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Osteogenesis, homology, and function of the intercostal plates in ornithischian dinosaurs (Tetrapoda, Sauropsida)

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Abstract Intercostal plates are bony structures positioned lateral to the anterior dorsal ribs in some ornithischian dinosaurs. Some propose these plates are homologous, or functionally analogous, with the uncinate processes of extant avian dinosaurs that assist in breathing, while others suggest they served a defensive function. To elucidate their osteogenesis, homology, and function, a histological survey of intercostal plates from three taxa (*Hypsilophodon*, *Talenkauen*, and *Thescelosaurus*) was undertaken. This study reveals that osteogenesis of intercostal plates closely resembles that of secondary centers of ossification in endochondral bone, typically present in the epiphyses of mammalian long bones. In contrast, ossification of avian uncinate processes begins at a primary ossification center via the development of a bony collar around a cartilaginous model. Based on these data, intercostal plates and avian uncinate processes are likely not evolutionary homologs. Dense packets of obliquely oriented Sharpey's fibers within the parallel-fibered bone of somatically mature intercostal plates indicate these plates were positioned medial to at least a portion of the hypaxial musculature, which does not support their use as bony armor. Rather, we propose that intercostal plates performed some biomechanical function, either assisting in breathing in a way analogous to avian uncinate processes, or working together with the sternal ribs and sternal plates of these ornithischian taxa to provide increased rigidity to the anterior portion of the ribcage.

Keywords Neornithischia · Histology · Uncinate processes · Aves

Introduction

Ossified or cartilaginous structures fused or otherwise attached to the posterior margin of the vertebral ribs surrounding the thoracic cavity are known from a variety of vertebrate taxa (e.g., the "uncinate processes" of avian dinosaurs, crocodylians, and *Sphenodon*). These posterodorsally oriented structures show a wide range of morphological variation in avian dinosaur taxa, but are generally anteroposteriorly longer than they are dorsoventrally tall. Alternatively, some basal neornithischian dinosaurs (sensu Boyd et al. 2009) possess dorsoventrally expanded, D-shaped plates positioned lateral to the thoracic portion of the rib cage (Fig. 1a). In specimens in which these structures are found in situ, the first plate is associated with the second rib in the dorsal series, and the anterior margin of the plate extends from the posterior margin of the distal portion of the

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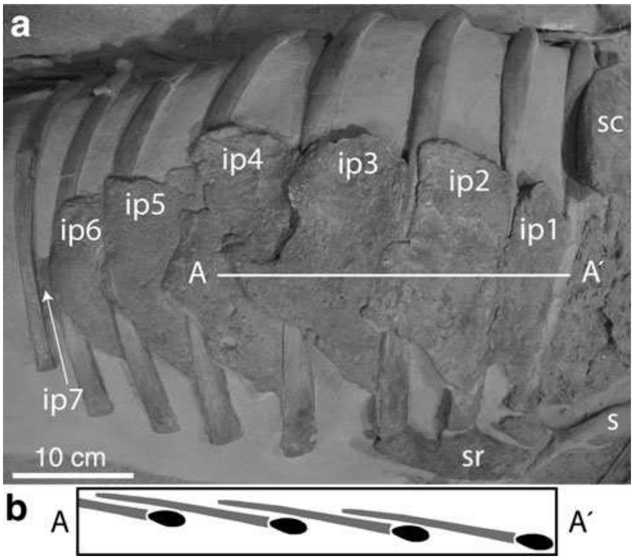


Fig. 1 **a** Right lateral view of the rib cage of NCSM 15728 (*Thescelosaurus* sp.) showing the morphology and placement of the intercostal plates on the thoracic cavity. The dorsal half of ip3 is reconstructed to match the portion of the plate that was removed for sampling. **b** Cartoon showing the position of the intercostal plates (*gray*) in relation to the dorsal ribs (*black*) in cross-sectional view along line A to A′. Abbreviations: *ip1-7* intercostal plates 1–7, *s* sternum, *sc* scapula, *sr* sternal ribs

rib shaft to overlap the external surface of the next rib in the series and the anterior portion of the adjacent intercostal plate (Fig. 1b). The presence of these intercostal plates (sensu Butler and Galton 2008) was proposed as an autapomorphy of the clade Elasmaria, which contains the Patagonian taxa *Talenkauen santacrucensis* Novas, Cambiaso, and Ambrioso, 2004 and *Macrogryphosaurus gondwanicus* Calvo, Porfiri, and Novas, 2007 (Calvo et al. 2007). However, these structures are also present in *Hypsilophodon foxii* Huxley, 1869, *Othnielosaurus consors* (Marsh, 1894), *Parksosaurus warreni* (Parks, 1926), and *Thescelosaurus* sp. (Butler and Galton 2008; Fisher et al. 2000), a relatively disparate assemblage of basal neornithischian taxa (Fig. 2).

Fragments of these plates were first recognized in association with a specimen of *H. foxii* (BMNH R2477) and were originally identified as osteoderms (Hulke 1874; Nopsca 1905). After further preparation and study of partial intercostal plates from BMNH R2477 and other specimens of *H. foxii*, this hypothesis was overturned, because of their "weak construction" (Butler and Galton 2008: p. 640), although no alternative hypothesis of function was advanced by these authors. Despite the structural variation between intercostal plates and uncinate processes, plates preserved in articulation on a specimen of *Thescelosaurus* (NCSM 15728) were referred to as "plates resembling uncinate processes" (Fisher et al. 2000: Fig. 1). Other authors suggested that these plates might be functionally analogous to the uncinate processes of avian and some maniraptoran dinosaurs (Novas et al. 2004), which act as lever arms for moving the sternum dorsally during respiration (Tickle et al. 2007; Codd et al. 2008). Before this or any other functional hypothesis for intercostal plates can be accurately assessed, the microstructure and ontogenesis of these plates need to be elucidated. We examine the histology of intercostal plates from four specimens of ornithischian dinosaur and propose a previously unsuspected developmental pathway for these structures. Additionally, we propose ontogenetic and taphonomic factors that may explain the infrequent preservation and phylogenetically disparate record of these structures on basal neornithischian specimens.

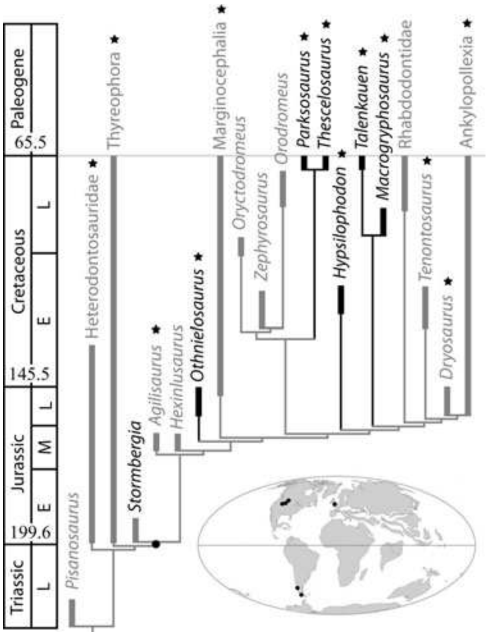


Fig. 2 Systematic and geographic relationships of basal neornithischian taxa that possess intercostal plates. The *black circle* on the tree indicates the base of the clade Neornithischia. Taxon names in *black* indicate those taxa known to possess intercostal plates. Terminal taxa marked with *black stars* include specimens found with articulated rib cages. The framework of the phylogeny is based on the comprehensive phylogeny by Butler et al. (2008). Relationships of basal neornithischians, which were largely unresolved in Butler et al. (2008), are based on the more restricted analysis by Boyd et al. (2009) focusing on these taxa. The position of *Macrogryphosaurus*, which was not included in either of these analyses, is based on the results of Calvo et al. (2007). Ages are given in mya. *Thickened lines* along the branches represent the known stratigraphic ranges of the terminal taxa. *Black dots* on the globe indicate the fossil localities where taxa possessing intercostal plates were recovered. Global reconstruction approximates the position of continents at 70 mya (after Scotese 2004). *E* early, *L* late, *M* middle

Materials and methods

Intercostal plates from the basal neornithischian taxa *Hypsilophodon foxii*, *Talenkauen santacrucensis*, and

Thescelosaurus sp., which are known from western Eurasia, Patagonia, and the Western Interior Basin of North America (Fig. 2: Weishampel et al. 2004), were sampled histologically. The original mediolateral orientation was noted for each specimen before sectioning. The original body position of the intercostal plate sample was known for only one specimen (NCSM 15728: *Thescelosaurus* sp.); all other samples were taken from disarticulated plate fragments. The intercostal plate sampled from NCSM 15728 was originally preserved in articulation in what is assumed to be original life position (Fig. 1), providing a valuable opportunity to confidently section a plate perpendicular to its long axis in an attempt to identify the presence or absence of a bony collar during osteogenesis. Ground sections were taken from each sample along a set of orthogonal planes to investigate whether the direction of sampling affected our observations. Histological samples were prepared following methods described in Green et al. (2010).

Histological criteria

Two criteria were used to differentiate calcified cartilage from ossified tissue. Calcified cartilage exhibits no extinction pattern under cross-polarized light, while bone exhibits extinction in accordance with original orientation of collagen fibers (Weiner et al. 1999; Francillon-Vieillot et al. 1990). Second, the chondrocyte lacunae observed in calcified cartilage are subspherical and bulbous, while prolate osteocyte lacunae interconnect via narrow canaliculi that radiate in three dimensions from the lacunae into the surrounding extracellular matrix (Francillon-Vieillot et al. 1990).

Institutional abbreviations

In order to trace back the original fossil material, the accession number is given in brackets in addition to the species name. The institutional abbreviations used are, BMNH: British Museum of Natural History, London, UK; BYU ESM: Brigham Young University, Earth Science Museum Collection, Provo, Utah, USA; MOR: Museum of the Rockies, Bozeman, Montana; MPM: Museo Padre Molina, Rio Gallegos, AR; NCSM: North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; NMNH: Smithsonian Institute National Museum of Natural History, Washington, D.C., USA; and UW: University of Wyoming, Laramie, Wyoming, USA.

Results

MOR 979 (*Thescelosaurus* sp.)

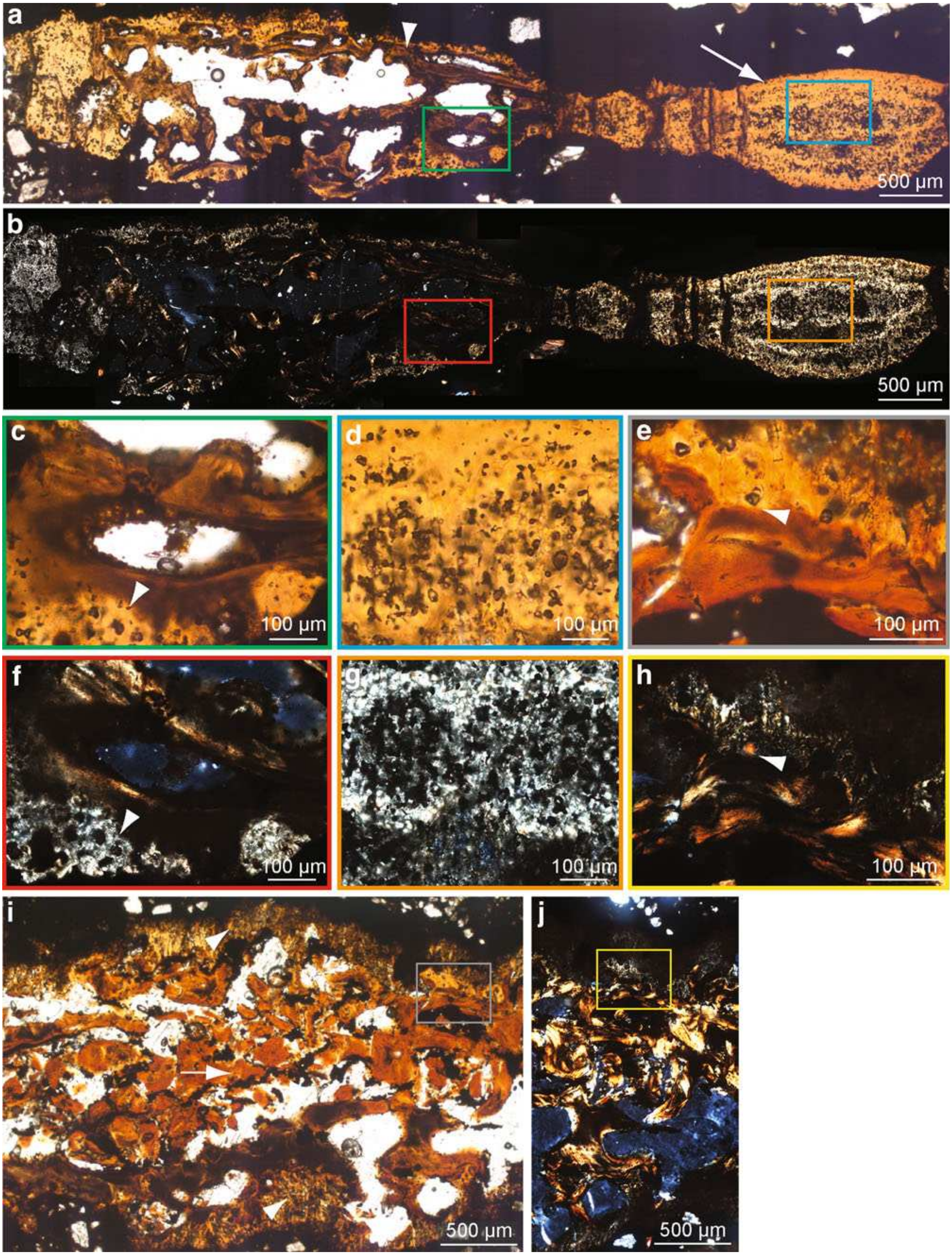
The morphology of the intercostal plate sampled from this specimen varies throughout the section (Fig. 3a, b). Calcified cartilage, identified by dense concentrations of chondrocyte lacunae, dominates large portions of the plate (Fig. 3a *arrow*, d, g). The plate is mediolaterally thin in this region, but in some areas, the plate is thickened and the center of the cartilaginous region is eroded, creating open cavities (Fig. 3a *arrowhead*). Thin layers of lamellar bone may be deposited along the periphery of the cavities (Fig. 3c, f), but in some places, there are small erosional cavities in the calcified cartilage where bone deposition has not yet occurred. Within these bony deposits, osteocyte lacunae are sparsely distributed relative to the dense concentration of chondrocyte lacunae present in surrounding calcified cartilage. In the thickest regions of the plate, erosional cavities are more extensive, and calcified cartilage is restricted to the medial and lateral margins of the plate, reinforced by a network of bony struts in the center of the plate (Fig. 3a, b).

NCSM 15728 (*Thescelosaurus* sp.)

Unlike in MOR 979 (*Thescelosaurus* sp.), bone is more abundant than calcified cartilage in this plate (Fig. 3i, j). Within regions of calcified cartilage, bone formation is more extensive relative to MOR 979 (*Thescelosaurus* sp.), possibly reflecting greater somatic maturity. Calcified cartilage is present along all external surfaces, entirely enclosing the bone (Fig. 3e, h). The cartilaginous regions vary in thickness, and occasional osteocyte lacunae are observed in the bony struts.

BMNH R2477 (*Hypsilophodon foxii*)

Portions of two overlapping plates were sampled and are referred to as plate A (Fig. 4a, b) and plate B (Fig. 4e, f). Plate A is positioned lateral to plate B, and the microstructure of plate A is intermediate between MOR 979 (*Thescelosaurus* sp.) and NCSM 15728 (*Thescelosaurus* sp.) in terms of bone formation and presence of calcified cartilage. Calcified cartilage is present along the exterior and interior margins of the plate, but is also sparsely distributed within the central portions of the plate. The erosional cavities are lined with newly deposited bone (Fig. 4c, d), but bone is not as extensively distributed as in NCSM 15728 (*Thescelosaurus* sp.). Plate B is composed of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◀ **Fig. 3** Histological sections of intercostal plates shown in plain polarized light and cross-polarized light from both *Thescelosaurus* sp. specimens. In all frames, the lateral (*exterior*) plate face is at the top, and the medial (*interior*) face is toward the bottom. *Colored boxes* on **a**, **b**, **i**, and **j** indicate the position of the corresponding magnified views shown in **c**–**h**. **a** Low-magnification view of the intercostal plate sampled from MOR 979 showing regions composed entirely of calcified cartilage (*arrow*) in plain polarized light. Other areas have ossified tissue formed around open internal cavities (*arrowhead*). **b** Cross-polarized light image of the same plate shown in **a**. **c** Higher magnification of **a** showing bone contacting calcified cartilage (*arrowhead*) adjacent to a simple vascular canal in plain polarized light. **d** Higher magnification of **a** showing calcified cartilage in plain polarized light. **e** Higher magnification of **i** showing the junction of bone and calcified cartilage (*arrowhead*) in plain polarized light. **f** Cross-polarized light image of **c** corresponding to **b**. Note the difference in extinction pattern between the bone and calcified cartilage. **g** Cross-polarized light image of **d** corresponding to **b**. **h** Cross-polarized light image of **e** corresponding to **j**. **i** Low-magnification view of the intercostal plate from NCSM 15728 in plain polarized light showing abundant bone (*arrow*) surrounded by calcified cartilage (*arrowheads*). **j** Cross-polarized light image of the plate in **i**

bony struts surrounding open cavities, with calcified cartilage lacking entirely (Fig. 4e, f). The external surfaces of the plate exhibit scalloped periosteal surfaces, but it is uncertain if this texture is natural or the result of some taphonomic process. Unlike in MOR 979 (*Thescelosaurus* sp.), NCSM 15728 (*Thescelosaurus* sp.), and plate A from BMNH R2477 (*Hypsilophodon foxii*), a few simple vascular canals are present (Fig. 4e, f: arrowhead).

MPM 10001 (*Talenkauen santacrucensis*)

The intercostal plate sampled from MPM 10001 (Fig. 4g, h) shows the most extensive ossification of all specimens examined. Calcified cartilage is absent. Although damaged by invasive plant roots, the central portion of the plate is composed of cancellous bone. The exterior and interior margins are composed of parallel-fibered, compact bone (Fig. 4i). Dense packets of obliquely oriented Sharpey's fibers are present along the lateral margin (Fig. 4j), but are less concentrated along the medial margin. A few primary (Fig. 4k, l) osteons are present within the compact bone, but most of the vascularization occurs as simple vascular canals.

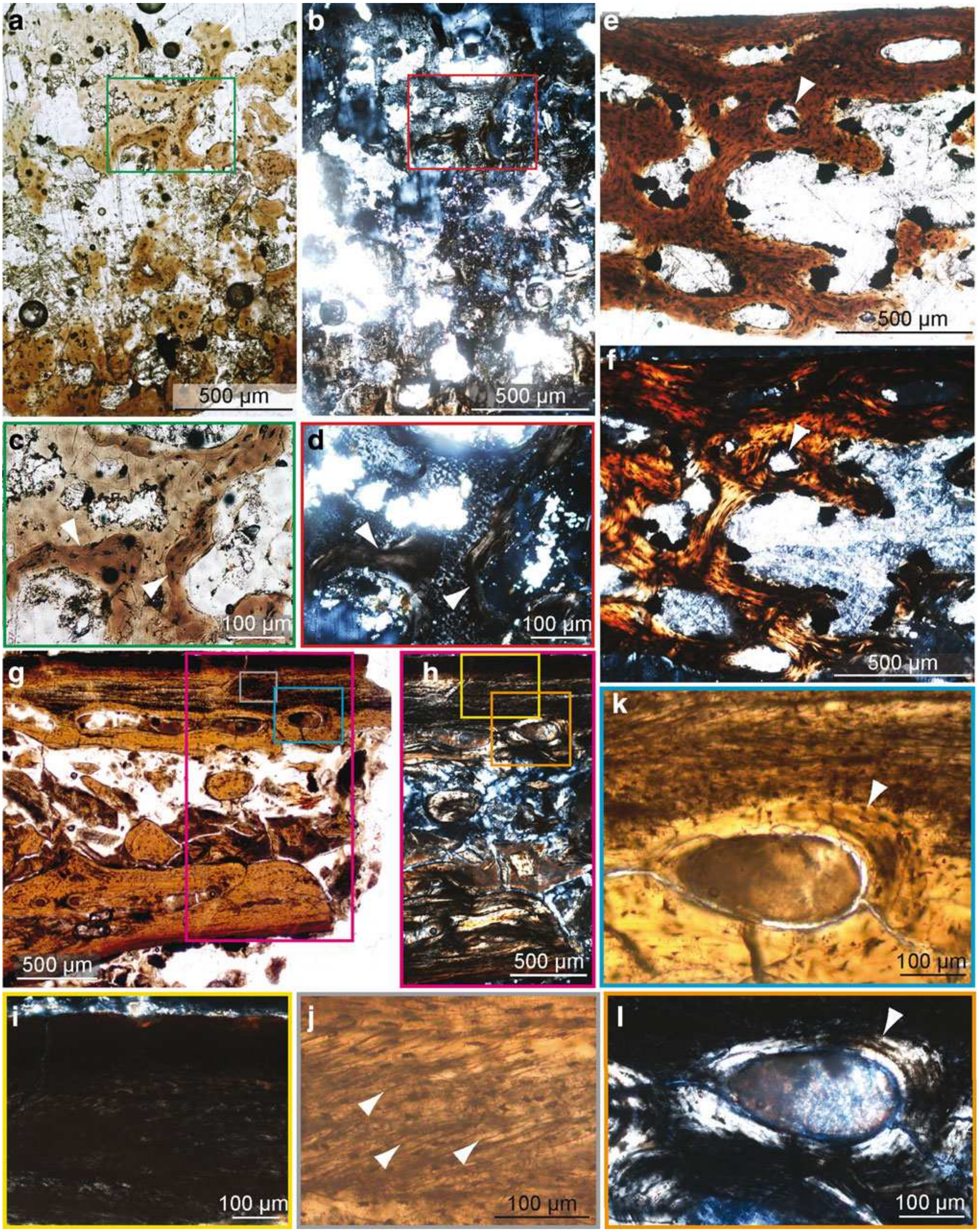
Discussion

Observed patterns of osteogenesis

Primary bone formation is typically divided into two broad categories: intramembraneous and endochondral; however, bone can be formed by other processes (e.g., metaplasia: Haines and Mohuiddin 1968). Intramembraneous bone is produced by direct transformation of mesenchymal cells to osteoblasts (Opperman 2000), which then secrete osteoid (organic phase) that is subsequently mineralized. Alternatively, endochondral bone is formed via the replacement of a cartilaginous precursor (Scott and Hightower 1991), where ossification expands outward from either primary or secondary ossification centers. Primary centers of ossification typically occur when the diaphysis of a cartilaginous precursor, or model, is surrounded by an intramembranous bony collar and later replaced by osseous tissue (Floyd et al. 1987; Francillon-Vieillot et al. 1990). Ossification continues from the diaphysis toward the epiphyses allowing for elongation of the bone (Francillon-Vieillot et al. 1990). At secondary centers of ossification, osteogenesis begins via innervation of blood vessels along cartilage canals within the cartilaginous model, leading to bone formation along the vasculature after calcification (Burkus et al. 1993). This type of endochondral bone formation most commonly occurs within the epiphyses of long bones in mammalians (Floyd et al. 1987).

Ossification within the endochondral uncinate processes of avian dinosaurs initiates with a bony intramembranous collar formed along the central part of the uncinate process, and bone is subsequently deposited similar to primary centers of ossification in long bones (Tickle and Codd 2009). No evidence of a bony collar is noted in any of the ornithischian specimens sampled, despite sectioning in multiple directions. Instead, ossification of intercostal plates examined in this study appears to begin in erosional cavities that open along cartilage canals, allowing vasculature to invade the interior of the plate. Initial bone deposition in the plates occurs at these central erosional cavities (Fig. 3a, b), gradually replacing the cartilage internally and then spreading to the periphery until the entire plate is ossified. Periosteal ossification then commences along the external surfaces, depositing layers of parallel-fibered bone (Fig. 4g, h, i). Thus, intercostal plates undergo endochondral ossification similar to secondary ossification centers, with no evidence of a bony collar indicative of primary ossification centers. As a result, basal neornithischian intercostal plates and avian uncinate processes are likely not evolutionary homologs owing to their developmental differences. However, the cartilaginous precursors for the uncinate processes and intercostal plates of tetrapod taxa may have a deeper homology (e.g., arose in a taxon positioned basal to the split between Dinosauria, Crocodylia, and *Sphenodon*) that remains unexplored, a topic that is beyond the scope of the current study to address.

The timing of osteogenesis of extant avian uncinate processes varies, with each uncinate process within an individual attaining somatic maturity at different times (Tickle and Codd 2009). Likewise, the two overlapping plates sampled from BMNH R2477 (*Hypsilophodon foxii*) show differing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◀ **Fig. 4** Histological sections of intercostal plates shown in plain polarized light and cross-polarized light from BMNH R2477 (*Hypsilophodon foxii*) and MPM 10001 (*Talenkauen santacrucensis*). In all frames, the lateral (*exterior*) plate face is at the top, and the medial (*interior*) is toward the bottom. *Colored boxes* on **a**, **b**, **g**, and **h** indicate the position of the corresponding higher magnification views shown in **c**–**d** and **i**–**l**. **a** Low-magnification view of intercostal plate A sampled from BMNH R2477 showing calcified cartilage and ossified tissue present in this plate in plain polarized light. **b** Low-magnification view of the plate in **a** under cross-polarized light. **c** Higher magnification of **a** showing bone contacting calcified cartilage (*arrowhead*) in plain polarized light. **d** Cross-polarized light view of **c** with contacts between bone and calcified cartilage labeled with *arrowheads*. **e** Low-magnification view of intercostal plate B sampled from BMNH R2477 showing the entire plate composed of bone with a few simple vascular canals present (*arrowhead*) in plain polarized light. **f** Cross-polarized light view of plate B, with simple vascular canal highlighted (*arrowhead*). Note that no calcified cartilage is visible, and bone extends to both periosteal surfaces. **g** Low-magnification view of the intercostal plate from MPM 10001 in plain polarized light. **h** Low-magnification view of the plate from MPM 10001 in cross-polarized light showing bone throughout. **i** Cross-polarized light image of **h** showing the full extinction of the parallel-fibered bone near the lateral margin of the plate. **j** Higher magnification view of **g** showing oblique Sharpey's fibers (*arrowheads*) along the lateral margin of this plate. **k** Higher magnification view of **g** showing an obliquely sectioned primary osteon from MPM 10001; however, most vasculature in this plate is non-osteonal. **l** Cross-polarized light image of **k** showing lamellar bone surrounding the vascular canal

stages of somatic maturity (Fig. 4a, e), suggesting similar timing offsets. Alternatively, these small fragments may be from different regions of the same plate and may occupy different positions along the advancing ossification front. However, our observations of the morphology across the entire length of the plate from NCSM 15728 (*Thescelosaurus* sp.) do not support the presence of this much variation within a single plate during osteogenesis. More thorough sampling of multiple plates from a single specimen is required to fully resolve this issue.

Factors influencing recovery of intercostal plates

It has been suggested that the observed distribution pattern of intercostal plates may be caused by ontogeny, based on a smaller articulated specimen of *Othnielosaurus consors* (BYU ESM-163R) lacking intercostal plates while a larger specimen (UW 24823) possesses them (Butler and Galton 2008). We note a similar pattern in *Thescelosaurus*. Smaller, articulated specimens of *Thescelosaurus* do not preserve intercostal plates (e.g., NMNH 7757), while larger, articulated specimens display intercostal plates that are in early stages of osteogenesis (i.e., MOR 979, NCSM 15728), lending support to this ontogenetic hypothesis. To fully understand the effect ontogeny may be having on our understanding of the distribution of these plates, additional work is needed to compare the somatic maturity of intercostal plates with the ontogenetic maturity of the specimen. This would provide a clearer understanding of the timing of ossification of intercostal plates during overall ontogeny and whether it is consistent across taxa, which may allow for more complete hypotheses of onset of intercostal plate formation, and their relationship to the maturity of each individual. The observed distribution pattern of intercostal plates among basal neornithischians closely matches the observed distribution of specimens preserving articulated rib cages (Fig. 2; starred taxa). Every taxon positioned above *Othnielosaurus* and below *Talenkauen* on the phylogeny in Fig. 2 for which specimens with articulated rib cages are known possess intercostal plates, excepting those taxa within the clade Marginocephalia. Based on these data, the lack of intercostal plates in some specimens may be because of a combination of ontogenetic and taphonomic factors, rather than non-occurrence, making it difficult to confidently trace the distribution of these structures within Ornithischia.

Hypotheses regarding function

One early hypothesis regarding the function of intercostal plates was that they served an active defensive function (i.e., bony armor: Hulke 1874). This hypothesis was challenged recently, when Butler and Galton (2008) argued that intercostal plates were too thin to function effectively in defense. We support this conclusion based upon the following additional evidence. Ornithischian dermal armor forms via metaplasia, which is the direct ossification of mature connective tissue into bone (Scheyer and Sander 2004; Main et al. 2005), and bones of dermal origin in general ossify via the intramembranous bone formation pathway (though see Scheyer 2007). Thus, the hypothesis that these structures are modified osteoderms (i.e., bony armor) is not supported by the endochondral bone formation pathway observed in these ontogenetically diverse samples. Additionally, the presence of Sharpey's fibers on both the lateral (Fig. 3i) and, to a lesser degree, medial margins indicates the insertion of tendons along their surfaces. These Sharpey's fibers suggest that: (1) the intercostal plates were not passively embedded in the surrounding tissue as is dermal bone (Main et al. 2005) and (2) intercostal plates were positioned medial to a portion of the hypaxial musculature. These data argue strongly against these structures serving as bony armor.

Alternatively, these structures have been suggested to be functionally analogous to the uncinate processes of avian dinosaurs (Novas et al. 2004; Calvo et al. 2007) and thus functioned as respiratory accessories. This hypothesis is partially supported by the presence of Sharpey's fibers along both the lateral and medial margins of the intercostal plates. Unfortunately, making muscular reconstructions strictly based on the presence of Sharpey's fibers is not possible (Hieronymus 2006), and the only plate sampled from original body position was incompletely ossified, making it difficult to determine exactly how/if it was attached to the adjacent ribs and or plates. As a result, this hypothesis cannot be fully evaluated until: (1) the presence and distribution of Sharpey's fibers within avian uncinate processes are better understood and (2) the nature of the connection, if present, between these plates and the adjacent ribs is determined.

A third hypothesis is suggested by these data. Intercostal plates, which are more broadly overlapping and cover a much wider area of the body than avian uncinate processes, may have worked in conjunction with the ossified sternal plates and sternal ribs to stiffen the thoracic cavity. Indeed, intercostal plates show a similar pattern of distribution to ossified sternal ribs among basal neornithischian taxa (Butler and Galton 2008), but without an extant analog, it is difficult to completely test this hypothesis.

Conclusions

This study provides unique insight into dinosaurian accessory structures associated with the dorsal ribs. The pattern of osteogenesis observed in this study for ornithischian intercostal plates is unlike that of avian uncinate processes (though the osteogenic pathway of the uncinate processes of non-avian, theropod dinosaurs remains uncertain). This difference, along with the extreme morphological differences noted between intercostal plates and avian dinosaur uncinate processes, implies that these structures are not evolutionary homologs. Although the exact function of ornithischian intercostal plates remains unclear, sufficient data are available to dismiss a defensive function for these structures. The hypothesis that ornithischian intercostal plates were functionally analogous to the uncinate processes of avian dinosaurs cannot be definitively confirmed or refuted at this time based on the available evidence. Additional research is needed to improve our understanding of the histology of somatically mature uncinate processes (e.g., to determine the presence and distribution of Sharpey's fibers) from a diverse array of avian dinosaurs, non-avian, theropod dinosaurs, crocodylians (which retain either cartilaginous or ossified "uncinate processes": Hofstetter and Gasc 1969), and similar structures in *Sphenodon* to help resolve this question. Further information is also needed regarding the nature of the connection between intercostal plates and their associated ribs, if present. Unfortunately, this information can only be obtained from well-preserved specimens that preserve mature intercostal plates in original body position, and no currently known specimen satisfies these requirements.

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