PALAEOHISTOLOGY AND EXTERNAL MICROANATOMY OF RAUISUCHIAN OSTEODERMS (ARCHOSAURIA: PSEUDOSUCHIA)

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Abstract: The presence of postcranial dermal armour is plesiomorphic for Archosauria. Here, we survey the external microanatomy and histology of postcranial osteoderms (i.e. dorsal paramedian and caudal osteoderms) of rauisuchians, a widely distributed assemblage of extinct predatory pseudosuchians from the Triassic. The osteoderms of eight rauisuchian taxa were found to be rather compact bones, which usually lack significant bone remodelling or large areas of cancellous bone. The presence of highly vascularized woven or fibrolamellar bone tissue deposited in the core areas indicates higher growth rates during earlier life stages, whereas a more compact parallel-fibred bone matrix indicates reduced growth rates in later development. This pattern of change corroborates earlier studies on long bone histology. With the exception of a bone tissue found in the sample of *Batrachotomus kupferzellensis*, which might be the result of metaplastic ossification, the general mode of skeletogenesis is comparable with intramembraneous ossification. The lack of cancellous bone tissue and remodelling processes associated with bone ornamentation, as well as the predominantly intramembraneous mode of ossification, indicates that rauisuchian osteoderm formation differs profoundly from that of the osteoderms of the only extant pseudosuchian lineage, the crocodylians.

Key words: bone histology, dermal armour, Rauisuchia, Crocodylia, archosaurs, intramembraneous and metaplastic ossification.

RAUISUCHIANS comprise an assemblage of mostly large terrestrial Triassic top predators, whose skulls are vaguely reminiscent of theropod dinosaurs (Gower 2000; Gower and Schoch 2009). Current research and phylogenetic analyses have provided evidence both for (Nesbitt 2007; Brusatte *et al.* 2010) and against (Nesbitt 2005, 2009; Gower and Nesbitt 2006; Weinbaum and Hungerbühler 2007) the monophyly of Rauisuchia. Together with other extinct clades including Phytosauria and Aetosauria, as well as the extant Crocodylia and their fossil relatives, they are grouped into Pseudosuchia. In turn, Pseudosuchia is the sister group of the other major archosaur lineage, Avemetatarsalia (*sensu* Benton 1999), which includes dinosaurs and pterosaurs. Pseudosuchian clades are generally characterized by osteoderms (Benton and Clark 1988).

Aside from being only scored as 'absent' or 'present' in phylogenetic studies, osteoderms and other dermal armour were largely neglected as a source of morphological data (see discussion in Hill 2005). This is surprising, given that osteoderms and other dermal armour occur in a large variety of extinct and extant amniotes, including turtles, crocodylians, lizards and armadillos.

Furthermore, for many peudosuchian species, osteoderms constitute the most common and best preserved fossil elements and often are used for taxonomic identification of taxa (e.g. aetosaurs), underscoring the need to access all available data for these structures, including microstructural details. Many rauisuchian taxa are too poorly known to provide detailed data on the osteoderm arrangement along the body, but a few of the better known taxa like *Batrachotomus* or *Ticinosuchus* carry a row of paired paramedian osteoderms covering the vertebral column dorsally in the precaudal region, whereas single median osteoderms cover the caudal region dorsally (e.g. Krebs 1965). The osteoderms show an anterior articular surface of overlap with a more or less prominent anterior projection. Dorsal paramedian osteoderms can also articulate medially. *Ticinosuchus* shows a ventral series of single median osteoderms in the caudal region (Krebs 1965), and small accessory osteoderms may have covered other parts of the body (e.g. belly, trunk and tail or limbs) in *Batrachotomus* (Gower and Schoch 2009).

In recent years, the value of the bone histology of archosaur osteoderms for systematics and functional morphology has been repeatedly shown (e.g. Scheyer and

Sander 2004; Main *et al.* 2005; Hill 2005; Parker *et al.* 2008; Hayashi *et al.* 2010; Cerda and Desojo 2010). The bone histology of several archosauromorph lineages has also been surveyed, but although osteoderms were sampled in some cases, only long bone data were presented (Ricqlès *et al.* 2003, 2008). For rauisuchian taxa, data on long bone histology are restricted to the Middle to Late Triassic rauisuchid *Postosuchus* from North America (e.g. Chinsamy 1994; Padian *et al.* 2001; de Ricqlès *et al.* 2003). Sectioned material previously interpreted to belong to specimens referred to *Luperosuchus* by Ricqlès *et al.* (2008) from the Chanares Formation (Anisian, Middle Triassic) of Argentina should be treated as an indeterminate tetrapod instead, because *Luperosuchus* Romer, 1971 is so far known only by skull remains and putative osteoderms (Desojo and Arcucci 2009). The available long bone data indicate that rauisuchians (as well as aetosaurs and phytosaurs) shared microstructural features and growth trajectories with modern crocodylians (see also Seymour *et al.* 2004; Scheyer *et al.* 2010). On the other hand, the deposition of fibrolamellar bone tissue, especially during early development, indicates that higher growth rates were potentially present in most pseudosuchian lineages, a character possibly retained from their archosauromorph ancestors (de Ricqlès *et al.* 2003, 2008).

Here, we examine the external microstructure and histology of the osteoderms of the rauisuchians (Pl. 1) in comparison to the osteoderms of other pseudosuchians (Pl. 2), including *Revueltosaurus*, phytosaurs and aetosaurs (Scheyer and Sander 2004; Parker *et al.* 2005, 2008; Cerda and Powell 2010; Cerda and Desojo, 2010; this paper). Furthermore, because rauisuchians are on the stem leading to the modern crocodylians, we compare the rauisuchian sample with published data on crocodylian osteoderm bone histology (e.g. Hutton 1986; Hua and Buffrénil 1996; Tucker 1997; Scheyer and Sander 2004, 2009; Vickaryous and Hall 2008; Klein *et al.* 2009), and we further elucidate whether the modes of skeletogenesis of osteoderms of both groups are comparable.

MATERIAL AND METHODS

For this study, six paramedian osteoderms (Pl. 1) could be sampled that represent a wide palaeogeographic, stratigraphic and taxonomic range of taxa which, following Brusatte *et al.* (2010, fig 5), belong to Rauisuchidae (*Rauisuchus tiradentes* von Huene, 1938, *Tikisuchus romeri* Chatterjee and Majumdar, 1987), Prestosuchidae (*Batrachotomus kupferzellensis* Gower, 1999, *Prestosuchus chiniquensis* von Huene, 1938 and '*Prestosuchus*' *loricatus* von Huene, 1938) and Poposauroidea (*Yarasuchus deccanensis* Sen, 2005) (Text-fig. 1). Although the analysis of Brusatte *et al.* (2010) is the most recent and most inclusive phylogenetic analysis published to date, another recent comprehensive analysis by Nesbitt (2009) indicates rauisuchians to be paraphyletic, but recovers monophyletic poposauroid, rauisuchid and crocodylomorph clades within the rauisuchian grade.

The specimens were sectioned transversely at the plate centre. Note that although the species *loricatus* von Huene, 1938 is valid, the material represents a separate genus (Desojo and Rauhut 2008, 2009). *Y. deccanensis*, initially classified as belonging to Prestosuchidae Romer, 1966 by Sen (2005), was recovered as a poposauroid by the phylogenetic analysis of Brusatte *et al.* (2010). However, because *Y. deccanensis* might actually represent more than one taxon (JBD, pers. obs.), its present taxonomic position as a rauisuchian should be treated with caution. Although all six osteoderms derive from the precaudal region, the exact location of the osteoderms on the body (cervical or dorsal part of the vertebral column) could not be identified with the exception of the specimen of *P. chiniquensis*, which comes from the sacral region. We assume that this minor positional variation will not have strong effects on the growth patterns of the various osteoderms and that observed differences stem from other factors.

Additionally, the paratype specimen of the rauisuchoid *Ticinosuchus ferox* (neural spines of six caudal vertebrae and an associated row of nine articulated, tightly overlapping osteoderms) was re-studied with a focus on

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EXPLANATION OF PLATE 1

Figs 1–20. Rauisuchian osteoderms sampled in the present study. Figs 1–12, the anterior side is pointing to the right of the image; Figs 13–20, the ridges are aligned anteroposteriorly (Figs 14, 18). Figs 1–4. *Batrachotomus kupferzellensis* in 1, dorsolateral view, 2, ventrolateral view, 3, thin-section, 4, close-up of the cross-hatching pattern of extrinsic fibres on the ventral bone surface. Figs 5–6. *Prestosuchus chiniquensis* in 5, dorsal view, 6, thin-section. Figs 7–9. *Rauisuchus tiradentes* in 7, dorsal view, 8, ventral view, 9, thin-section. Figs 10–12. '*Prestosuchus*' *loricatus* in 10, dorsal view, 11, ventral view, 12, thin-section. Figs 13–16. *Tikisuchus romeri*. 13, dorsal view, 14, general shape of osteoderm with position of fragment, 15, ventral view, 16, thin-section. Figs 17–20 *Yarasuchus deccanensis*. 17, dorsal view, 18, general shape of osteoderm with position of fragment, 19, ventral view, 20, thin-section. The two columns on the left (with the exception of 4) share the same scale (= 10 mm), and the column on the right depicting the thin-sections of the specimens in normal transmitted light also share one scale (= 4 mm).

PLATE 1
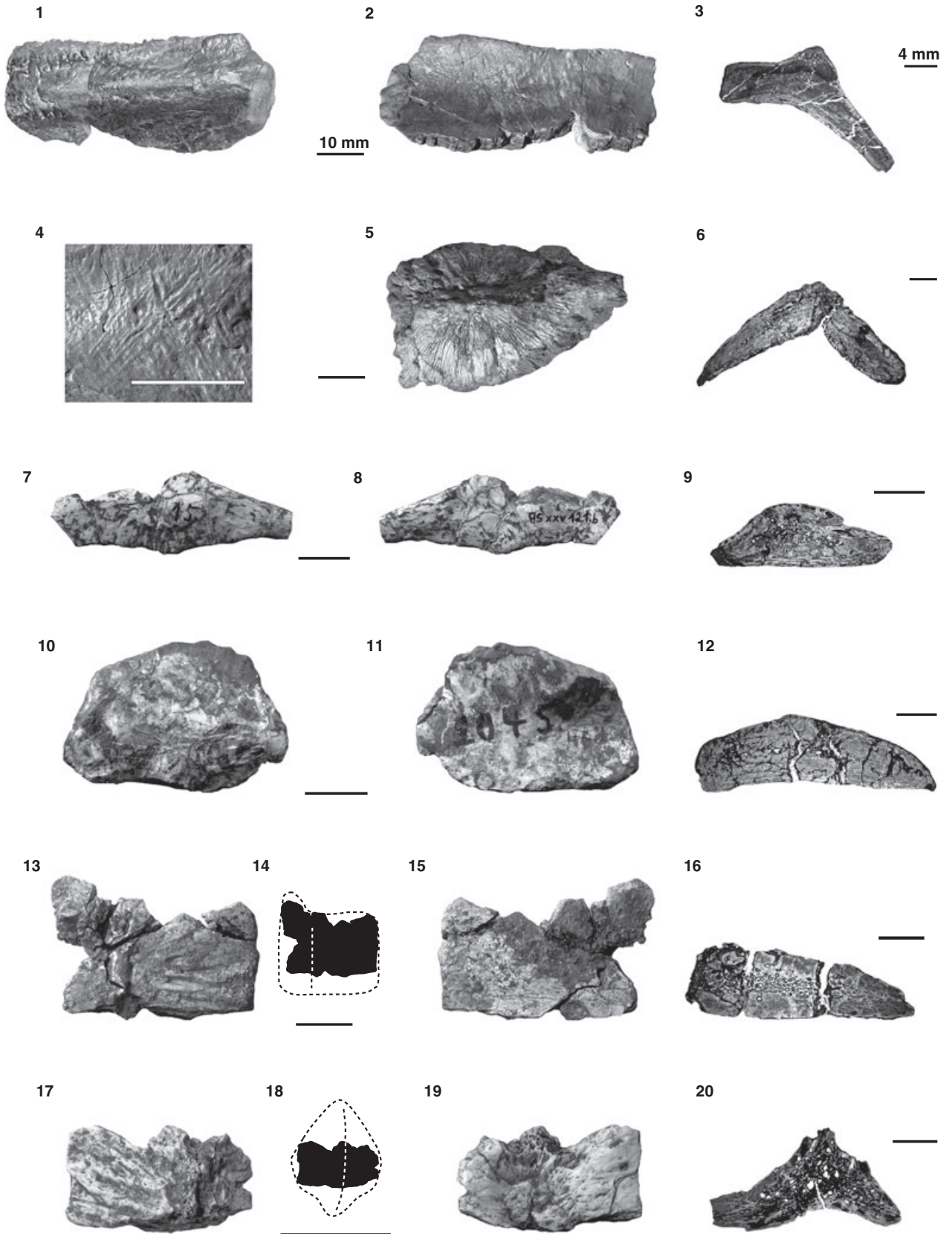
the external microanatomy of the osteoderms (Text-fig. 2A–C). Owing to the preservation of the osteoderms, only the external surfaces and the broken-off parts of the anterior-most and posterior-most plates were studied. An osteoderm associated with a caudal vertebra of a possibly juvenile rauisuchian from the Prosanto Formation (Ladinian) of Canton Grisons, Switzerland (Furrer 2009), was also included in the study (Text-fig. 2D).

Data on authority, accession numbers, age and locality of all specimens sampled were compiled in Table 1. The general morphology of the specimens was recorded prior to destructive sampling, which followed the well-documented standard procedures of petrographic thin-sectioning, which were developed and refined over the last decades (e.g. Scheyer *et al.* 2010). The thin-sections were then analysed with a composite polarizing microscope LEICA DM 2500M and mounted digital camera DFC420 C. Histological and morphological terminology of osteoderms follows Scheyer and Sander (2004).

The terms 'external' and 'internal' are used instead of 'dorsal' and 'ventral' to indicate the superficial and deep/visceral sides or bone surfaces of the osteoderms, whereas the term 'interior' pertains to the core or central area of the osteoderms.

For comparison, fossil osteoderms of *Revueltosaurus* (PEFO 35283, see also Parker *et al.* 2005), the phytosaur cf. *Mystriosuchus* sp. (SMNS 91013), the marine thalattosuchian *Steneosaurus jugleri* (NMS 7152; Mesoeucrocodylia) and the alligatoroid *Diplocynodon* (PIMUZ A/III 0997; IPB R144/1; Crocodylia) have been compiled in Plate 2. Detailed descriptions of these taxa are in preparation elsewhere and will not be reproduced here.

Institutional abbreviations. BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; IPB, Steinmann-Institut für Geologie, Mineralogie und Paläontologie (formerly Institut für Paläntologie), University of Bonn, Germany; ISI, Geology Museum, Indian Statistical Institute, Calcutta, India; NMS, Naturmuseum Solothurn, Switzerland; PEFO, Petrified Forest National Park, Arizona, USA; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

RESULTS

General morphology and external microanatomy

Batrachotomus kupferzellensis. The general shape and morphology of the paramedian dorsal osteoderms of *Batrachotomus kupferzellensis* were thoroughly described by Gower and Schoch (2009); therefore, only a short description is given here for the specimen sampled. The specimen is an elongate paramedian osteoderm composed of a medial horizontal part and an angled lateral part, which form a thickened keel or ridge (Pl. 1, fig. 1). The external bone surface is partly sculptured with low ridges and tubercles. Gower and Schoch (2009) mentioned briefly that the internal bone surface of paramedian osteoderms lacks contours (i.e. sculpturing) and that the external surface is smoothly finished cortical bone. The external microanatomy of the plates is roughened because of a cross-hatching pattern of extrinsic mineralized fibres (Pl. 1, fig. 4; see also Gower and Schoch 2009, text-fig. 7K) that lie superficial to the main internal bone surface, similar to e.g. crocodylian, aetosaur, phytosaur, ankylosaur and sauropod osteoderms (Seidel 1979; Rossmann 2000; Scheyer and Sander 2004; Parker *et al.* 2008; D'Emic *et al.* 2009; Cerda and Powell 2010), as well as placodont armour plates (e.g. Westphal 1976; Rieppel 2002; Scheyer 2007, 2008 and references therein).

Prestosuchus chiniquensis. The specimen is heart- or drop-shaped, with a strong keel, an anterior projection and a rounded posterior margin (Pl. 1, fig. 5). Because the internal side of the osteoderm is still embedded in sediment, the strongly concave internal bone surface and the tapering in thickness towards the margins are visible only in section.

Rauisuchus tiradentes. The specimen is elongated and slightly spindle-shaped (48 mm in length) with an oval anterior projection and a small posterior excavation (Pl. 1, figs 7–8). The external bone surface is convex, the internal one flat (with the exception of the anterior projection). Both internal and external bone surfaces appear
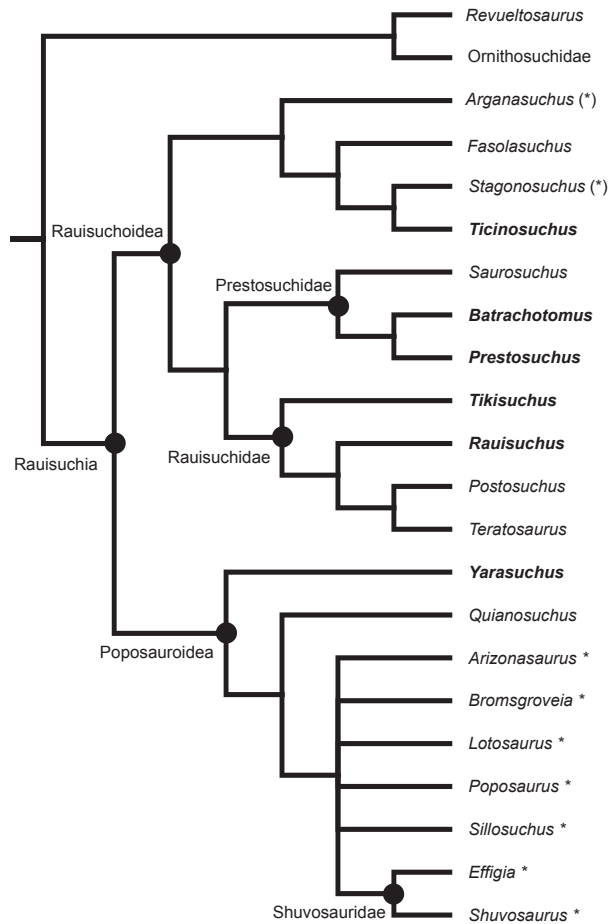

EXPLANATION OF PLATE 2

Figs 1–13. Pseudosuchian osteoderms included for comparison with rauisuchian osteoderms. In all figures, the anterior side is pointing to the top of the image. 1–4. *Revueltosaurus* (PEFO 35283) in 1, dorsal view, 2, ventral view, 3, transverse thin-section, 4, longitudinal thin-section with the anterior bar pointing towards the left. Figs 5–7. cf. *Mystriosuchus* sp. (SMNS 91013) in 5, dorsal view, 6, ventral view, 7, transverse thin-section. Figs 8–10. *Steneosaurus jugleri* (NMS 7152) in 8, dorsal view, 9, ventral view, 10, transverse thin-section. Figs 11–13. *Diplocynodon* sp. osteoderm PIMUZ A/III 0997 in 11, dorsal view, and 12, ventral view. 13, Transverse thin-section of osteoderm IPB R144/1 of cf. *Diplocynodon* sp. Note that this thin-section was described by Scheyer and Sander (2004), and it was used to calculate a compactness profile in Bone Profiler Version 3.20 (Girondot and Laurin 2003) by Scheyer and Sander (2009).

PLATE 2

1

2

10 mm

3

10 mm

4

5 mm

5

6

10 mm

7

5 mm

8

9

10 mm

10

10 mm

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10 mm

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13

5 mm
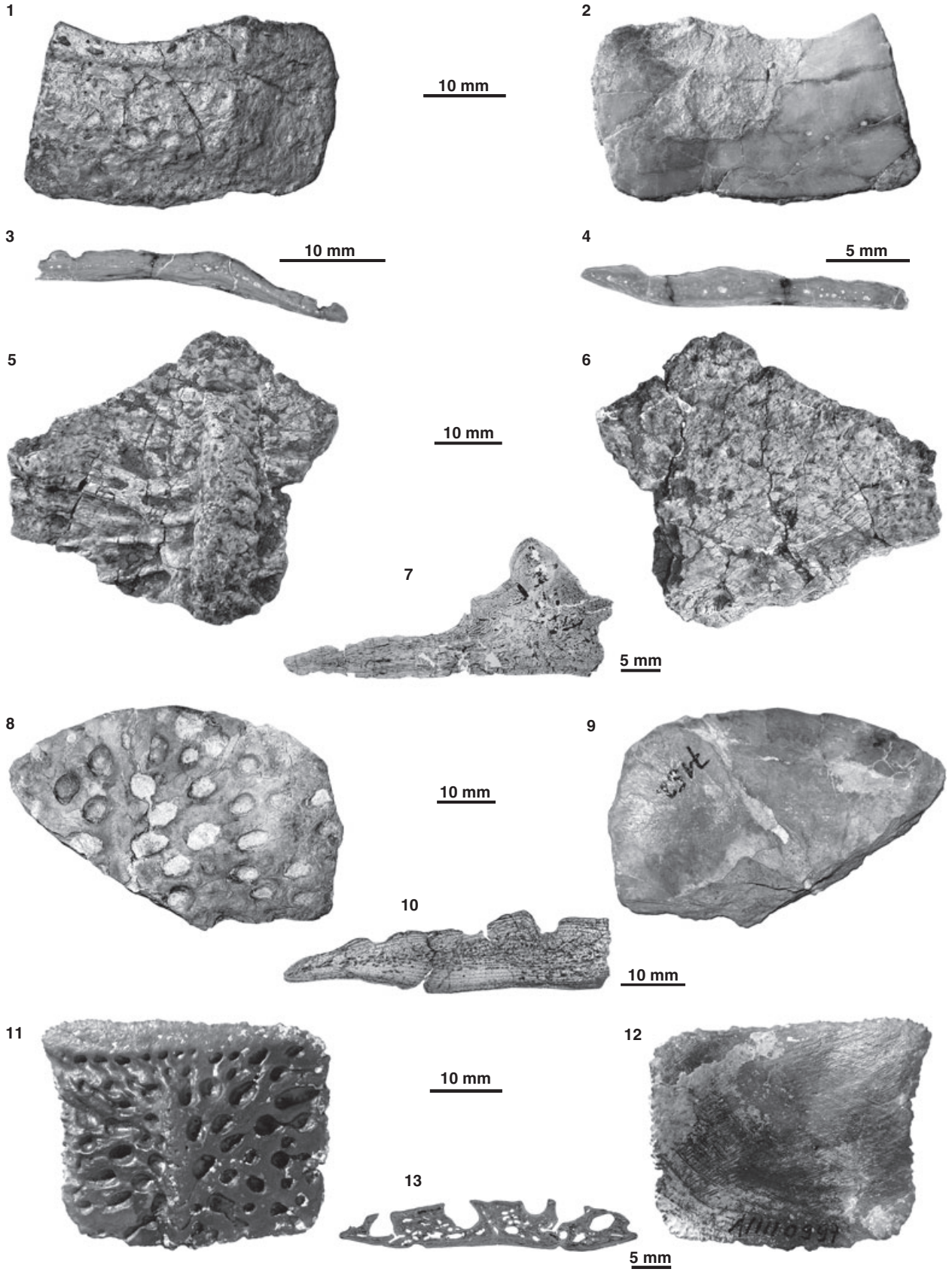
SCHEYER and DESOJO, pseudosuchian osteoderms

TEXT-FIG. 1. Phylogenetic hypothesis of rauisuchian taxa (plus *Revueltosaurus*) based on and modified from consensus tree of archosaurs (Brusatte *et al.* 2010, text-fig. 5). Taxa that were sampled in the present study are marked in bold. Taxa that lack osteoderms, a derived condition in archosaurs, are marked with an asterisk (see Nesbitt 2005, 2007; Weinbaum and Hungerbühler 2007; Brusatte *et al.* 2010). In the case of the poorly known *Arganasuchus* (Carnian, Late Triassic of Morocco, Africa) and *Stagonosuchus* (Anisian, Middle Triassic of Tanzania, Africa), the presence of osteoderms remains ambiguous at present.

to be smooth without any sculpturing. The osteoderm tapers in thickness towards the margins.

'*Prestosuchus*' *loricatus*. The specimen is roughly oval, with a rounded anterior projection (Pl. 1, figs 10–11). The osteoderm tapers in thickness from a low keel towards the margins. The internal bone surface is straight to slightly concave. Both internal and external bone surfaces are not sculptured and appear smooth.

Tikisuchus romeri. The specimen of *T. romeri* is a strongly fragmented osteoderm with a low central anteroposterior

ridge (Pl. 1, fig. 13). Comparison with other more complete osteoderms suggests that the original shape of the osteoderm was roughly rectangular with slightly concave anterior and slightly convex posterior margins, as well as a laterally positioned anterior projection. The external bone surface is sculptured with long, shallow grooves. The internal bone surface is smooth (Pl. 1, fig. 15). Only one edge is preserved, showing that the osteoderm tapers in thickness from the centre towards the margin.

Yarasuchus deccanensis. The specimen is a small fragment of a strongly ridged osteoderm (Pl. 1, fig. 17). According to Sen (2005), the ridge extends anteroposteriorly along the midline. The internal bone surface is only slightly concave and shows a faint cross-hatching pattern of mineralized fibres (Pl. 1, fig. 19). The external bone surface is sculptured with grooves, which extend from the keel towards the margins of the osteoderm. The margins and the apical region of the keel are not preserved in the sampled specimen. However, comparison with other more complete osteoderms shows that the bone was roughly leaf-shaped (*sensu* Sen 2005), with a short medially positioned anterior projection. The osteoderms do not show sutures at their margins.

Ticinosuchus ferox. A formal description of the osteoderms of *Ticinosuchus ferox* was given by Krebs (1965), so only a short description of the dorsal caudal osteoderms of the paratype PIMUZ T 2471 is given here. The paratype includes a row of nine unpaired and articulated osteoderms. The overlapping dermal bones are symmetrical with a posterior concave margin and a round anterior projection (Text-fig. 2A). Krebs (1965) noted briefly that the external bone surface shows a fine reticulation as well as a few larger scattered pits or depressions of *c*. 1 mm in diameter. These depressions are present on each of the osteoderms, but they can be situated at different locations on the keel or at the margins. At present, it remains unclear whether these pits were caused by a pre- or post-mortem microbial infection or some kind of preparatory or erosive artefact. A closer inspection of the external bone surfaces further reveals that the reticular pattern is caused by a rugose relief of vascular canal systems that open up and extend on the external bone surface of the osteoderms. The reticular pattern is not uniformly distributed over the surface but occupies a triangular patch starting centrally at the keel and extending backwards over the posterior flanks of the keels. Towards anterior, the external bone surfaces are smoother, the rugosity is less conspicuous, and the reticulation is substituted by shallow canals that radiate from the keel towards the margins. The natural breaks at the first and the ninth osteoderm further reveal a compact bone structure and growth marks in the lateral margins.
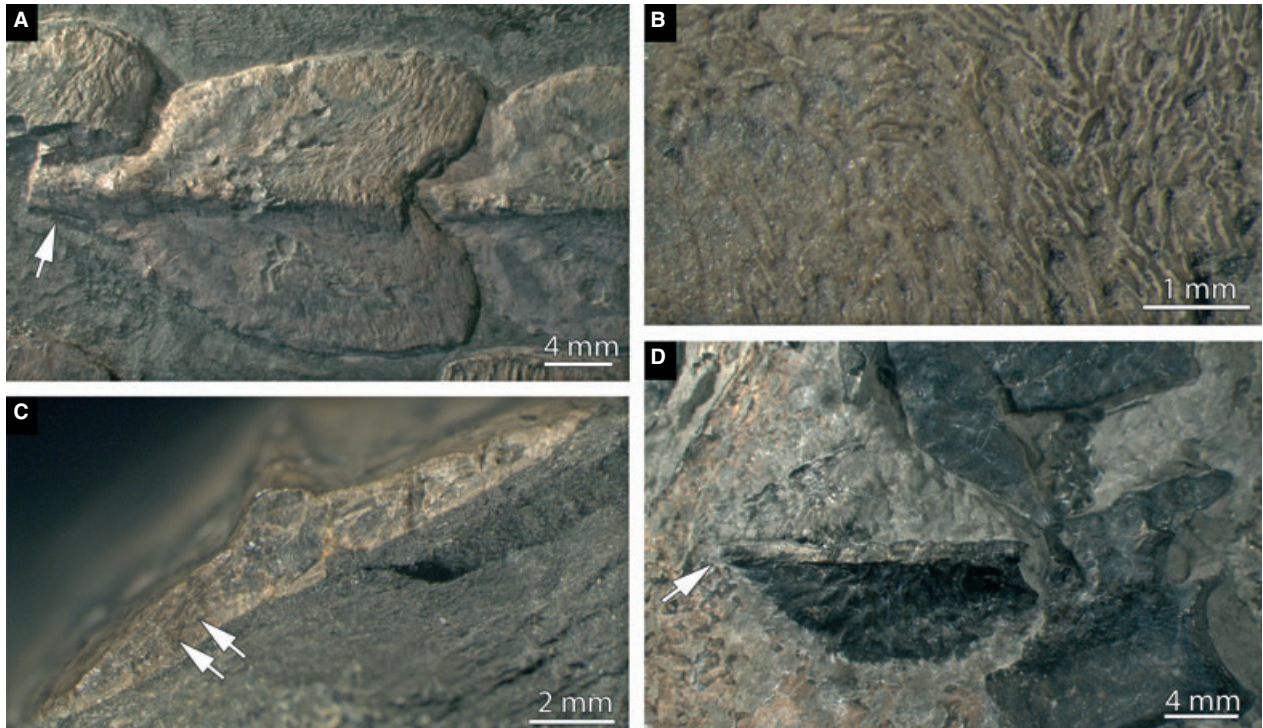
TEXT-FIG. 2. External microanatomy of the dorsal caudal osteoderms of *Ticinosuchus ferox* (A–C; PIMUZ T 2471) and a presumably juvenile rauisuchian (part of specimen PIMUZ A/III 1090) from Canton Grisons, Switzerland (D). A, articulated fourth to sixth osteoderm of paratype in dorsal view. Note rounded anterior projection of the fifth osteoderm pointing towards the left. B, close-up of the transition between the anterior smooth and the posterior rugose reticular pattern of the external bone surface of the first preserved osteoderm. C, natural transverse cut through the anterior part of the first preserved osteoderm. The cut reveals a compact interior bone core, a rather flat internal bone surface (note that specimen is also taphonomically flattened), as well as a dorsal keel. Growth marks are visible as thin dark lines in the plate margins (white arrow). D, dorsal caudal osteoderm in dorsal view. White arrow indicates the short anterior projection. Note the sculpturing pattern, which covers about the posterior two-thirds of the external bone surface and the rough margins of the osteoderm.

Possibly juvenile rauisuchian. The associated bones (PIMUZ A/III 1090), which possibly belong to a juvenile rauisuchian, include the left half and the anterior part of the right half of a dorsal caudal osteoderm. The dermal plate is spade- or drop-shaped, with a strong, high keel, a short anterior projection and a concave almost notched posterior margin (Text-fig. 2D). The apical region of the keel is slightly damaged. The posterior two-thirds of the external bone surface show a sculpturing with ridges and the osteoderm margins appear irregular. In comparison to the osteoderms of PIMUZ T 2471, this specimen seems not to be dorsoventrally flattened.

Bone histology

General notes. Rauisuchian osteoderms are generally compact bone structures, with a less vascularized cortex surrounding a more vascularized core (Pl. 1). External and internal cortices are of overall similar thickness in these taxa. There is variability, though, in the amount of vascularization of the cortex and the core area among the taxa studied. Otherwise, bone tissue types are very similar in the external and the core regions of the osteoderms, with the amount and orientation of Sharpey's fibres being the only difference observable.

Cortical bone. The cortical bone consists of parallel-fibred bone tissue (Text-fig. 3A, B). The amount of Sharpey's fibres inserting into the cortical bone is generally high, and the fibres are most conspicuous in the marginal areas of the osteoderms (Text-fig. 3C, D). Depending on the overall shape of the osteoderm, these margins are smooth to slightly undulating or show a weak suturing as in *Tikisuchus romeri*. In *Y. deccanensis* and *B. kupferzellensis*, the cross-hatched extrinsic mineralized fibres on the ventral osteoderm surface extend into the internal cortical bone layers as coarse Sharpey's fibres (Text-fig. 3A, B). Growth marks are present in the bone tissue as well. In some specimens (e.g. in *B. kupferzellensis*), the complete growth record is visible because of the low rate of remodelling (Text-figs 3C, D, 4).

TABLE 1. Taxon names, specimen numbers and information on the locality, where the rauisuchian specimens are recovered.

Taxon sampled	Specimen no.	Age and locality information
Batrachotomus kupferzellensis Gower, 1999	SMNS 80317 (paramedian dorsal osteoderm)	Late Ladinian (upper Middle Triassic), Erfurt Formation (Upper Lettenkeuper), Kupferzell, southern Germany
Prestosuchus chiniquensis von Huene, 1938	BSPG AS XXV 7 (part of paralectotype)	Santa Maria 1 Sequence (Late Ladinian/Early Carnian), late Middle – early Late Triassic, Brazil
'Prestosuchus' loricatus von Huene, 1938	BSPG AS XXV 46 d (part of lectotype)	Santa Maria 1 Sequence (Late Ladinian/Early Carnian), late Middle – early Late Triassic, Brazil
Rauisuchus tiradentes von Huene, 1938	BSPG AS XXV 121 b (part of holotype)	Santa Maria 2 Sequence (Late Carnian/Early Norian), lower Late Triassic, Brazil
Ticinosuchus ferox Krebs, 1965	PIMUZ T 2471 (dorsal caudal osteoderms of paratype; not thin-sectioned)	Anisian/Ladinian (Middle Triassic), Besano Formation, Cava Tre Fontane, Monte San Giorgio, Ticino, Switzerland
Tikisuchus romeri Chatterjee and Majumdar, 1987	ISI R 305/1 (part of holotype)	Carnian (lower Late Triassic), Tiki Formation, Gondwana Supergroup, Son-Mahanadi Valley, India
Yarasuchus deccanensis Sen, 2005	ISI R 334 (part of referred material)	Anisian (Middle Triassic), Yerrapalli Formation, Pranhita-Godavari valley, India
Possible juvenile rauisuchian specimen	PIMUZ A/III 1090 (dorsal caudal osteoderm; not sectioned)	Ladinian (Middle Triassic), Prosanto Formation, Ducanfurgga 1, Sertig, Davos, Grisons, Switzerland

In *Prestosuchus chiniquensis* and 'Prestosuchus' loricatus, the cortex is usually vascularized by a reticular network of primary vascular canals and scattered primary osteons, the latter being identifiable as longitudinally sectioned canals surrounded by a thin layer of lamellar bone (Text-fig. 3E, F).

Interior core. In *R. tiradentes*, *P. chiniquensis* and *B. kupferzellensis*, the core area of the osteoderms appears very compact with only primary osteons and scattered secondary osteons and smaller erosion cavities pervading the tissue. A diploe structure, in which external and internal compact bone layers frame interior cancellous bone, is missing in these osteoderms. The bone tissue is either woven or parallel-fibred, or a mixture of both (Text-fig. 4A–C). On the other hand, the osteoderm of *B. kupferzellensis* (SMNS 80317) is the only specimen studied in which the core is composed of a primary fibrous bone tissue, i.e., structural fibres, which could be of metaplastic origin (Text-fig. 4D–F). A primary growth centre is easily identifiable in this specimen. The coarse fibres of this tissue are of even thickness, spatially ordered with an interwoven character, and are clearly more birefringent as in typical woven bone. SMNS 80317 of *B. kupferzellensis* was also the only specimen studied, which shows a larger amount of transversely sectioned primary osteons in its core area, whereas longitudinally sectioned primary osteons and reticular primary canals are restricted mostly to the cortical bone layers.

Diploe structure. Cancellous or trabecular bone is present only in the osteoderm cores of the Indian rauisuchians, *T. romeri* and *Y. deccanensis*. The trabeculae, which are often secondarily remodelled, are composed of secondary lamellar bone. In these taxa, the marginal areas of the osteoderms in particular show a diploe organization, with compact cortical bone framing an interior cancellous centre (Text-fig. 5).

DISCUSSION

The presence of woven or fibrolamellar bone tissue, together with increased vascularization in the core regions of the rauisuchian osteoderms, is an indication of higher growth rates during earlier stages of development. These growth rates are elevated in comparison to those of extant crocodylians, as well as in phytosaurs, aetosaurs and *Revueltosaurus*, which generally show parallel-fibred or lamellar-zonal bone tissue in osteoderms and long bones (e.g. Ricqlès *et al.* 2003, 2008; Scheyer and Sander 2004; Parker *et al.* 2008). Somewhat higher rates of bone deposition have been reported in the small crocodylomorph *Terrestrisuchus* (Ricqlès *et al.* 2003), indicating that the 'typically reptilian' condition in modern crocodylians is secondarily
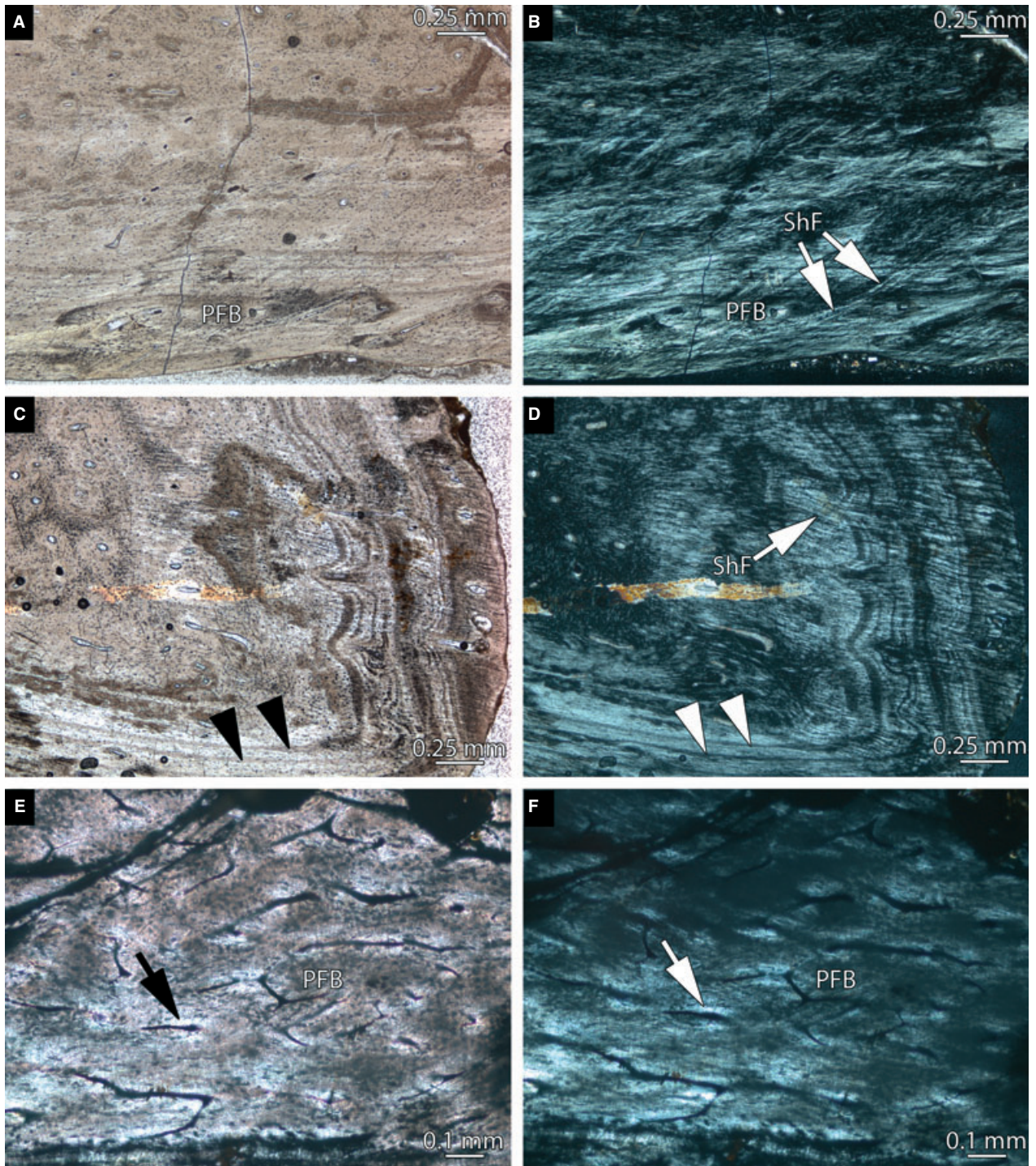
TEXT-FIG. 3. Bone histology of rauisuchian osteoderms of *Batrachotomus kupferzellensis* (A–D) and '*Prestosuchus*' *loricatus* (E, F). A, B, external compact bone in (A) normal and (B) polarized light. Note angled Sharpey's fibres (ShF) inserting into the parallel-fibred bone tissue (PFB). C, D, marginal bone tissue in (C) normal and (D) polarized light, showing growth marks (black and white arrow heads) and coarse Sharpey's fibres (ShF) inserting perpendicular into the compact bone. E, F, parallel-fibred compact bone tissue (PFB) with reticular vascularization pattern in (E) normal and (F) polarized light. Note longitudinally sectioned primary osteon marked by black and white arrows.
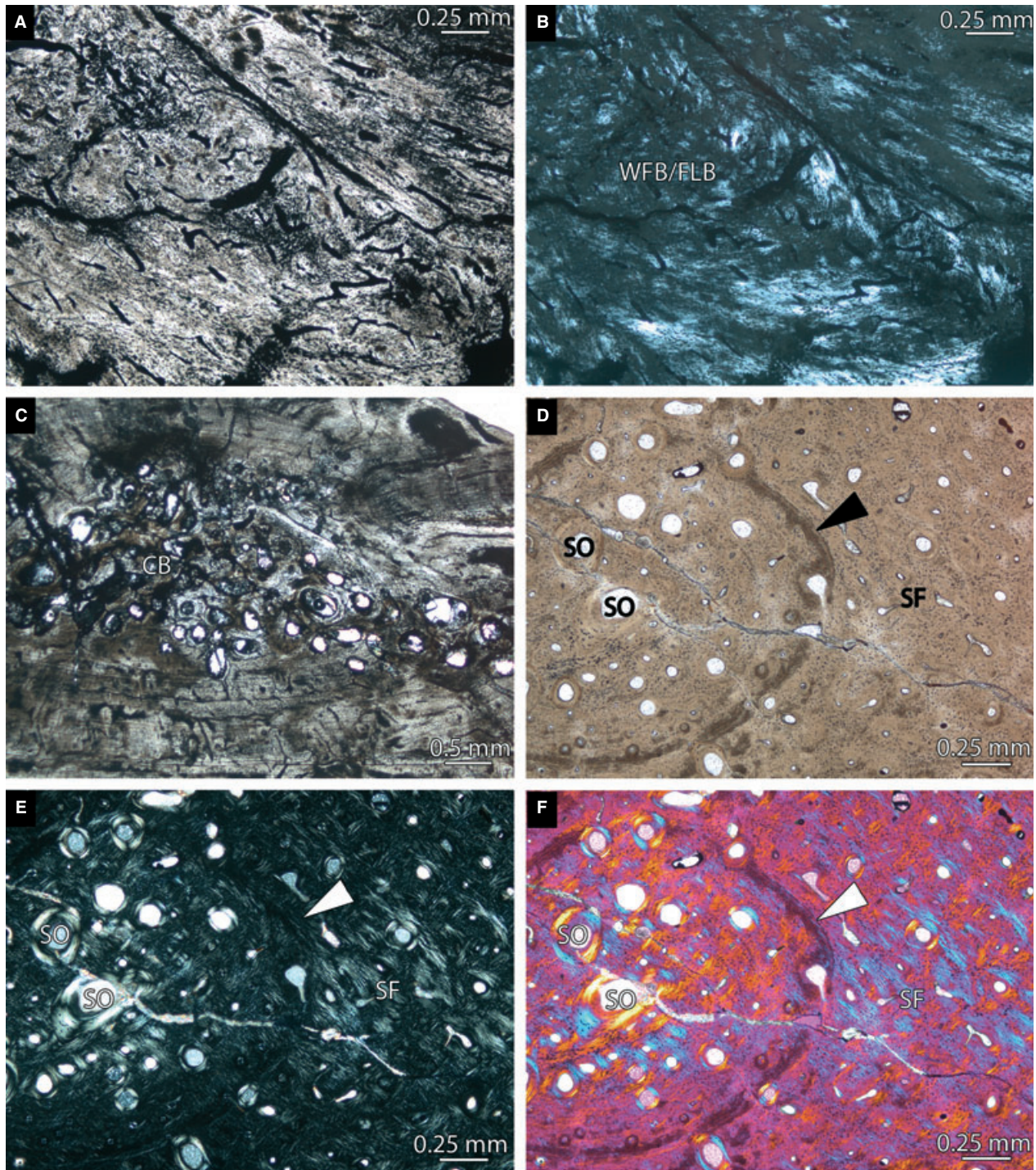
TEXT-FIG. 4. Bone histology of the interior core areas of rauisuchian osteoderms of *Prestosuchus chiniquensis* (A, B), *Rauisuchus tiradentes* (C) and *Batrachotomus kupferzellensis* (D–F). A, B, dense core of woven or fibrolamellar bone tissue (WFB∕FLB) with reticular vascularization in (A) normal and (B) polarized light. C, Small interior core of cancellous bone (CB) surrounded by compact bone layers in normal transmitted light. D–F, dense core tissue in (D) normal, (E) polarized light and (F) polarized light and lambda compensator. The primary centre of growth is marked by black and white arrow heads in (D–F). Note primary structural fibres (SF) of bone tissue purportedly of metaplastic origin. The coarse fibres are spatially ordered with an interwoven character. Scattered larger secondary osteons (SO) are present inside and outside of the core area. Unlike the bone tissue in (A) and (B), the images in (E) and (F) clearly show stronger birefringence of the structural fibre matrix.
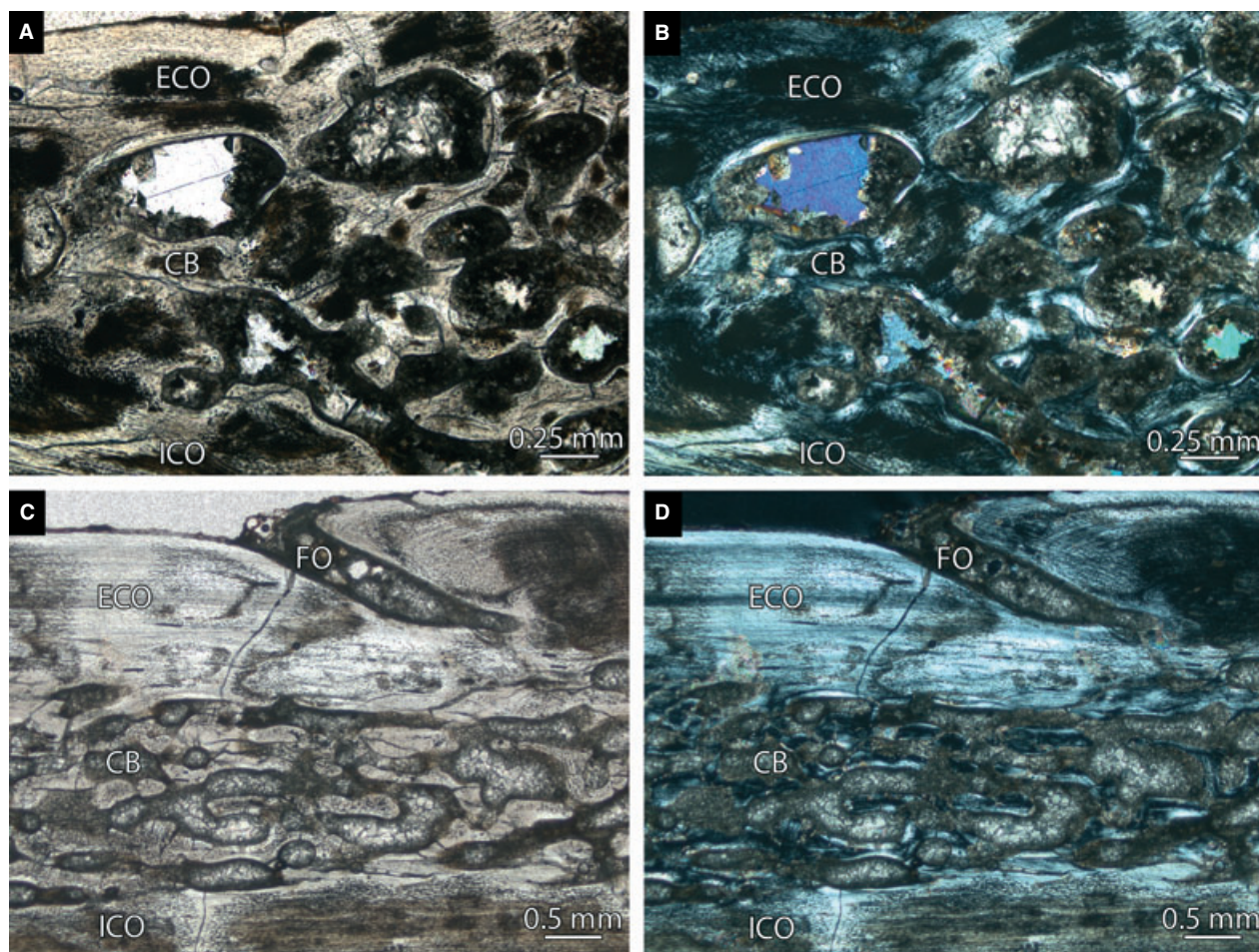
TEXT-FIG. 5. Interior cancellous bone in rauisuchian osteoderms from India. A, B, *Yarasuchus deccanensis* in (A) normal and (B) polarized light. C, D, *Tikisuchus romeri* in (C) normal and (D) polarized light. Note the diploe structure of the osteoderms with external (ECO) and internal (ICO) compact bone layers framing interior cancellous bone (CB). In (C) and (D), a foramen (FO) opening onto the external bone surface is visible.

derived. In rauisuchian osteoderms, however, vascularization never reaches laminar organization, i.e., anastomosing longitudinal and circular vascular canals (including radial canals in plexiform tissue) pervading fibrolamellar bone tissue, as is found for example in some of the very fast growing dinosaurs or birds (see review by Scheyer *et al.* 2010). The parallel-fibred matrix of the cortical bone and the presence of growth marks in the rauisuchian osteoderms, on the other hand, imply reduced growth rates in later development. Similar to crocodylian osteoderms, rauisuchian osteoderms thus appear well suited to complement long bone data for the study of skeletochronology or life history of these extinct animals. Some rauisuchian osteoderms are even better as sources of life history data and for counting growth cycles than crocodylian osteoderms (see Hutton 1986; Tucker 1997), which are generally submitted to stronger resorption and remodelling processes especially in egg-laying females (see discussion in Klein *et al.* 2009).

The ornamentation in the rauisuchian osteoderm sample is only slightly variable, ranging from unsculptured, smooth bone surfaces to ornamentations with small pits, grooves and tubercles, which develop through differential growth of the external compacta. Together with the overall shape of the osteoderms, these microanatomical differences have a taxonomic value. The differential superficial resorption processes described in the skeletal pitting ornamentation of crocodylians (e.g. de Buffrénil 1982) were not found in the rauisuchian osteoderms sampled herein, nor in aetosaur or phytosaur osteoderms (Scheyer and Sander 2004; Parker *et al.* 2008; Cerda and Desojo 2010).

Besides the taxonomic value, the changes in ornamentation, relief and vascularization pattern encountered in our osteoderm sample also have a biomechanical benefit in the sense that the smoother anterior surfaces serve as a 'hinge zone' with the overlapping osteoderms, allowing sideways bending movement of the whole osteodermal row. In this regard, the 'hinge zone' is similar to the flat-

tened, unsculptured anterior bars, or anterior external articular surface, of *Revueltosaurus* (see Parker *et al.* 2005) and other suchian osteoderms, including those of aetosaurs and crocodylomorphs (e.g. Frey 1988; Parker *et al.* 2008; Heckert *et al.* 2010). In modern crocodylians, an interosteodermal ligament inserts between the posterior internal and anterior external articular surfaces (i.e. the zone of overlap) of adjacent osteoderms, thus facilitating the bending movement of the individual osteoderm rows of the paravertebral shield (Salisbury and Frey 2001).

Ridged ornamentation and the rough margins of the osteoderm of the presumably juvenile specimen from Grisons, Switzerland, appear more similar to the osteoderms of *B. kupferzellensis* (Gower and Schoch 2009) rather than to *T. ferox* osteoderms. This could indicate that more than one species and genus of rauisuchian were present in the Middle Triassic of Switzerland. On the other hand, ontogenetic changes or sexual dimorphism are not yet understood well enough in this group to be ruled out as potential sources of variation.

The lack of larger areas of cancellous tissue and large resorption cavities in most of the rauisuchian osteoderms further indicates that the growth dynamics, i.e., the rates of bone apposition and resorption, differ from that of modern crocodylian osteoderms. The latter develop as a spongeous mass of spiculae that radiate out from a centre of origin into the surrounding dermal connective tissue and are usually subject to ongoing resorption and deposition processes, especially in relation to the external ornamentation patterns later in development (Schmidt 1914; Vickaryous and Hall 2008). Metaplastic ossification was hypothesized by Vickaryous and Hall (2008) to be the main mode of bone formation for osteoderms of *Alligator mississippiensis*. The predominant mode of osteoderm formation in rauisuchians appears to be compatible with intramembraneous ossification, although a clear diagnosis of one mode or the other remains tentative in fossils, because of the lack of soft-tissue staining (Vickaryous and Sire 2009). The presence of bone tissue of possible metaplastic origin in *B. kupferzellensis* osteoderms, however, indicates that there might be more than one mode of skeletogenesis active in this group. The plasticity of microstructures, growth dynamics and possible modes of ossification encountered in the osteoderms is overall consistent with differences in rauisuchian morphotypes, such as long necked, stout rauisuchians (Trotteyn *et al.* 2011) such as *Saurosuchus*, *Fasolasuchus*, *Prestosuchus*, *Stagonosuchus* and short necked and more gracile (slender, lightly built) animals such as *Batrachotomus*, *Ticinosuchus* and *Rauisuchus*.

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