey's fibres in H are dense, contacting the internal osteoderm boundary in a low acute angle. Scale bars: A, C, 0.5 mm; B, D, F–H, 0.1 mm; E, 0.05 mm.

Chroniosuchus osteoderms and the density of such fibres is higher below valleys of the dorsal ornamentation than at the saddle tops.

Middle region

The structure of the osteoderm middle region is variable among the sampled chroniosuchid taxa (see Table 2). Mostly its thickness accounts for approximately 50% of the total thickness, but it can constitute up to 70% in *Chroniosuchus* (Figs 4G and 7A) and cf. *Uralerpeton* or <40% in the *Chroniosaurus* osteoderms (Fig. 6A,C). In *Chroniosuchus*, the thickness of the cancellous layer depends on the dorsal ornamentation relief, i.e. it is extended below sculptural saddles. With the exception of some *Chroniosaurus* sections (see Fig. 6A), the degree of remodelling is high, as indicated by voluminous erosive cavities, and only minor areas of parallel-fibred primary bone (Figs 4G, 5A, 6C, 7A, and 8).

In the Poteryakha-2 specimens of *Chroniosaurus*, the unaltered primary bone matrix accounts for a relatively high amount of the total volume. Well separable from the homogenous parallel-fibred bone of the external cortex in cross-polarised light, the bone matrix of the osteoderm middle region of these specimens is either structured by distinct fibre bundles of coarse parallel-fibred bone or by networks of overcrossing collagen fibres alternating with zones of parallel-fibred bone (in FG 612/7; Fig. 6A,B). These fibre networks appear to represent 'interwoven structural fibres' similar to those described for osteoderms of the *Plagiosuchus pustuliferus* and *Bystrowiella schumanni* (Witzmann and Soler-Gijón 2010),

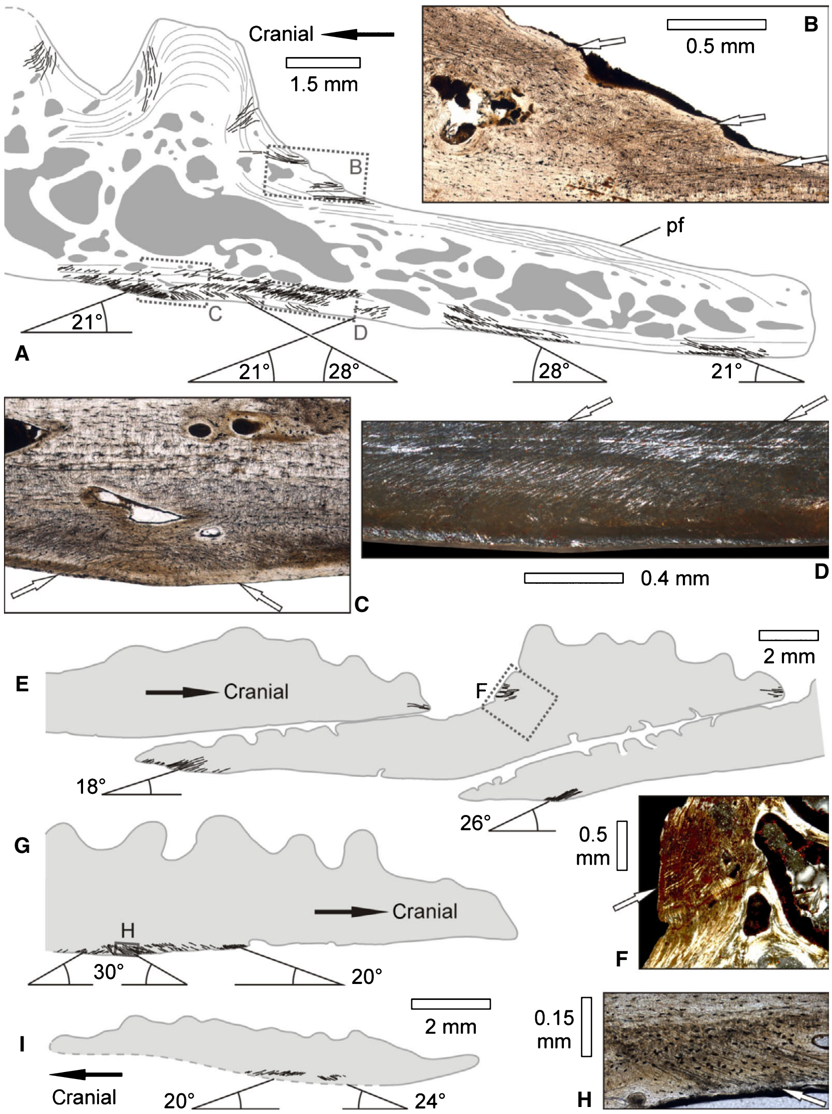

Fig. 7—Sharpey's fibres within the internal cortex and close to the facet areas. —**A–D**. *Chroniosuchus licharevi*, specimen FG 612/2: A, schematic drawing; B, C, detail photomicrographs of the internal and external cortices in normal light; D, detail photomicrograph of the internal cortex in cross-polarised light. —**E, F**. Schematic drawing and detail photomicrograph of *Madygenerpeton pustulatus*, specimen FG 596/V/13. —**G, H**. Schematic drawing and detail photomicrograph of cf. *Uralerpeton tverdochlebovae* specimen FG 612/8. —**I**. Schematic drawing of *Chroniosaurus dongusensis*, specimen FG 612/7. All depicted thin sections have a parasagittal orientation. White arrows and angle diagrams indicate the trend of Sharpey's fibres (black lines). Dotted rectangular frames designate the position of B–D, F, and H.

anurans (Ruibal and Shoemaker 1984) and various amniote groups (e.g. Scheyer and Sander 2004; Main *et al.* 2005; Hill 2006; Scheyer and Sánchez-Villagra 2007; Scheyer and Anquetin 2008; Vickaryous and Hall 2008). Osteoderm sections displaying structural fibres are marked by irregularly arranged lacunae without canaliculi.

The compactness of the middle region varies with the shape and size of the erosive cavities and often it increases at the lateral, anterior and posterior ends. In *Chroniosuchus* and cf. *Uralerpeton*, the middle region is dominated by large cavities that have a polygonal shape and are separated by only thin trabeculae of secondary bone. Medially, the interior of *Chroniosuchus* osteoderms comprises a central layer of large polygonal cavities surrounded by more dense secondary bone tissue with numerous smaller elongated and irregularly branching cavities (see FG 612/1, Fig. 4G). *Chroniosaurus* and *Madygenerpeton* are marked by erosive cavities that have rather roundish than polygonal outlines and are not as dense as in *Chroniosuchus* and cf. *Uralerpeton* (see Figs 6A,C and 8). Among the *Chroniosaurus* specimens, the osteoderm samples from Dongus-6 (FG 612/4 and 5; see Fig. 4H) display a cancellous layer with lower amounts of primary bone and more channel-like transversally oriented cavities than osteoderms from Poteryakha-2, whose isometric cavities are lined with thick secondary bone (FG 612/6 and 7, Fig. 6A–D). Between anterior-end and trunk osteoderms of *Chroniosaurus*, the overall compactness may differ slightly but no marked dissimilarity occurs.

Internal cortex

The internal cortex usually forms the thinnest layer of a chroniosuchid osteoderm and may locally taper off. In most specimens, it consists of homogenous or coarse parallel-fibred

Table 2 Variation in the osteoderm microstructure of four studied chroniosuchid taxa and the bystrowianid *Bystrowiella schumanni* (from Witzmann and Soler-Gijón 2010, p. 99-101). The asterisk marks terms that describe differences in compactness according to the scheme of Francillon-Vieillot *et al.* (1990)

	Primary bone matrix			
Taxon	ec	mid region	ic	Structure of the osteoderm middle region
Chroniosuchus	pfb	pfb	pfb - lb	Highly remodelled, trabecular to coarse cancellous*
Chroniosaurus	pfb	(c)pfb + isf	pfb - lb	Moderately to highly remodelled, coarse cancellous*
cf. *Uralerpeton*	cpfb	cpfb	cpfb	Highly remodelled, trabecular*
Madygenerpeton	pfb	pfb	pfb	Highly remodelled, coarse cancellous*
Bystrowiella	pfb	isf	pfb	Lowly remodelled, fine cancellous*

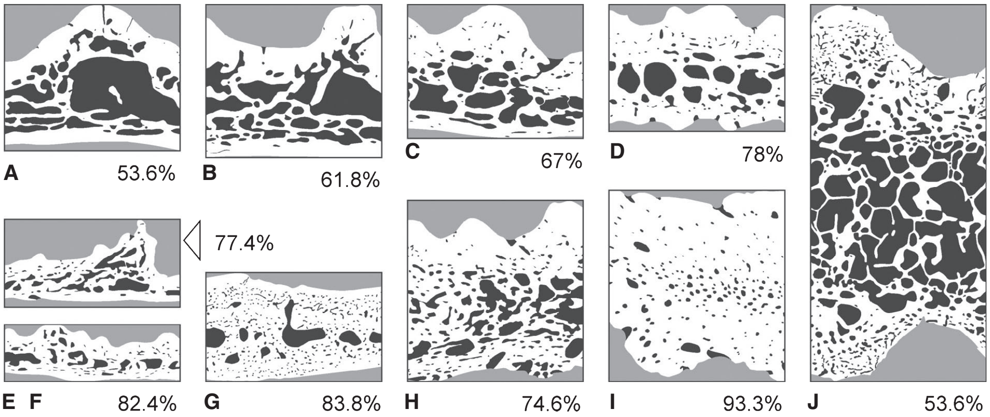

Fig. 8—Amount and distribution of internal space in exemplary compactness measurement sections (5 mm width) of all sampled taxa (see Fig. 2, Supporting information). —**A**, **B**. *Chroniosuchus licharevi*, sections FG 612/3-t and 2-t-1. —**C**. cf. *Uralerpeton tverdochlebovae*, section FG 612/8-t-2. —**D**. *Madygenerpeton pustulatus*, section FG 596/V/12-t-1. —**E**, **F**. *Chroniosaurus dongusensis*, sections FG 612/5-t-3 and 5-t-2; **G**, *Bystrowiella schumanni*, section SMNS 91226-t-1. —**H**. *Gerrothorax* sp., section SMNS 91330-t-1. —**I**. *Plagiosuchus pustuliferus*, section SMNS 91327-t. —**J**, *Aspidosaurus* sp., MCZ 1477-p-1.

primary bone. The internal cortex may have a more orderly structure than the primary bone matrix of the contacting layer of the osteoderm middle region (Fig. 6D,F). Some osteoderm sections of *Chroniosuchus* and *Chroniosaurus* feature homogenous parallel-fibred bone with local transitions to lamellar bone which are indicated by contrasting zone-wise extinction in cross-polarised light (Fig. 6E,G). The oval or roundish shape of bone cell lacunae in successive layers of this bone type reflects the corresponding change of cell and fibre orientations in successive zones of contrasting extinction (see Fig. 6E; Francillon-Vieillot *et al.* 1990).

In chroniosuchid osteoderms, the internal cortex is avascular to moderately interspersed by primary vascular channels, mostly in accordance with the degree of vascularisation in the external cortex. Growth zonations in the internal cortex are common and often as defined (see Fig. 6D,F), but may be of lower contrast than in the external cortex. In *Madygenerpeton*, lines of arrested growth are rare and only barely recognisable in cross-polarised light despite a very pronounced pattern of growth marks which probably was to some degree synchronous to the resting lines in the external cortex.

Only in four parasagittal thin sections which were cut close to the dorsal midline, Sharpey's fibres have been found within the internal cortex. In cross-polarised light the parasagittal sections of FG 612/2, 612/7, 612/8, and FG 596/V/13 (representing each of the four considered chroniosuchid taxa) display dense bundles of thin fibres running oblique to the zonation of the parallel-fibred cortical bone (Figs 6H and 7). In FG 612/2 and 612/8, these fibres are also visible in normal light (Fig. 7B,C,H). Unlike the more variable configuration in the external cortex, the fibre orientation within a bundle of Sharpey's fibres in the internal cortex displays only minor variation (see Figs 6H and 7). The fibre bundles only occur in the posterior non-overlapping part of the inner cortex and display a posteroventral trend in FG 596/V/13 and both, anteroventral and posteroventral trends in FG 612/2, 7, and 8 (see Fig. 7A). Mostly the Sharpey's fibres are dipping shallowly at angles between 20° and 30° towards the internal osteoderm boundary. Whereas in the specimens, FG 612/7 and 8 one posterior bundle of posteroventral fibres and one anterior bundle of anteroventral fibres are preserved, the *Chroniosuchus* specimen FG 612/2 features several bundles with alternating orientations (see Fig. 7A,C,G,I). The contrasting orientations of Sharpey's fibres close to the internal osteoderm boundary and close to the osteoderm middle region leads to a conspicuous herring-bone pattern in one part of the internal cortex of FG 612/2.

Central body and ventral process

Chroniosuchid osteoderms are marked by a medial to lateral differentiation in morphology and osteohistology. In the transversal sections of FG 612/1, 4, 5, and 7 as well as FG 596/V/12, a characteristic edge on the internal surface and an associated bend in the parallel-fibred bone of the internal cortex mark the boundary line between the lateral osteoderm wings and the osteoderm central body (*corpus scutulumi*) that forms a prominent plateau from which the ventral process as well as to the anterior wings and posterior processes arise (see Figs 5A and 11).

In the transversal sections of *Chroniosuchus* specimen FG 612/1 and *Madygenerpeton* specimen FG 596/V/12, the thickness of the cancellous middle region considerably increases towards the medial plane, enlarging the contact zone between the main plate of the osteoderm (i.e. the platy part parallel to the dorsal body surface) and the midsagittal ventral process (Fig. 5A). In FG 596/V/12 the internal cortex also contributes much to the medial thickening. It features an increased density of primary vascular channels – as in the medial part of some *Chroniosaurus* osteoderms – and wide-spaced bone growth marks that end unconformably at older growth marks of the ventral process (Fig. 5E). Both osteoderms, FG 612/1 and FG 596/V/12, display medially a layer of lowest compactness that is further away from the internal osteoderm surface than in the lateral osteoderm sections. The medial contact zone of the ventral process is marked by a ventrolateral trend of trabeculae in the cancellous layer (oblique to the main plate and ventral process of the osteoderm (Fig. 5A: dash-dotted lines; see also Fig. 4G).

Similar to the lateral wings of the osteoderm, the ventral process has a diploë structure with a cancellous interior and cortices which form a seamless connection to the internal cortex of the central osteoderm body. In *Madygenerpeton* specimen FG 596/V/12, the asymmetrical pocket-like incision of the ventral process that encloses the neural spine of the adjacent vertebrae is preserved (Fig. 5A). As the growth mark pattern around the incision demonstrate, the distance between vertebra and main plate of the osteoderm was not static but changed during the ontogenesis.

Facet areas

Unlike the external cortex in the ornamented part of the chroniosuchian osteoderms, the thinner external cortices below the posterodorsal articulation facets are devoid of Sharpey's fibres in all considered specimens. With the exception of the *Madygenerpeton* osteoderms, the degree of vascularisation of the cortex is similar to that of the ornamented sections. In the *Madygenerpeton* specimens, numerous primary vascular channels end on the facets which appear to be pockmarked by roundish foramina (denoted for specimen FG 596/V/13 in Fig. 7E). The foramina often occur within the grooves of the groove-and-ridge-system relief which is characteristic for the articulation facets of *Madygenerpeton* osteoderms (Schoch *et al.* 2010).

The rear sides of the dorsal sculptured areas immediately adjoining the posterodorsal facet areas of *Chroniosuchus* specimen FG 612/2 and *Madygenerpeton* specimen FG 596/V/13 display thin distinct bundles of Sharpey's fibres with a conspicuous posterior trend (Fig. 7A,B,E,F). In FG 696/V/13, corresponding bundles of anteriorly trending peripheral fibres occur at the anterior osteoderm margin.

A pair of anteroventral facets constitutes the contact zone of the posteriorly following osteoderm towards the posterodorsal facets of its anterior neighbour. Similar to the state of the external cortex below facet regions, Sharpey's fibres are generally lacking for the overlapping zones of the internal cortex. Whereas the anteroventral facets are morphologically indistinct from the rest of the internal surface in other chroniosuchids, those of *Madygenerpeton* reproduce mirror-inverted groove and ridge pattern of the posterodorsal facets and display similar foramina (see Buchwitz and Voigt 2010, figs 2, 3).

Results of the compactness analysis

The compactness of 31 measured sections varies between 51.8% and 93.3%. The values for chroniosuchians appear to be continuously distributed over the whole spectrum and their compactness profiles overlap with both, the dissorophid and the plagiosaurid sample (Table 3; Figs 8 and 9A). While compactness profiles of *Bystrowiella*, *Chroniosaurus*, and *Madygenerpeton* osteoderms are closer to those of plagiosaurids, profiles of *Chroniosuchus* and cf. *Uralerpeton* sections show more similarity to those of the dissorophid *Aspidosaurus* (Fig. 9A,B).

Most often the compactness values of the five successive 20%-thickness layers (L1 to L5 in Fig. 4) are correlated or highly correlated with each other and with the overall compactness of the measured sections (Table 4). The compactness of the external-most 20% layer (L5), however, is only poorly correlated with other compactness measures. In particular, its correlation with the compactness of the second fifth (L2) is low. Plotting the compactness ratio of L2 and L5 against the overall compactness, a difference in the distribution of internal space between chroniosuchid sections and other measured osteoderms is revealed (Fig. 9C): Among osteoderm sections with a similar total amount of compactness, the chroniosuchid sections display a compactness ratio

Table 3 Results of the compactness measurements: Overall compactness values ('total') and compactness of layers L1 to L5 for all considered taxa. The number of measured sections/osteoderms is listed in column '*n*'

		Compactness [%]					
Taxon	*n*	L1	L2	L3	L4	L5	Total
Temnospondyli	7/3	71–91	35–93	21–90	44–96	74–97	54–93
Aspidosaurus	3/1	71–80	35–50	21–30	44–56	74–85	54–56
Gerrothorax	3/1	70–88	62–69	50–77	83–92	91–97	75–83
Plagiosuchus	1/1	91	93	90	96	96	93
Chroniosuchia	24/10	70–99	7–97	19–90	49–96	81–99	52–93
Bystrowiella	3/1	93–99	76–97	66–90	88–94	93–95	83–93
Chroniosuchidae	21/9	70–99	7–74	19–75	49–96	81–99	52–85
Chroniosuchus	5/3	72–87	7–62	20–36	57–73	81–98	53–68
Chroniosaurus	5/2	89–99	60–74	63–72	79–91	85–97	77–85
cf. *Uralerpeton*	6/2	70–92	25–52	19–63	49–82	95–98	52–74
Madygenerpeton	5/2	90–96	44–60	48–75	61–96	96–99	72–85

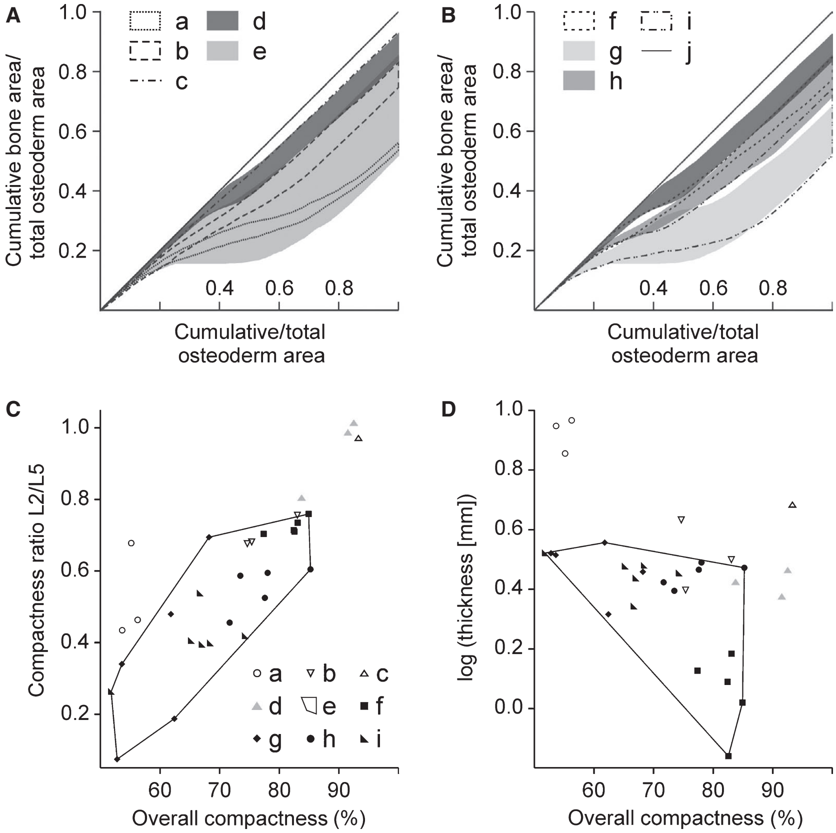

Fig. 9—Results of compactness analysis. —**A**, **B**. Cumulative compactness plots. —**C**. Compactness ratio of 20%-layers L2 and L5 plotted against overall compactness. —**D**. Logarithm of section thickness plotted against overall compactness. Labels: a, *Aspidosaurus* sp.; b, *Gerrothorax* sp.; c, *Plagiosuchus pustuliferus*; d, *Bystrowiella schumanni*; e, Chroniosuchidae (convex hull of associated data points in C, D); f, *Chroniosaurus dongusensis*; g, *Chroniosuchus licharevi*; h, *Madygenerpeton pustulatus*; i, cf. *Uralerpeton tverdochlebovae*; j, line of 100 per cent compactness.

which is mostly lower. Furthermore, there appears to be a dependence of thickness and compactness as a consequence of the markedly deviant thicknesses of the *Aspidosaurus* and *Chroniosaurus* samples (Fig. 9D).

Discussion

Homology of the chroniosuchian osteoderms

The assumption that dorsal osteoderms of the two principal chroniosuchian groups, Bystrowianidae and Chroniosuchidae, are homologous structures was questioned by Golubev (1998) who considered the overlap of the posterodorsal osteoderms facets in chroniosuchids by a posteriorly following osteoderm as antithetic to the overlap of the broad dorsal facets on the anterior wings of bystrowianid osteoderms (see *Bystrowiella* in Fig. 10A) by an anteriorly following osteoderm. He argued that this disparity in morphology and arrangement contradicted the hypothesis of their homology (Golubev 1998; p. 280). Novikov and Shishkin (2000), however, proposed a homology hypothesis that could solve this paradox: Assuming that bystrowianid osteoderms correspond only to

Table 4 Correlation matrix for compactness values of the 20% thickness layers L1- L5 and total compactness. In the lower left half, correlation coefficients for the chroniosuchid sample ($n = 21$) are listed; upper right half: values for the complete sample ($n = 31$)

	L1	L2	L3	L4	L5	Total
L1	–	0.525	0.686	0.691	0.350	0.800
L2	0.701	–	0.813	0.662	0.152	0.885
L3	0.745	0.815	–	0.770	0.378	0.941
L4	0.761	0.652	0.627	–	0.506	0.885
L5	0.278	0.042	0.127	0.215	–	0.455
Total	0.869	0.911	0.924	0.846	0.228	–

the central body of chroniosuchid osteoderms, the peg-like anterior processes of chroniosuchids (see Fig. 2A) may be homologous to the platy anterior wings of bystrowianids (further congruencies in Novikov and Shishkin 2000, p. 168). An independent test of this kind of morphology-based homology hypothesis is provided by the comparison of histological characteristics of the two osteoderm types.

The only yet considered sample of the bystrowianid *Bystrowiella* (specimen SMNS 91226; Witzmann and Soler-Gijón 2010) differs markedly in its histology from the chroniosuchid osteoderms described in this study (see Fig. 10A): Whereas the interior of chroniosuchid osteoderms is of low compactness, featuring large erosive cavities lined with secondary bone and only minor areas of parallel-fibred primary bone, the middle region of the *Bystrowiella* osteoderm is dominated by a homogenous primary bone matrix with a regular pattern of interwoven structural fibres. The cancellous layer accounts for less than one forth in *Bystrowiella* and divides the osteoderm symmetrically (Fig. 10B,C) – unlike the state in chroniosuchids, whose thick cancellous layer separates the thin internal and relatively thick external cortices. In chroniosuchids, Sharpey's fibres are not only abundant in the external cortex, but also occur as distinct bundles in the internal cortex. Featuring

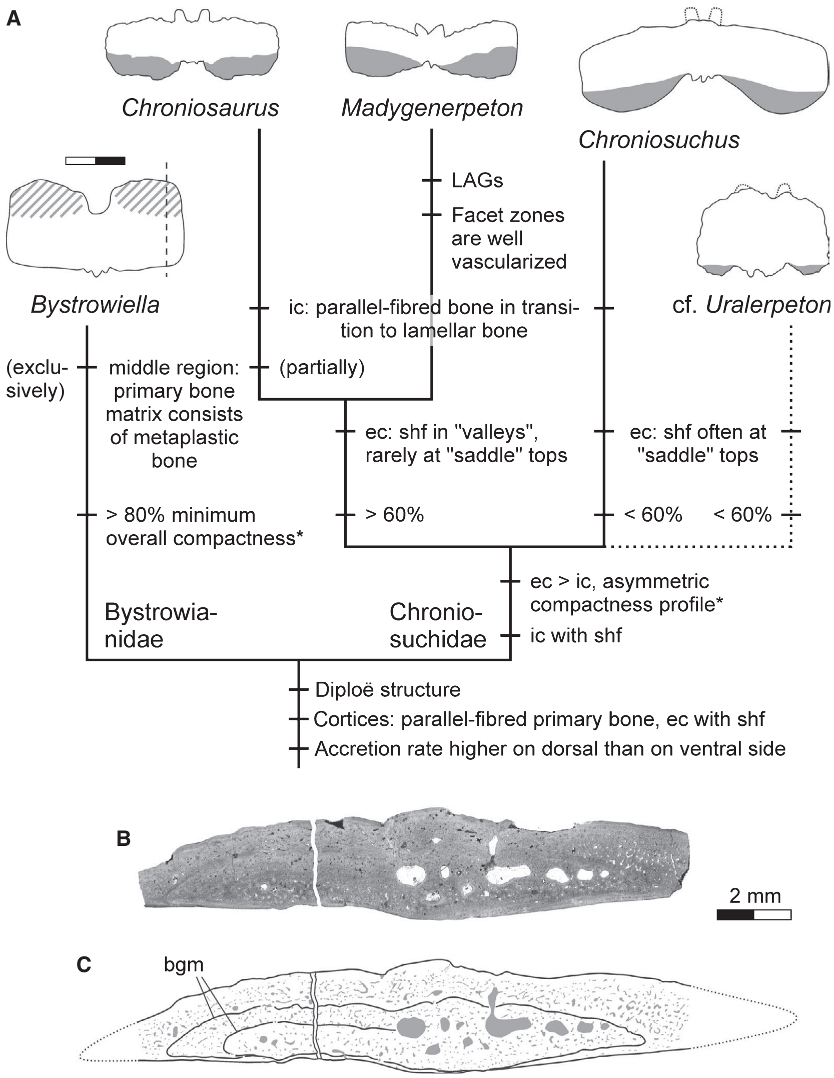

Fig. 10—Osteoderm histology of *Bystrowiella schumanni* compared to that of chroniosuchids. —**A**. Tree diagram for the Chroniosuchia; topology modified from Schoch *et al.* (2010). *Bystrowiella* and cf. *Uralerpeton* have been incorporated on the basis of the assumption that Chroniosuchidae is a monophyletic group. The asterisk marks characters based on the compactness analysis of 5-mm-wide dorsoventral transects (see Figs 3, 8 and 9). Posterodorsal facets are grey-shaded; the lined areas indicate the position of facets on the anterior wings of *Bystrowiella* (after Witzmann *et al.* 2008). The dashed line marks the position of the thin section depicted below. —**B**, **C**. *Bystrowiella schumanni*, parasagittal section through specimen SMNS 91226 displaying growth marks (black lines) that indicate a high dorsal and low ventral accretion of bone throughout the preserved part of the ontogenesis. Cavities and vascular channels are grey-shaded. Note that the central position of the cancellous layer is not concordant with the pattern of growth marks.

a high overall compactness, domains of interwoven structural fibres and often an only moderately remodelled middle region the osteoderm samples of *Chroniosaurus* display the highest similarity with the *Bystrowiella* specimen. As no bystrowianid osteoderms have been studied histologically apart from this one specimen, conclusions regarding the distinctness of bystrowianid osteoderm histology have to be treated with caution. In view of all mentioned aspects, the hypothesis that chroniosuchid and bystrowianid osteoderms are homologous skin derivatives cannot be rejected on the basis of present histological data.

Mode of skeletogenesis

The bone microstructures of chroniosuchian osteoderms indicate similar modes of skeletogenesis as in the dermal bone types of other crown-group tetrapods: Ossification via metaplasia in *Bystrowiella* and some of the *Chroniosaurus* specimens can be inferred from the presence of interwoven structural fibres, i.e. remnants of the former dense dermal or connective tissues that were transformed into dermal bone (see Scheyer and Sander 2004), and from absence of canaliculi in the bone cell lacunae (see Haines and Mohuiddin 1968; Main *et al.* 2005). Osteoderms that formed partially by metaplasia also occur in the plagiosaurid temnospondyl *Plagiosuchus* (Witzmann and Soler-Gijón 2010), anurans (Ruibal and Shoemaker 1984), squamates (Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986), crocodylians (Vickaryous and Hall 2008), dinosaurs (e.g. de Ricqlès *et al.* 2001; Scheyer and Sander 2004; Main *et al.* 2005; Cerda and Powell 2010) and some xenarthrans (Hill 2006). Often, metaplastic primary bone does not form the outermost layer but it is enclosed in periosteal bone. As in the *Chroniosaurus* osteoderms from the locality Poteryakha-2, which comprise domains of metaplastic bone within a primary bone matrix dominated by parallel-fibred bone, intermediate states between metaplastic bone and periosteal bone have also been observed within dermal bones of other basal tetrapods and reptiles (e.g. Main *et al.* 2005; Scheyer and Sánchez-Villagra 2007; Witzmann 2009; Witzmann and Soler-Gijón 2010). Lacking interwoven structural fibres, most of the sampled chroniosuchian osteoderms comprise parallel-fibred bone as the only type of primary bone, indicating that they may have formed entirely through intramembraneous ossification similar to the mode of skeletogenesis in the dermal armour of the extant armadillo *Dasypus* (Vickaryous and Hall 2006), pareiasaurs (Scheyer and Sander 2009), placodonts (Scheyer 2007), some temnospondyls (Witzmann and Soler-Gijón 2010) and some aetosaurs (Cerda and Desojo in press).

Similarities in the initial development and microstructure of chroniosuchian osteoderms and those of other tetrapods cannot be explained by simple homology as the dorsal osteodermal shields of chroniosuchians have no equivalent among related stem-group amniotes (see Fig. 1A,B). In fact, with the exception of some microsaur species, which display a minor osteoderm cover in the throat or shoulder girdle region (Carroll and Gaskill 1978), osteoderms appear not to be present at all in other groups of the amniote stem. Thus, we find likely that chroniosuchian osteoderms represent another example for the multiple independent origin of osteoderms within the dermis of tetrapods (see also Ruibal and Shoemaker 1984; Hill 2005; Scheyer and Sander 2009; Witzmann and Soler-Gijón 2010).

Aspects of osteoderm development

The presence of zonal periosteal bone in the cortices of all sampled chroniosuchid osteoderms allows us to infer allometries during the latter part of the ontogenesis. Chroniosuchid osteoderms display a marked difference between internal and external cortices (see Figs 4G,H, 6A,C, 8A–F and 9C): Whereas the external cortex is relatively thick, usually displays a high ornamentation relief and is composed of parallel-fibred bone, the thin internal cortex can show transitions to slower growing lamellar bone as indicated by zones of contrasting extinction in cross-polarised light (Fig. 6E,G). The interpretation that accretion on the inside of the chroniosuchian osteoderm was actually slower than on its outside is in agreement with the higher distinctness of LAGs in the external cortex of *Madygenerpeton* samples and with the structure of circumferentially preserved growth marks in the *Bystrowiella* specimen which demonstrate that at some point of the ontogenesis the growth on the inside of the osteoderm came almost to a rest and only the external cortex grew further (Fig. 10B,C).

Whereas the thin *Chroniosaurus* osteoderms display a T-shape when sectioned transversally, the thicker osteoderms of *Madygenerpeton* and *Chroniosuchus*, which belonged to larger individuals, display an increased thickening in the contact region between the horizontal plate of the osteoderm and the ventral process. Wide-spaced growth marks and a higher density of primary vascular channels in the internal cortex of *Madygenerpeton* indicate that its medial thickening is in fact reached by higher growth rates of the internal cortex (see Fig. 5A). In *Chroniosuchus*, the internal cortex close to the ventral process was probably growing faster as well but its late growth phase is obscured by a stronger bone remodelling than in *Madygenerpeton* which resulted in an expansion of the cancellous middle layer at the expense of the internal cortex. Apart from the thickening, the medial cancellous layer in the contact zone to the ventral process of *Madygenerpeton* specimen FG 596/V/12 displays a conspicuous oblique trend of bone trabeculae (Fig. 5A). Probably both the thickening and the orientation of trabeculae strengthened the attachment of the ventral process and increased the loading capacity of the osteoderm. The length of the ventral process which determines the distance between the osteoderm main plate and the transversal processes of the vertebrae is only slightly increasing in specimen FG 596/V/12.

According to a generalised growth scheme for chroniosuchid osteoderms, an initially T-shaped osteoderm, consisting

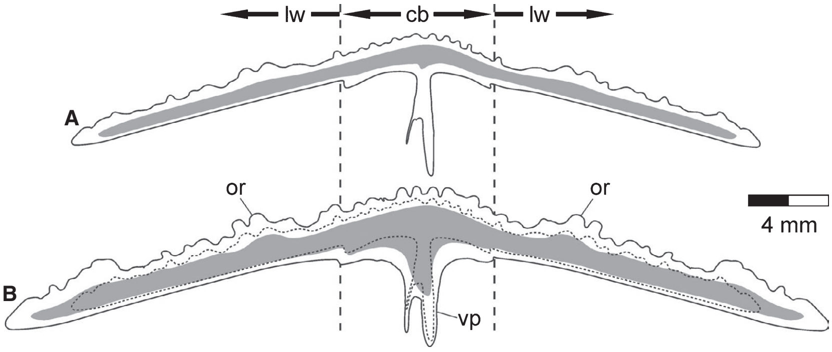

Fig. 11—Osteoderm shape change during the latter part of the ontogeny. —**A**. Schematic transversal section through the dorsal osteoderm of a pre-adult chroniosuchid. —**B.** Transversal osteoderm section for an adult individual (scheme modified from specimen growth series in FG 596/V/12, see Fig. 5). The dashed line represents the earlier osteoderm outline; the cancellous layer is grey-shaded. Scale bar: 4 mm.

of a thin ventral process and a thin and narrow main plate (Fig. 11A), develops by dominating lateral and dorsal accretion, and, after a certain size limit is reached, by thickening of the anchoring of the ventral process (Fig. 11B). Notwithstanding the distance between osteoderm and the vertebral centrum might have changed only slightly given the simultaneous medial thickening of the internal cortex and elongation of the ventral process. The position of parasagittal ornamentation ridges appears to be relatively constant over time and the gradient of the dorsal relief apparently increases with raising osteoderm thickness.

Resting lines within bone cortices of fossil and extant poikilotherm tetrapods are often interpreted as the result of an annual growth cycle and form the basis of skeletochronology (e.g. Peabody 1961; Castanet *et al.* 1993; Scheyer *et al.* 2010). Assuming that resting lines in the osteoderms of *Madygenerpeton* reflect an annual periodicity as well, we infer growth rates and a minimum individual age for specimen FG 596/V/12: The thickest growth increments of its external cortex demonstrate that its maximum growth rate exceeded 0.3 mm per period. If the period was 1 year, this osteoderm would have belonged to an individual that was more than 12 years old. The spacing of increments towards the external surface reflects a continuous decrease in accretion of periosteal bone at the beginning of the recorded time span and during the last 6 years of life accretion occurred at a constant low growth rate (Fig. 5B,C,F). Given this kind of growth profile, we interpret the individual to whom FG 596/V/12 belonged as an adult.

Sharpey's fibres and muscle attachment

Sharpey's fibres in the external cortex of the sculptured osteoderm parts can vary considerably in thickness, abundance and orientation (Fig. 4D–E). They often have perpendicular or high-angle orientations towards the outer osteoderm surface and probably represent anchoring fibres from an overlying dermal connective tissue. To some degree, the distribution patterns of Sharpey's fibres in the external cortex vary between the chroniosuchid species (see Fig. 10A) and may be related to the type of ornamentation. In contrast, Sharpey's fibres in the internal cortex of chroniosuchid osteoderms form strictly localised dense bundles with low variation in the orientation of individual fibres, which run towards the internal boundary of the osteoderm at acute angles of 30° or less (see Fig. 7). Previous studies documented Sharpey's fibres in the internal cortex or basal layer of dorsal osteoderms of various tetrapod groups, such as, squamates (de Buffrénil *et al.* 2010), phytosaurs, crocodylians (Scheyer and Sander 2004; Vickaryous and Hall 2008; Klein *et al.* 2009), thyreophoran dinosaurs (Scheyer and Sander 2004) and temnospondyls (Witzmann and Soler-Gijón 2010). In most groups, these fibres have been interpreted as incorporated tissue of the skin, muscles, tendons or ligaments that effected a more forceful attachment of the osteoderms.

However, such an attachment function cannot explain the patterns of Sharpey's fibres observed in the craniocaudally segmented crocodylian dorsal shields which have the two middle osteoderms of each multi-osteoderm shield segment inflexibly attached to the spinous process of one associated vertebra through an intermediate layer of apical cartilage and cingular ligaments (Frey 1988*a,b*; Salisbury and Frey 2000). Two or four osteoderm rows in the middle of the dorsal shield constitute the so-called paravertebral shield which functions as an attachment site for the epaxial musculature. The epaxial muscles systems span several vertebral segments between the transverse processes of the vertebrae and the ventral side of the paravertebral osteoderms. This particular suspension considerably contributes to the support of the trunk during raised gait on land and forms a crucial component of the various trunk constructions in fossil and recent Crocodylia (*sensu* Martin and Benton 2008) referred to as bracing systems (see Frey 1988*b*; Salisbury and Frey 2000; Schwarz-Wings *et al.* 2009).

Apart from crocodylians, dorsal osteoderm systems with a rigid connection to the vertebral column occur as well in dissorophid temnospondyls (Dilkes and Brown 2007; Dilkes 2009), but in the internal cortex of their osteoderms Sharpey's fibres have not been found. Arguably, they are absent because a further soft tissue anchoring of the osteoderms was not required (Witzmann and Soler-Gijón 2010). Chroniosuchids and crocodylians, however, share dense bundles of shallowly dipping Sharpey's fibres in the internal cortex of the shield segments (consisting of one only osteoderm in chroniosuchians)

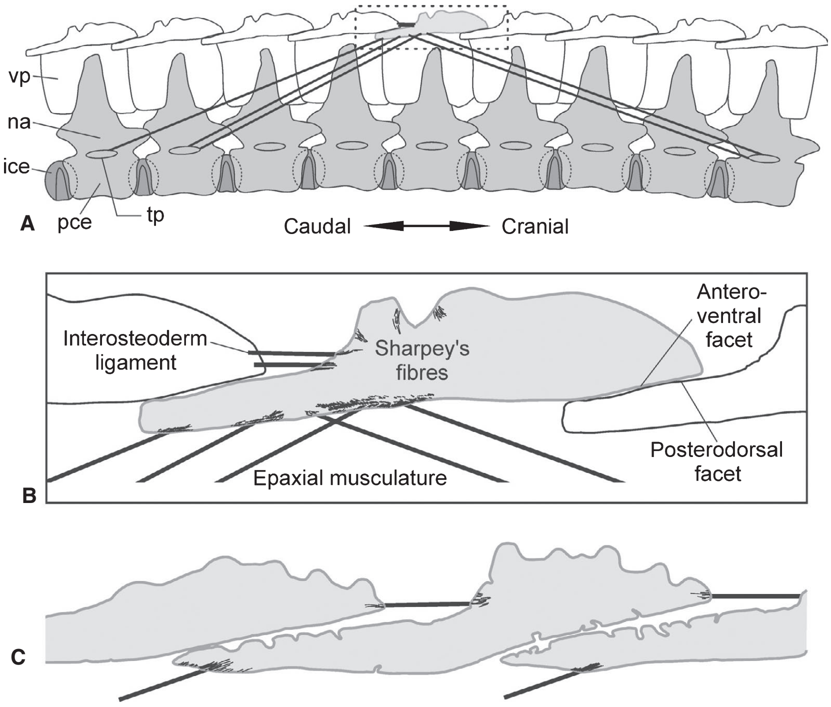

Fig. 12—Schematic reconstruction of epaxial muscle suspension and interosteoderm ligaments in the chroniosuchid trunk. —**A, B**. Reconstruction on the basis of osteoderm specimen FG 612/2 (parasagittal thin section), a ratio of height to segment length of 1.4, and a dorsal curvature of 1° per segment. Vertebral structure and osteoderm contact according to V'yushkov (1957*a*) and Buchwitz and Voigt (2010). —**C**. Orientation of muscles and ligaments for the osteoderms of specimen FG 696/V/13 which has been sectioned more laterally than FG 612/2.

and a stiff or joint-like connection between the shield segments and associated vertebrae (see also Discussion by Clack and Klembara 2009; Buchwitz and Voigt 2010). Our conclusion is that the insertion of the epaxial musculature to the ventral side of chroniosuchian osteoderms evolved convergent to the arrangement in crocodylian bracing systems and was not functionally related to the already sophisticated anchoring of the osteoderms but supported the carrying of the trunk during terrestrial locomotion. In agreement with such an analogy Sharpey's fibres in the internal cortex of chroniosuchian osteoderms have only been documented in parasagittal thin sections cut close to the midsagittal plane and not further laterally (see all documented occurrences in Fig. 7); they do not occur in the zone of anteroventral overlap by the neighbouring osteoderm, and they have an either anteroventral or posteroventral orientation, meeting the osteoderm surface at acute angles smaller than 30° – as expected for sets of longitudinal muscles that connect distant vertebral segments. The conspicuous medial thickening and diagonal trend of bony trabeculae in some larger osteoderms (Figs 4G and 5) could be explained as an adaptation to the loadings imposed by their participation in the carrying of the trunk.

Given the knowledge about the height of neural spines in chroniosuchians and about the distance between the main plate of the osteoderm and the transverse processes of the vertebrae (see Golubev 1998; Novikov *et al.* 2000; Clack and Klembara 2009), which possibly formed the counter-attachment for the epaxial muscles as in crocodylians, we can constrain further aspects of a chroniosuchian trunk bracing system (Fig. 12A,B): Assuming a moderate dorsal curvature of 1° per segment and a distance between osteoderm and the transverse processes which was 1.4 times as large as the axial segment length the epaxial muscles would have spanned 3–4 vertebrae. The herring-bone pattern of Sharpey's fibres in the internal cortex of the *Chroniosuchus* osteoderm FG 612/2 (Fig. 7A) probably documents an ontogenetic change in the position of neighbouring muscle insertion fields. The lack of anteroventrally dipping fibre bundles in the somewhat more laterally positioned section through three *Madygenerpeton* osteoderms (FG 596/V/13) might reflect a specific mediolateral differentiation in the attachment system (Figs 7E and 12C).

Apart from the general lack of knowledge about chroniosuchian soft body anatomy, the hypothesis of functional analogy between chroniosuchian and crocodylian osteoderm systems faces several limitations: Unlike the state of muscle attachment inferred here for chroniosuchian osteoderms, the epaxial musculature of recent eusuchians features suspension angles of <10° and only for the hyposaurine dyrosaurids, a fossil group of crocodylians with particular long neural spines, steeper angles of 20° have been suggested (Schwarz-Wings *et al.* 2009). A further dissimilarity occurs in the observed patterns of Sharpey's fibres: Despite the longitudinal trend of epaxial muscles, Sharpey's fibres in the internal cortex of *Alligator mississippiensis* (Vickaryous and Hall 2008; Klein *et al.* 2009) and fossil crocodylian osteoderms (Scheyer and Sander 2004) have transversal orientations perpendicular to the parasagittal dorsal osteoderm ridges but parallel to the orientation of cingular ligaments which are underlying the paravertebral osteoderms and form the actual attachment sites instead of a direct insertion of the muscle systems on the bone (Frey 1988*b*).

In crocodylians, successive shield segments are connected through interosteoderm ligaments that are dorsally attached to the anterior end and ventrally attached to the posterior end. Some fossil crocodylian groups display a serial overlap of narrow anterodorsal and posteroventral facets which form the insertion sites of interosteoderm ligaments (Frey 1988*b*; Salisbury and Frey 2000). In contrast, chroniosuchids display broad anteroventral and posterodorsal facets with no indication of ligament attachment (Fig. 7A,E,G,I). However, at the anterior end of two osteoderms in specimen FG 696/V/13 (Fig. 7E,F) and at posterior end of the raised ornamented dorsal area in FG 696/V/13 and FG 612/2 (Fig. 7A,B), thin bundles of craniocaudally trending Sharpey's fibres occur, and we compare them to so-called peripheral Sharpey's fibres of some squamates (Levrat-Calviac and Zylberberg 1986; de Buffrénil *et al.* 2010) and the armadillo (Vickaryous and Hall 2006) which mark the insertion of ligaments connecting neighbouring osteoderms (see Fig. 12B,C). Considering the differences in the orientation of Sharpey's fibres, the distinct articulation between osteoderms, and the position of the interosteoderm ligaments with respect to the articulation facets, the crocodylian trunk bracing systems probably shared not much more than the basic principle with chroniosuchian trunk constructions and all conclusions by analogy have to be treated with caution.

Apart from osteohistological similarities, Clack and Klembara (2009) compared the morphology of chroniosuchian osteoderm systems to the 'closed' osteoderm shields of certain fossil crocodylians, such as *Goniopholis*, whose overlap of shield segments was probably efficient in the mitigation of damaging shear and torsional loads acting on the vertebral column during raised gait on land (see Salisbury and Frey 2000). Given the lack of Sharpey's fibres in the internal cortex of *Bystrowiella schumanni* (see Witzmann and Soler-Gijón 2010) and considering the multifold overlap in the osteoderm articulations of chroniosuchians, exceeding those of crocodylians in complexity, Buchwitz and Voigt (2010) argued that the stabilisation provided by osteoderm interlock and fixation to the vertebral column was the major function of chroniosuchian osteoderm shields and probably present in the ancestor of all yet known members of the Chroniosuchia. However, if the skeletal and soft body elements forming the chroniosuchian trunk bracing system evolved closely linked in the context of terrestrialisation, both functions, i.e. suspension of epaxial muscles and support by high-degree interlock of bone, could have arisen simultaneously. To assess the ancestral state in chroniosuchians phylogenetically, further histological evidence from bystrowianid osteoderms, which have not been sufficiently covered here, is required.

Lifestyle inference from the compactness analysis of osteoderm bone

Variation in the compactness and relative thickness of spongious and compact bone layers has been shown to be correlated with lifestyle: In aquatic tetrapods inhabiting shallow water, the average compactness and overall mass of the skeleton are often higher than in the skeletons of similarly sized terrestrial dwellers, effecting a relatively low buoyancy (e.g. Francillon-Vieillot *et al.* 1990; Laurin *et al.* 2004). Secondarily, aquatic tetrapods increase the amount of bone by pachyostosis, i.e. additional accretion of cortical bone, or by osteosclerosis, i.e. increase in bone compactness, or a mixture of both (see de Ricqlès and de Buffrénil 2001; Houssaye 2009). To quantify the lifestyle-dependent variation in bone compactness, several recent approaches on extant and fossil tetrapods employ the software Bone Profiler for extracting compactness parameters from medial sections of limb bones (e.g. Laurin *et al.* 2004, 2006; Germain and Laurin 2005; Kriloff *et al.* 2008; Canoville and Laurin 2009, 2010). On the basis of the digitalised bone outline and internal spaces Bone Profiler calculates a centre to surface compactness profile and deduces several compactness parameters related to an interpolated compactness curve (see Girondot and Laurin 2003). As the known aquatic or terrestrial habitat preference of recent tetrapods is well reflected by variation in the long bone compactness parameters, lifestyle inference is feasible for fossil taxa whose ecology is poorly known or ambiguous.

Apart from the long bones, the integumentary skeleton also varies in its compactness and distribution of internal space and these variations may depend on lifestyle as well. In a first quantification approach, Scheyer and Sander (2009) have carried out Bone Profiler analyses on 15 osteoderms of pareiasaurs, crocodylians, ankylosaurs, turtles and lepidosaurs. They found some accordance between the previously assumed lifestyle and overall compactness but sample size and interfering signals (e.g. osteoderm size, variability within an individual) prevented a numerical discrimination on the basis of compactness parameters. We use a somewhat different approach here (see Fig. 3) as flat dermal bone is rather badly described by a measurement scheme that integrates over concentric osteoderm zones for a single centre to surface compactness profile and thereby neglects the strict orientation dependence of dermal bone growth and marked difference of developmental processes on the outer and inner bone surfaces.

The results for 24 dorsoventral compactness profiles of ten chroniosuchian osteoderms and their comparison to temnospondyl profiles and to the data set of Scheyer and Sander (2009) lead us to question the idea that chroniosuchians had a homogenous lifestyle: For osteoderms of *Chroniosuchus* and cf. *Uralerpeton*, which feature a relatively thick trabecular middle region, the measured overall compactness varies between 52% and 74% (see Table 3, Fig. 8A–C) – covering a range that also comprises the much thicker osteoderms of the dissorophid temnospondyl *Aspidosaurus* (Figs 8J and 9), pareiasaurs and an indeterminate nodosaur (Scheyer and Sander 2009, table 2). According to this overlap with chiefly terrestrial groups, the osteoderms of *Chroniosuchus* and cf. *Uralerpeton* did probably not serve as a means to decrease buoyancy, indicating that their bearers were probably no aquatic animals. In contrast, the one included osteoderm of *Bystrowiella* delivers high overall compactness values between 83% and 93% similar to the dorsal osteoderms of the aquatic plagiosaurids (see Fig. 8H,I) and to amphibious crocodylomorphs but also in the range of various terrestrial amniotes (from the sample of Scheyer and Sander 2009). Nonetheless, given the relatively thick cortices which are unusually well vascularised compared to other chroniosuchians – as in the case of pachyostotic thickening (see de Ricqlès and de Buffrénil 2001) – as well as the only thin cancellous layer and lack of secondary bone, which may indicate osteosclerosis by inhibition of remodelling, we consider the osteoderm bearer as an aquatic or amphibious animal.

In accordance with a total compactness of 72–85% which is intermediate between the *B. schumanni* specimen and the osteoderms of cf. *Uralerpeton* and *Chroniosuchus*, the osteoderm samples of *Chroniosaurus* and *Madygenerpeton* display cortices of intermediate thickness and resorption of primary bone in the middle region is either not as high as in the two other chroniosuchids or a thick lining of secondary bone occurs that causes a relatively high compactness of the cancellous middle region (see Figs. 3, 5A, 6A and 8D–F). The straightforward interpretation that *Chroniosaurus* and *Madygenerpeton* had a more waterbound lifestyle than *Chroniosuchus* and cf. *Uralerpeton* but not as waterbound as *Bystrowiella* is weakened by the uncertain ontogenetic status of the individuals from which the samples of *Chroniosaurus* and *Bystrowiella* have been taken and by the possibility that the thinnest osteoderms of *Chroniosaurus* could not have been as lightly built as thicker ones for mechanical reasons (as for the lepidosaur samples of Scheyer and Sander 2009; see also size/compactness relationship in Fig. 9D). The largest osteoderms of *Chroniosaurus dongusensis* reached a medial length of about 1.4 cm whereas the specimens sectioned here were below 1 cm in length. Similarly, the sectioned *Bystrowiella* specimen SMNS 91226 is more than 40% smaller than the holotype (see Witzmann *et al.* 2008). Accordingly, only for *M. pustulatus*, whose preserved pattern of LAGs suggests an adult stage, a clear implication of more aquatic lifestyle than in *Chroniosuchus* and cf. *Uralerpeton* is given. In contrast, the high compactness of the *Chroniosaurus* and *Bystrowiella* osteoderms might be the consequence of an earlier ontogenetic stage and is thus a less compelling indication for a more waterbound lifestyle.

The inference of a more aquatic lifestyle from the compactness profiles of *M. pustulatus* osteoderms is in agreement with the peculiar morphology of their osteoderm-osteoderm articulation which indicates that the osteoderm-bearer had a laterally more flexible trunk than the wide-armoured Permian chroniosuchids and was probably more capable of axial undulation swimming (Buchwitz and Voigt 2010). The unique presence of resting lines in the cortices of the *Madygenerpeton* osteoderms could be either lifestyle-related as well or the consequence of a distinct palaeoenvironment. As the Kyrgyz depositional area of the Madygen Formation was lying between 30° and 40°N during the Middle to Late Triassic (Fedorenko and Miletenko 2002) at a similar latitude as the Russian chroniosuchid localities during the Late Permian (see Ziegler *et al.* 1997, fig. 8.3, 8.4), a higher seasonality or a lower annual average temperature are arguably not the answer to why periodical growth cessations occurred in *Madygenerpeton* and not in the Russian chroniosuchids.

Considering the strong correlation of the 20%-layer compactness values L1 to L5 for our sample of 31 measurement sections (Table 4), we have not carried out a multivariate analysis (see Laurin *et al.* 2004 and subsequent approaches) to discriminate taxa or lifestyles on the basis of these data. However, the compactness ratio of the second and fifth layer (L2/L5) provides a systematic distinction between chroniosuchids and other considered taxa: Chroniosuchid osteoderms of similar total compactness mostly have a lower L2/L5 ratio than non-chroniosuchids (Fig. 9C) which is a consequence of their typical disproportionateness between internal and external cortices. Arguably, our model of the osteoderm as a platy object that consists of locally parallel layers of homogenous compactness could yield a functioning lifestyle discrimination model – if a large enough sample of osteoderm sections and a refined layering are considered.

Conclusions

Unique among stem-amniotes, the dorsal osteoderm systems of chroniosuchians evolved convergent to similar dermal ossifications in temnospondyls and amniotes but with a common inventory of microstructures and developmental processes. Given certain similarities, such as the involvement of metaplastic ossification and a marked difference in the bone accretion rates on the inside and outside of the osteoderms, their independent origin within the two principal groups of Chroniosuchia, Chroniosuchidae and Bystrowianidae, cannot be confirmed on the basis of the present histological comparison of 13 chroniosuchid osteoderms from four species and one bystrowianid osteoderm. The chroniosuchid osteoderms feature sets of antero- and posteroventrally trending Sharpey's fibres in the non-overlapping medial part of the internal cortex which indicate the insertion of epaxial muscle systems to the ventral side of the osteoderms. Considering their attachment to the spinous processes of the vertebrae, the highly sophisticated interlocking mechanism, and their allometric medial thickening that led to a higher mechanical resistance, we interpret the muscle connection of the osteoderms not as a further anchoring element but as the part of a trunk-carrying construction that parallels the crocodylian trunk-bracing systems. This finding supports the hypothesis that the chroniosuchian osteoderm series evolved in a terrestrial context and primarily served as a device that supported terrestrial locomotion. In conflict with a homogenous terrestrial habitat and lifestyle, however, the compactness of chroniosuchian osteoderms is highly variable, indicating a differentiation of the Chroniosuchia within the aquatic-terrestrial spectrum.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Data S1 Results of the compactness analysis.