

Morphology, histology and identification of the ‘granicones’ from the Purbeck Limestone Formation (Lower Cretaceous: Berriasian) of Dorset, southern England



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The identification of the ‘granicones’, small, conical and shield-like phosphatic structures with a pustulate surface ornamentation, from the Purbeck Limestone Formation of Dorset, has been problematic for over 130 years. They have been interpreted as the osteoderms of theropod or ornithischian dinosaurs, lizards or crocodiles, though only circumstantial evidence was presented in support of these hypotheses. Here, we provide anatomical, histological and geological evidence that demonstrates the true affinities of the granicones: they are the limb osteoderms of turtles and may be referable to either *Helochelydra* (= *Tretosternon*) *anglica* or ‘*Tretosternon*’ *bakewelli*.

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1. Introduction

The Purbeck Limestone Formation in Dorset consists of interbedded clays, limestones and shales that represent a succession of depositional environments: intertidal marginal marine, intertidal brackish, and freshwater with rare episodes of fully emergent, terrestrial sedimentation (Clements, 1993; Allen, 1998). This unit has yielded the remains of a diverse vertebrate fauna including fish, amphibians, lizards, turtles, crocodylians, pterosaurs, dinosaurs and mammals (e.g., Ensom *et al.*, 1991, 1994; Clarke, 1993; Benton & Spencer, 1995; Howse & Milner, 1995; Wright *et al.*, 1998). Invertebrate and plant remains are also common (see Allen, 1998 for a brief review). Most authors accept an earliest Cretaceous (Berriasian) age for this deposit on the basis of biostratigraphical correlations (Allen & Wimbledon, 1991; Feist *et al.*, 1995). The high taxonomic diversity of the Purbeck fauna and flora, and the limited spatial and temporal

distribution of the Purbeck depositional regime, provides an important window on an earliest Cretaceous terrestrial/marginal marine biome.

This paper considers the ‘granicones’: small, conical phosphatic objects obtained from the Cherty Freshwater Member of the Purbeck Limestone Formation (Owen, 1878a, 1879; Figure 1). The discovery of granicones in blocks of sediment containing isolated teeth of the Purbeck reptile *Nuthetes* led Owen to suggest that they represented dermal bones of this taxon (Owen, 1878a, 1879). Comparison of granicone histology with that of fish, lizard and crocodile dermal bone indicated that granicone microstructure was most similar to that of lizards (Owen, 1878a). Owen also noted that the gross morphology of the granicones was comparable to that of epidermally derived ossicles from the extant lizard *Moloch*: as *Nuthetes* was originally thought to be a lizard (Owen, 1854, 1861), these observations appeared to provide support for this referral. However, the inclusion of the granicones (and other *Nuthetes* material) in a monograph on the Purbeck crocodylians (Owen, 1879)

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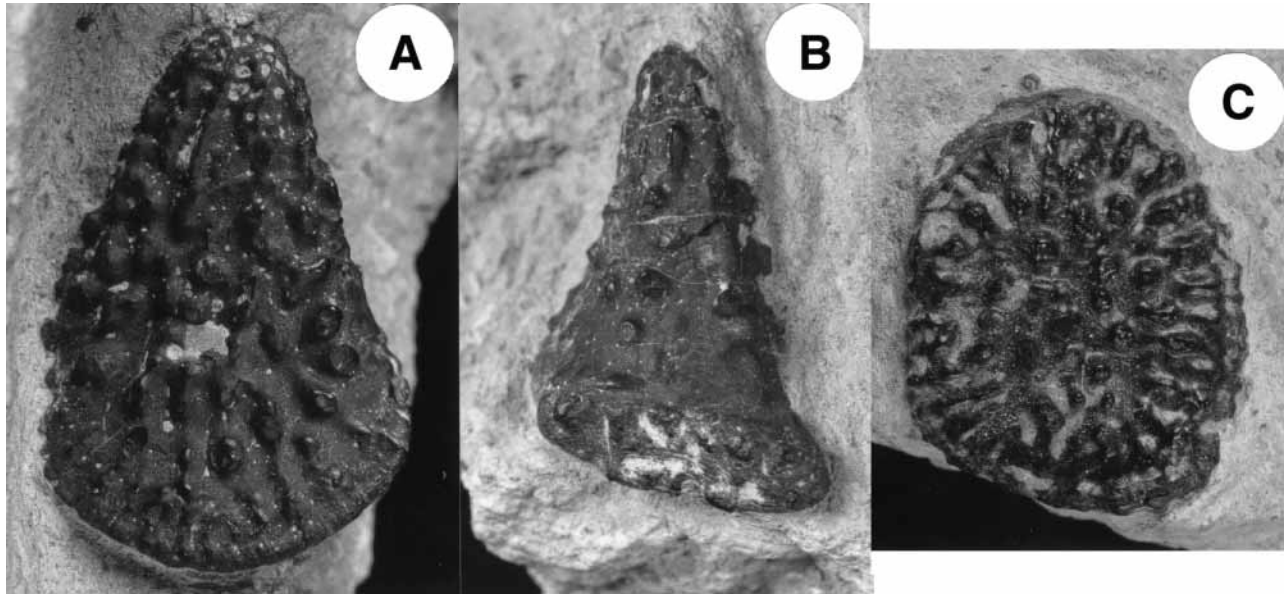


Figure 1. ‘Granicones’ from the Purbeck Limestone Formation (Berriasian), Durlston Bay, Dorset, England. A, conical granicone (BMNH R16310 in part); $\times 5$. B, conical granicone (BMNH R16310 in part); $\times 6$. C, a ‘shield-like’ granicone (BMNH R16312); $\times 5$. Note the strongly pustulate surface texture.

implies that Owen may have regarded *Nuthetes* as a crocodylian at this time, in spite of the emphasis that he placed on the histological similarities between the granicones and lizard dermal elements. Nevertheless, Owen (1879) did not explicitly refer *Nuthetes* to either the Crocodylia, the ‘Lacertilia’ (lizards) or to any other group. This ambiguity might reflect doubts on Owen’s part regarding the systematic affinities of this material; the text of the paper, and the context in which it is set, provide some support for either assignment. Owen (1878a) also mentioned the resemblance between the granicones and the osteoderms of the thyreophoran dinosaurs *Hylaeosaurus* and *Scelidosaurus*: the small size of the granicones, however, was thought to preclude them from referral to either of these taxa.

Lydekker (1888) referred *Nuthetes* (including the granicones) to the Dinosauria, but did not assign it to any named order. Swinton (1934) suggested that *Nuthetes* was a theropod dinosaur, though he did not provide any characters to support this hypothesis and did not mention the systematic status of the granicones. Further work has since confirmed Swinton’s (1934) referral: detailed examination of tooth morphology has demonstrated that *Nuthetes* is a dromaeosaurid theropod dinosaur (Delair, 1959; Molnar *et al.*, 1992; A. C. Milner, *in press*). Recent authors either contest the referral of the granicones to *Nuthetes* (Delair, 1959; A. C. Milner, *in press*), or do not address this issue (Molnar *et al.*, 1992). Delair (1959) suggested that the granicones might have pertained

to an ornithischian dinosaur, as they resembled the dermal ossicles of stegosaurs. Galton (1981, 1985, 1986) referred the granicones to the Purbeck ornithischian *Echinodon* on the basis of supposed similarities between *Echinodon* and the primitive armoured dinosaur *Scutellosaurus* (see Norman & Barrett, *in press*, for a historical account of *Echinodon* systematics).

Although previous authors have assumed that the granicones are osteoderms of dinosaurian origin (Lydekker, 1888; Delair, 1959; Galton, 1981, 1985, 1986), none has provided convincing arguments to support this thesis. In this paper we re-examine granicone morphology and histology in an attempt to deduce their biological origins and affinities.

Institutional abbreviations. BMNH, The Natural History Museum, London, UK; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; DORCM, Dorset County Museum, Dorchester, Dorset, UK; FMNH, Field Museum of Natural History, Chicago, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMZ, University Museum of Zoology, University of Cambridge, Cambridge, UK; UOP, School of Earth and Environmental Sciences, University of Portsmouth, UK.

2. Material and methods

2.1. Material

The ‘granicones’ described by Richard Owen were collected by S. H. Beckles from the ‘Middle Purbeck

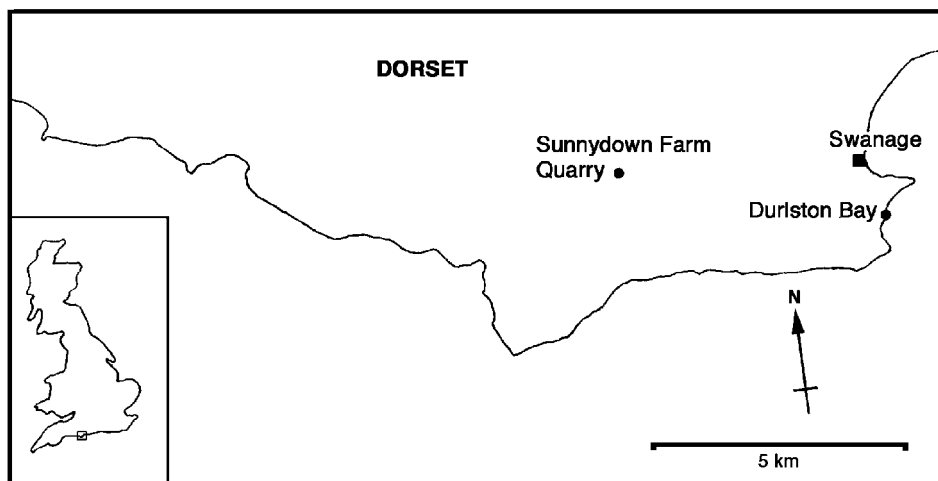


Figure 2. Map of the Dorset coast showing the localities from which granicones have been collected.

Beds' of Durlston Bay, near Swanage, Dorset, south-west England (Owen, 1878a, 1879; National Grid Reference SZ 035780; Figure 2). Contemporary reports state that they were recovered from a stratum known to local quarrymen as the 'Feather Bed' (cf. Owen, 1878a, 1879), which is currently considered to lie within the Cherty Freshwater Member of the Purbeck Limestone Formation (Clements, 1993).

Until recently, most of the granicones from Durlston Bay were accessioned under a single specimen number in the collections of The Natural History Museum, London (BMNH 48247). This specimen number included the five 'original' granicones figured by Owen (1878a, 1879) and many others that were obtained by several collectors at different times. To facilitate identification of the various granicones, the specimen number BMNH 48247 has now been restricted to the five granicones figured by Owen (1878a, 1879): four of the latter have been identified (Owen, 1879, pl. 2, figs 18–21), but one (Owen, 1879, pl. 2, fig. 17) cannot be located at present. The other granicones later accessioned under this specimen number have been re-accessioned: the histological sections were taken from a granicone now catalogued as BMNH R16311; the remaining granicones are catalogued as BMNH R16310 and BMNH R16418–47; and a large block of matrix containing granicones and indeterminate reptilian phalanges has been transferred to BMNH 16448. Three granicones from the same block of matrix as a partial jaw referred to *Nuthetes* (BMNH 48207) have been re-accessioned (as BMNH R16312 and BMNH R16416–7) in order to avoid confusion. All of these specimens pertain to the Cherty Freshwater Member of the Purbeck Limestone Formation.

A second locality, Sunnydown Farm, near Langton Matravers, Dorset (Ensom, 1988; Ensom *et al.*, 1991, 1994; National Grid Reference SY 98227880; Figure 2), has also yielded granicones. Isolated examples (DORCM uncatalogued) have been extracted from bulk samples of a well-laminated, calcareous, carbonaceous shale (West, 1988) taken from the Cherty Freshwater Member (equivalent to the interface between beds DB 102 and 103; cf. Clements, 1993). The same locality also yielded a bulk sample containing approximately 60 granicones in association with numerous shell and limb elements (probably representing a single individual) referable to a solemydid turtle (DORCM GS.1488; see below).

In several cases, granicones are present on the same blocks of matrix as disarticulated vertebrate specimens (either isolated elements or associated elements from a single individual) from the 'Middle Purbeck Beds' of Durlston Bay. Taxa associated with the granicones include: a turtle (BMNH 48349: a referred specimen of *Tretosternon bakewelli*) and crocodiles (*Theriosuchus*: BMNH 48270; and indeterminate crocodylians: BMNH 48239, BMNH 48244 in part, BMNH 48227). Unfortunately, detailed stratigraphic information for many of these specimens was not recorded at the time of collection, though it is likely that most, if not all, were collected from either the Cherty Freshwater Member or the Marly Freshwater Member of the Purbeck Limestone Formation.

2.2. Histological methodology

Owen's (1878a) original histological sections of granicones could not be located and are currently lost, although some figures were published. Therefore, in

order to examine the microscopic anatomy of the granicones, one specimen (BMNH R16311) was bisected longitudinally through the apex using a diamond-impregnated lapidary saw (Figure 3A). The base of one half of the granicone was ground flat using 400-mesh carborundum grit on plate glass. The flattened surface was bonded to a roughened microscope slide using epoxy glue. Most of the remaining section of the granicone was then cut away from the specimen, using a lapidary saw, leaving a slice approximately 0.5 mm in thickness bonded to the glass; custom-built jigs were used to ensure that the specimen was ground flat and parallel to the plane of the slide. The slice attached to the slide was then ground down using 200- and 400-mesh carborundum grits on glass until it reached a thickness of approximately 70 μm , allowing detailed examination of granicone histology in both plane and cross-polarised light (basal section 1). A second section, parallel to the first, was prepared in similar fashion, using the remaining portion of this half of the granicone (basal section 2; Figure 3A). The same technique was used to prepare a longitudinal section through the other half of the granicone (Figure 3A). The histology was examined using a trinocular Swift Polarising Microscope (series MP3500 BL) and the micrographs were taken with a Pentax MV1 reflex camera.

3. Description

3.1. Gross morphology

There are two distinct granicone morphotypes (see also Norman & Barrett, *in press*; Figure 1). The majority of the granicones (BMNH 48247, BMNH R16310–11, BMNH R16418–48 and DORCM GS.1488 in part) are small conical ossicles (ranging in length from approximately 5 to 20 mm) with either a planar or slightly concave base (Figure 1A, B). The main part of the granicone projects obliquely from the base forming an angle of approximately 45° with the basal surface. The base is smooth and unornamented; the rest of the granicone is studded with numerous small circular or subcircular tubercles, producing a pustulate texture. The tubercles are evenly distributed around the external surface of the granicones. They are largest near the base of the granicone and decrease in size towards the apex. A distinct rim of bone encircles the base of the granicone (Figure 1A, B).

Some granicones (BMNH R16312, BMNH R16416–7 and DORCM GS.1488 in part) have a different morphology and are flat to mildly convex, plate-like structures with a crenulated, suboval outline and planar or slightly concave bases (referred to

hereafter as ‘shield-like’ granicones; Figure 1C). The bases are unornamented, but the central portion of the upper surface displays a pustulate texture very similar to that of the conical granicones. The ornament around the margins of some of the plate-like granicones (e.g., BMNH R16312) is more reticulate or vermiculate in pattern as the tubercles in this area are elongated, rather than circular or subcircular in outline. These elongated tubercles appear to radiate outwards from the centre of the upper surface of the granicones (e.g., BMNH R16312; Figure 1C).

3.2. Histology

The histology of the granicone shows a division between basal and apical regions. The basal area is composed of densely woven bundles of collagen fibrils, while the apical area is composed largely of remodelled cancellous bone. Periosteal ossification is absent.

In basal section 1, bundles of collagen fibrils are visible under cross-polarised light. These bundles form an interwoven mat-like fabric, with the bundles crossing at approximately 90° to each other (Figure 3B; see also Owen, 1878a, pl. 12, fig. 7). The bundles of fibrils do not appear to interdigitate, but remain as discrete bundles that interweave with each other (Figure 3C). Basal section 2 shows that the cortex is composed of bundles of collagen fibrils that run parallel to the outer surface of the granicone (Figure 3D). Towards the centre of the granicone secondary Haversian systems are superimposed on the woven fabric (Figure 3E). In the central area the Haversian canals are relatively large, occupying about half of the cross-sectional area of each Haversian system.

The longitudinal section confirms the presence of secondary Haversian replacement and of large Haversian canals. The woven fabric is not so clearly defined in longitudinal section, but a section through one of the external tubercles shows that it is composed of loosely bundled collagen fibrils oriented parallel to the outer surface of the granicone (Figure 3F).

4. Discussion

4.1. Histological evidence

Osteoderm histology has not been studied extensively and only a limited amount of comparative information is available. Nevertheless, histology confirms that the granicones represent dermal ossifications. Granicone histology is similar to that reported for the osteoderms of some anurans (Ruibal & Shoemaker, 1984),

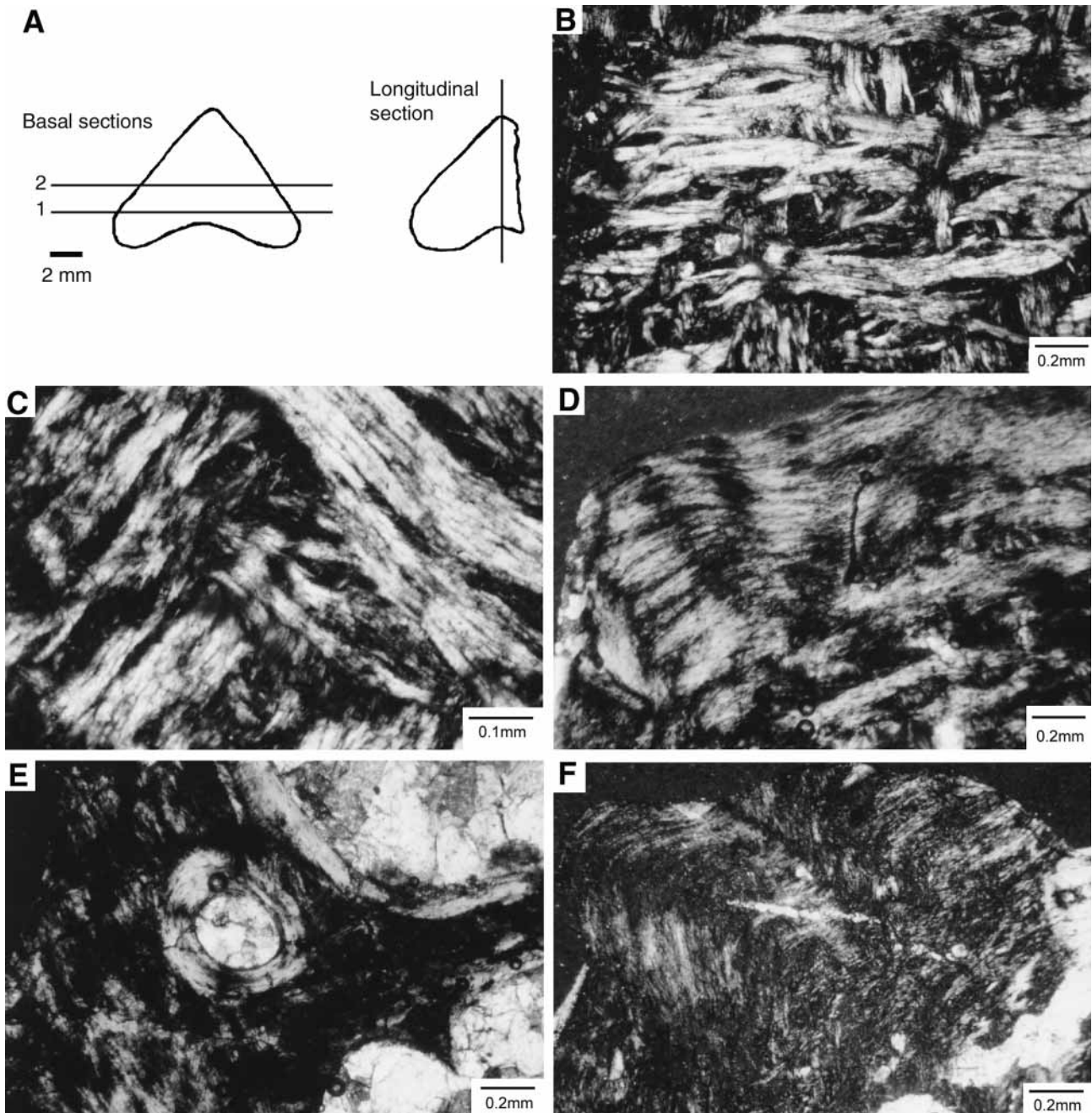


Figure 3. Granicone histology (based on BMNH R16311). A, sketch of granicone sectioning scheme; two basal sections and one longitudinal section. B, interwoven bundles of mineralised collagen fibrils from basal section 1. C, detail of mineralised collagen fibril bundles that do not interdigitate. D, loosely bundled collagen fibrils oriented parallel to the outer surface of the cortex of basal section 1. E, a secondary Haversian ring replacing the woven fabric from basal section 2; portions of other larger Haversian rings are also visible. F, longitudinal section through a surface tubercle composed of loosely bundled collagen fibrils following the contours of the tubercle. Photographs in B–F were taken through crossed polarisers.

squamates (Zylberberg & Castanet, 1985; Levrat-Calviac & Zylberberg, 1986), basal thyreophorans (*Scelidosaurus*; Figure 4A) and ankylosaurs (JBC, pers. obs.; de Ricqlès *et al.*, 2001; Figure 4B–D). In

general, the osteoderms of all of these taxa are composed of a basal section (‘basal plate’) composed of regularly arrayed bundles of mineralised collagen fibrils, and an outer part consisting of remodelled

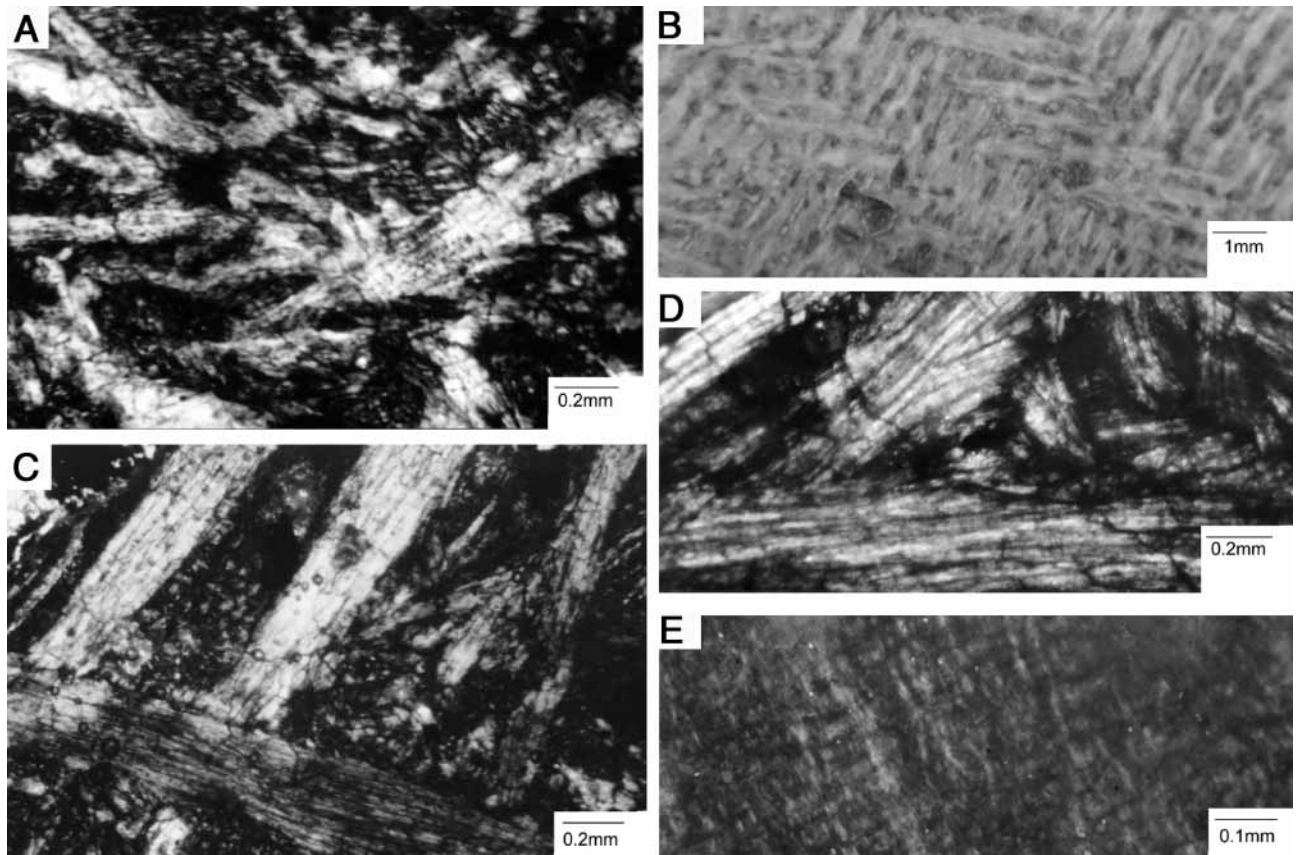


Figure 4. Comparative histology of dinosaur osteoderms and turtle shell. A, *Scelidosaurus* (BRSMG Ce12875); woven bundles of collagen fibrils from a basal section of an osteoderm. B, cf. *Hylaeosaurus* sp. (BMNH 35494); woven bundles of collagen fibrils visible on a broken, polished margin of an osteoderm. C, *Polacanthus foxii* (BMNH R9293); woven bundles of mineralised collagen fibrils in a basal section from the sacral shield. D, indeterminate ankylosaur (BMNH R16369); woven bundles of collagen fibrils from an osteoderm. E, indeterminate turtle (UOP/01/101); woven, regular bundles of mineralised fibrils of very small diameter from the basal section of a pleural plate. Photographs in A and C–E were taken through crossed polarisers.

cancellous or woven bone (though it should be noted that there is a great deal of diversity in the fine histological structure of both anuran and squamate osteoderms: Moss, 1969; Ruibal & Shoemaker, 1984). In lizards, the bundles of collagen fibrils in the basal plate continue into the surrounding dermis, anchoring the osteoderm within the dermis and linking it to both the dermal-epidermal junction and to neighbouring osteoderms. This observation has suggested that the osteoderms were formed by ‘metaplastic ossification’, whereby pre-existing dermal connective tissue structures were mineralised to form hard tissues (Moss, 1969; Zylberberg & Castanet, 1985; Levrat-Calviac & Zylberberg, 1986; de Ricqlès *et al.*, 2001). The detailed histological similarities shared by lizard and ankylosaur osteoderms and the granicones suggests that all of these structures were formed by metaplastic ossification. The granicones, therefore, probably arose from condensations of

dermal collagen fibrils that became ossified; the bone in the apical region was later remodelled.

Turtle shell and crocodylian osteoderms possess a bone microstructure that is broadly similar to that described in the above-mentioned taxa, but which differs from the latter in several important respects. Viewed in transverse section, the basal plate of a crocodylian osteoderm apparently lacks discrete bundles of collagen fibrils; this area is composed of compact fibrolamellar bone that appears to have been deposited periosteally. The fibrolamellar layer is overlain by a transitional zone containing rare Haversian systems, in which the primary bone has been heavily remodelled to form a zone of secondary, cancellous bone that comprises the central portion of the osteoderm (see also de Buffrénil, 1982). As the external surface of the osteoderm is approached, this zonal pattern is repeated in reverse, such that a transitional zone overlies the central cancellous zone and the outer

surface of the osteoderm is composed of fibrolamellar bone. However, sections cut parallel to, and within a short distance of, the lower (inner) surface of the osteoderm reveal the presence of a thin basal layer composed of interwoven collagen fibril bundles that lies beneath (i.e., internal to) the zone of fibrolamellar bone (Figure 4E; see also de Buffrénil, 1982). These collagen fibril bundles are more densely packed and narrower in diameter (10–20 µm in diameter) than those observed in either the granicones or in ankylosaur dermal armour (bundle diameter of up to approximately 0.4 mm). This basal layer may correspond to the basal plate of lissamphibian, squamate and dinosaur osteoderms (see above); the external surface of the crocodylian osteoderm lacks this layer of collagen fibril bundles. The histology of the outer part of the turtle shell displays the same sequence of bone fabrics as the crocodile osteoderm (Zangerl, 1969), but below the lower transition zone, instead of fibrolamellar bone, the fabric of the bone consists of interwoven layers of narrow, closely packed interwoven bundles of collagen fibrils that are identical to the thin woven inner layer of the crocodylian osteoderm. However, it should be noted that there is some variation in the histology of turtle shell; in several marine forms (e.g., *Allopleuron*) the outer layers of compact fibrolamellar bone are either reduced in thickness or lost entirely (Zangerl, 1969).

Several clades with representatives that possess osteoderms are known from the Purbeck Limestone Formation, including chelonians, squamates, crocodylians and ankylosaurian dinosaurs (e.g., Ensom *et al.*, 1991, 1994). At present, comparative osteoderm histology is too poorly documented to allow the determination of unambiguous character states that would permit the identification of the animal that possessed the granicones. However, on the basis of this brief survey, gross differences in the composition of the bone fabrics and in the distribution and diameter of the collagen fibril bundles indicate that the granicones are neither crocodile osteoderms nor component parts of chelonian thecal shell (*sensu* Zangerl, 1969).

4.2. Geological and taphonomic evidence

The initial referral of the granicones to the theropod dinosaur *Nuthetes* was based upon an association of the former with isolated teeth of the latter (Owen, 1878a, 1879). However, such taphonomic associations are not necessarily reliable indicators of biological affinity. Within the Purbeck Limestone Formation there is evidence for a wide range of taphonomic histories for the vertebrate specimens preserved (PCE, pers. obs.). Specimens range from: complete and fully

articulated fish (Woodward, 1916–19); partial, articulated skeletons of crocodiles and turtles (e.g., Owen, 1853, 1879); associated, but disarticulated, specimens of lizards (Evans, 1994); a range of well-preserved isolated elements (limb bones and jaws of crocodylians, dinosaurs, mammals, pterosaurs; turtle shell; dorsal fin spines of hybodontid sharks); to small, localised accumulations of disarticulated material, which may contain representative elements of many different taxa; and isolated teeth, scales and bone fragments. A small amount of material is heavily abraded and may have been reworked from older deposits, though there is currently little evidence to support this assertion on the basis of the vertebrate material alone. However, there is evidence for the reworking of material from lower horizons within the Purbeck Limestone Formation (the ostracod *Mantelliana purbeckensis*; Clements, 1981) and from the older Late Jurassic Kimmeridge Clay (the ammonite *Pavlovia* sp.; Ensom, 1985).

Granicones have been found in direct association with turtle, crocodile and theropod specimens (see section 2.1). It is possible that they were also associated with many other Purbeck taxa, but that these field relationships have been lost. There is evidence to suggest that, in some cases, large slabs of Purbeck matrix containing accumulations of vertebrate material were subdivided for easier dispatch to museums and/or to facilitate later study; this practice might have obscured the full complement of granicone field associations. Sieving of bulk samples from the Sunnydown Farm locality has yielded granicones in loose association with many different taxa, including mammals, dinosaurs, crocodylians, pterosaurs, lizards, sphenodontians, turtles, lissamphibians and fish (Ensom *et al.*, 1991, 1994; PCE, pers. obs.).

This wide variety of field associations between granicones and different Purbeck taxa suggests that, in the majority of cases, geological occurrence and taphonomic evidence can provide only limited evidence for the referral of the granicones to any particular taxon. However, one exception to this general rule may be provided by specimens from an unusual bulk sample that was collected from the Sunnydown Farm locality. This sample contained many associated limb and shell fragments of a solemydid turtle (DORCM GS.1488 in part; see locality data in section 2.1), approximately 60 granicones (DORCM GS.1488 in part) and a small amount of other vertebrate material (DORCM uncatalogued). The pustulate surface texture on the carapace and plastral elements indicates that they are referable to either *Helochelydra* (= *Tretosternon*) *anglica* or '*Tretosternon*' *bakewelli* (taxonomy after A. R. Milner, in press). The sample is

unusual as it contained a concentration of relatively large, associated bone fragments from both the limbs and shell. This contrasts with the usual modes of preservation for turtle specimens from the Purbeck Limestone Formation: usually they consist of either well-preserved, fully articulated carapaces and/or plastra or partial specimens that include only small fragments of either shell, girdle or limb material. The high concentration of turtle material in the sample and the mixture of limb and shell elements suggest that the majority of these remains pertain to a single individual (DORCM GS.1488 in part). The association between this individual and the large number of granicones (in the absence of appreciable amounts of other vertebrate material) provides strong circumstantial evidence for the referral of the granicones to the turtle taxon represented in the sample. Consequently, it is possible that the granicones might be skeletal elements of either *Helochelydra* (= *Tretosternon*) *anglica* or '*Tretosternon*' *bakewelli*. This prospect is discussed further, below.

4.3. Anatomical evidence

Squamates

Cephalic and body osteoderms (i.e., those that cover the dorsum and other regions of the body) are present in a wide variety of squamates (Camp, 1923; Romer, 1956; Estes, 1983; Richter, 1994). The majority of lizards with osteoderms are members of the Anguimorpha and are included in the families Anguidae, Helodermatidae, Xenosauridae and Lanthanotidae (Camp, 1923; Estes, 1983; Gao & Norell, 1998). Some gekkotans (e.g., *Geckonia*, *Tarentola*, *Lygodactylus*) and scincormorphs (e.g., *Scincus*, *Gongylus*, *Lygosoma*) also possess osteoderms, but the occurrence of this feature is much rarer in these clades (Camp, 1923; Romer, 1956; Estes, 1983; S. E. Evans, pers. comm. 1999).

The ovate morphology of the shield-like granicones suggests that they are not lizard body osteoderms as the majority of the latter are usually rectangular, subrectangular or trapezoidal in shape [for example, in the anguimorphs *Ophisaurus* (BMNH R8942) and *Helodermoides* (Gilmore, 1928; Meszoely & Ford, 1976; Sullivan, 1979; Estes, 1983; Richter, 1994) and the scincormorphs *Chalcides*, *Cordylus* and *Zonosaurus* (Camp, 1923; Richter, 1994)]. Several taxa (e.g., *Zonosaurus*, *Helodermoides*: Sullivan, 1979; Richter, 1994) possess a small number of polygonal body osteoderms, but these elements are straight-sided, rather than rounded in outline (Estes, 1983; Richter, 1994). *Apodosauriscus* and *Chalcides* bear subovate body osteoderms along the dorsum; however, these

osteoderms differ from the shield-like granicones as they have smooth, rather than crenulated, margins (Estes, 1983; Richter, 1994). Moreover, the body osteoderms of both *Apodosauriscus* and *Chalcides* display large articular facets on their external surfaces. These facets permitted mobility between adjacent, overlapping osteoderms and lack the ornament that covers the remainder of the external surface of the osteoderm (Estes, 1983; Richter, 1994); articular facets are absent from the shield-like granicones. Conical osteoderms are, apparently, rare in lizards; for example, the large conical spines of the thorny devil (*Moloch horridus*) are composed entirely of epidermally derived keratinous material and lack a bony core (Owen, 1878a). The gekkotan *Geckonia* possesses small, conical osteoderms that are arranged in parasagittal rows along the sides of the trunk and tail (PMB, pers. obs.; S. E. Evans, pers. comm. 1999). These structures are similar to the conical granicones in overall morphology, but they lack the basal rim of bone (see section 3.1), are much smaller (maximum length of *Geckonia* osteoderm from tip to base is approximately 1 mm) and differ in their surface ornamentation (see below).

The pustulate ornamentation of the shield-like granicones precludes their referral to many lizard taxa. The body osteoderms of most lizards are either only lightly sculptured, bearing small, irregularly spaced pits and ridges (Estes, 1983; Richter, 1994) or have a well-developed reticular ornamentation (e.g., *Ophisaurus*; Meszoely & Ford, 1976; Estes, 1983; Richter, 1994). Body osteoderms of both *Apodosauriscus* (Estes, 1983) and glyptosaurine anguids (Gilmore, 1928; Sullivan, 1979) do display strongly tuberculate ornamentation that is very similar to that present on the granicones; however, the polygonal outline of glyptosaurine body osteoderms (Gilmore, 1928; Sullivan, 1979) and the presence of articular facets on the osteoderms of *Apodosauriscus* (see above) prevent referral of the shield-like granicones to either of these taxa. Keels are also present on the body osteoderms of several lizard taxa (Meszoely & Ford, 1976; Richter, 1994); they are not present on any of the granicones. The conical osteoderms of *Geckonia* are covered with many small, circular pits, and are traversed by shallow troughs and grooves, particularly in the basal region of the osteoderm; pustulate ornamentation is absent (PMB, pers. obs.).

The shield-like granicones bear a strong resemblance to the cephalic osteoderms of glyptosaurine anguids (e.g., Sullivan, 1979) and non-varanid platynotans (including helodermatids, carusiids and xenosaurids; e.g., Gao & Norell, 1998, 2000). The

cephalic osteoderms in these squamates are hexagonal, subhexagonal or ovate in outline, possess smooth or crenulated margins and bear pronounced ornamentation. However, several subtle differences in ornament pattern and distribution suggest that the granicones cannot be referred to any of these taxa. For example, the cephalic osteoderms of xenosaurids and carusiids display well-developed vermiculate ornamentation (strongly pitted surfaces with thin, raised ridges of bone delimiting and separating the pits from each another), in contrast to the pustulate ornament present on the granicones (Camp, 1923; Estes, 1983; Gao & Norell, 1998; *Xenosaurus* BMNH 1913.7.19.97). Helodermatid and glyptosaurine cephalic osteoderms possess a pustulate, tubercular ornament that is strikingly similar to that of the granicones (Shufeldt, 1890; Camp, 1923; Gilmore, 1928; Sullivan, 1979, 1989; Estes, 1983; Pregill *et al.*, 1986; Figure 5). However, the tubercles on glyptosaurine cephalic osteoderms are often arranged in regular, geometric patterns (with rows of tubercles aligned parallel to the osteoderm margins), are very numerous and densely packed, and are always circular in outline (e.g., Gilmore, 1928; Sullivan, 1979, 1989). In contrast, the tubercles on the granicones are arranged irregularly, less densely packed, less numerous and occasionally elongated (see section 3.1). The central portions of the cephalic osteoderms of *Heloderma* (e.g., BMNH 1911.6.9.1, BMNH 1969.830, UCMZ R.9321) are extremely similar to the shield-like granicones; they are pustulate and the tubercles are irregularly disposed across the osteoderm surface. However, the margins of *Heloderma* cephalic osteoderms bear a reticulate ornamentation and lack distinct tubercles. Moreover, the granicones are much larger than lizard cephalic osteoderms; those of *Heloderma* reach a maximum length of 5 mm (BMNH 1911.6.9.1, BMNH 1969.830, UCMZ R.9321) whereas the largest granicones reach lengths of approximately 20 mm (see above).

Two lizards from the Purbeck Limestone assemblage are known to have possessed osteoderms: the scincomorphs *Becklesius* and *Paramacellodus* (Estes, 1983; Richter, 1994; Evans & Chure, 1998). Osteoderms from these taxa (Richter, 1994; *Paramacellodus*: BMNH R8209 and BMNH R8210) are either rectangular or subrectangular in outline; there are no known examples of either conical or ovate osteoderms in either taxon. The external surfaces of the osteoderms bear a variable number of small, circular pits and are usually lightly sculptured, though some examples are completely lacking in ornament. Where present, the sculpturing produces a reticulate pattern; the pustulate ornamentation that is

characteristic of the granicones is not seen in either *Becklesius* or *Paramacellodus* (Richter, 1994; PMB, pers. obs.). Moreover, the granicones are far too large to have been borne by any of the described Purbeck lizards, most of which had snout/vent lengths of 150–200 mm or less (Evans, 1994; Richter, 1994; S. E. Evans, pers. comm. 2001). There is currently no evidence to suggest that squamates of sufficient size to bear the granicones were present in the fauna of the Purbeck Limestone Formation (S. E. Evans, pers. comm. 1999).

Osteoderms are associated with the holotype specimen of the Purbeck anguimorph *Parviraptor* (Evans, 1994; BMNH 48388), but these are not lizard and are referable to a small atoposaurid crocodylian, possibly *Theriosuchus*. None of the articulated lizard specimens from the Purbeck Limestone Formation is associated with granicones (BMNH 48388, BMNH R8209 and BMNH R8210), though a loose association has been documented on the basis of bulk sampling (see above).

Crocodylians

Many taxa have been based upon the crocodylian material from the Purbeck Limestone Formation (e.g., Owen, 1878b, 1879), but the taxonomy of these animals has received scant attention (e.g., Joffe, 1967; Steel, 1973). A recent, comprehensive review of the Purbeck crocodylian taxa recognises the presence of five species in three genera: the goniopholidids *Goniopholis crassidens*, *G. simus* and *G. gracilidens*, the pholidosaurid *Pholidosaurus purbeckensis*, and the atoposaurid *Theriosuchus pusillus* (Salisbury, *in press*). On the basis of the holotype and referred specimens, osteoderms can only be assigned confidently to three of these taxa: *Goniopholis crassidens*, *Pholidosaurus purbeckensis* and *Theriosuchus pusillus* (Salisbury, *in press*).

All crocodylians possess an extensive covering of dermal armour, with osteoderms situated on the dorsal and ventral surfaces of the body and tail (e.g., Romer, 1956; de Buffrénil, 1982; Ross & Mayer, 1983). The osteoderms vary in size and shape according to their position but, in general, they are rectangular to subrectangular in outline, are rather thin and plate-like, and have external surfaces that are heavily sculptured. The sculpture is characteristically reticulate or 'waffle-like' and consists of a series of deep subcircular to subrectangular pits that are separated from each other by thin, but distinct, ridges of bone (de Buffrénil, 1982). Crocodylian osteoderms often possess a longitudinal keel that extends across the external surface (Romer, 1956). The osteoderms of *Goniopholis crassidens* (e.g., BMNH 44818, BMNH

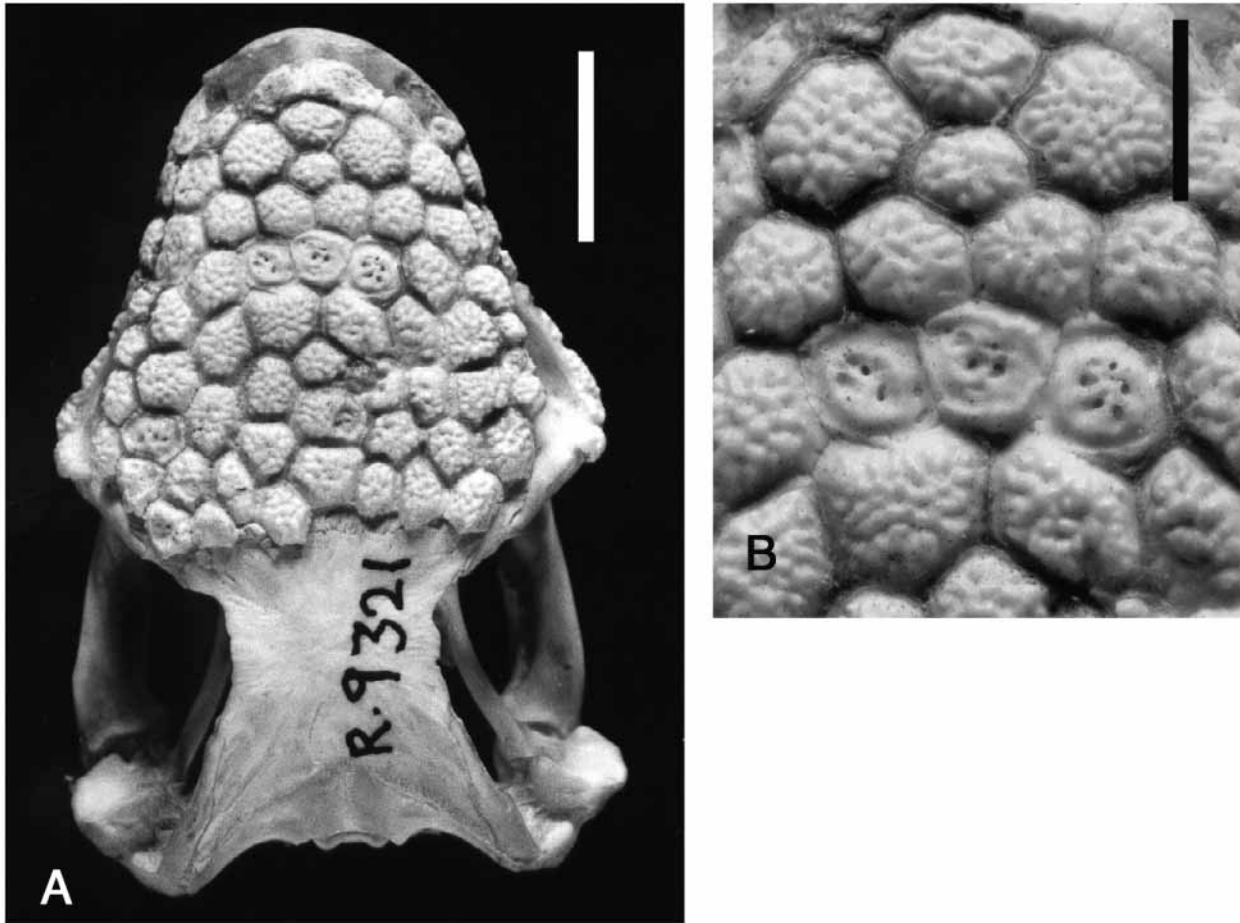


Figure 5. Osteoderms of the Gila Monster, *Heloderma suspectum* (Helodermatidae) (UCMZ R.9321). A, skull in dorsal view, showing the mosaic pattern created by the closely packed osteoderms; scale bar represents 10 mm. B, detail of the osteoderms close to the anterior midline of the skull in dorsal view; note the pustulate texture; scale bar represents 5 mm.

R3415, BMNH R6865 and many others), and some of those of *Pholidosaurus purbeckensis* (e.g., BMNH R3884 and BMNH R3956), are ‘typically’ crocodylian, with strong ‘waffle-like’ ornamentation and, in some cases, longitudinal keels. The remainder of the osteoderms associated with *P. purbeckensis* and with *Theriosuchus* (e.g., BMNH 48216, BMNH 48275, BMNH 48329 and many others) are less heavily sculptured, bearing only a few small circular pits, though many osteoderms of *Theriosuchus* possess a prominent midline keel (Figure 6).

Crocodylian osteoderms possess several obvious features that distinguish them from the granicones. These include: the presence of longitudinal keels (which are absent in the granicones); the possession of either a ‘waffle-like’ or pitted surface texture (contrasting with the pustulate texture of the granicones); and a subrectangular to rectangular outline in dorsal view (as opposed to the ovate outline of the granicones

in dorsal view). Moreover, conical osteoderms have not been reported in any crocodylian. Consequently, referral of the granicones to the Crocodylia seems highly doubtful, a conclusion that is supported by the histological evidence (see above).

Dinosaurs

Dermal armour is present in a variety of dinosaur taxa, but is particularly well-developed in the Thyreophora, a monophyletic assemblage that contains the stegosaurs, ankylosaurs and a number of basal forms, such as *Scelidosaurus* and *Scutellosaurus* (Norman, 1984; Sereno, 1986, 1997). Rare remains of nodosaurid ankylosaurs have been recovered from the Purbeck Limestone Formation (Galton, 1983; Norman & Barrett, in press).

Some nodosaurid ankylosaurs (e.g., *Polacanthus*, BMNH R9293; Blows, 1987; Figure 7) possess small, conical osteoderms that are superficially similar to the

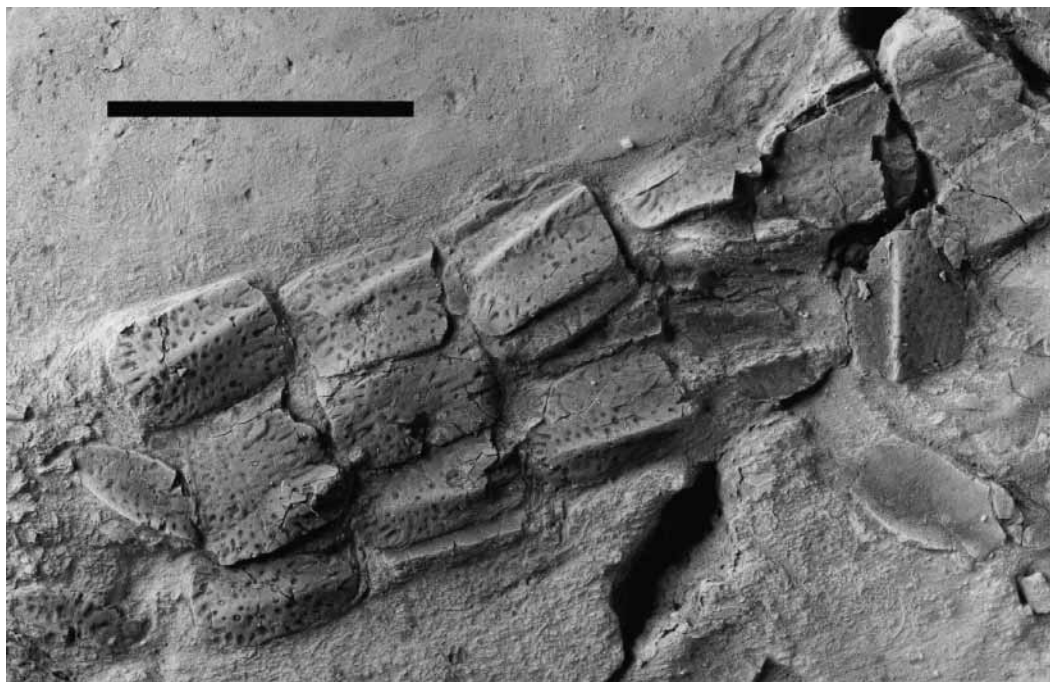


Figure 6. Osteoderms from the dorsal region of the tail in the atoposaurid crocodilian *Theriosuchus pusillus* (BMNH 48216) from the 'Middle Purbeck Beds' (Berriasian) of Durlston Bay, Dorset, UK. Note the small circular pits that are unevenly distributed across the dorsal surfaces of the osteoderms and the prominent longitudinal keels. Scale bar represents 20 mm.

conical granicones. Moreover, the small polygonal osteoderms that comprise the sacral shield of *Polacanthus* (BMNH R9293; Blows, 1987) and those that cover the dorsum of the ankylosaurid *Euoplocephalus* (BMNH R5161) are similar in size and shape to the shield-like granicones. However, all ankylosaur osteoderms, and those of the basal thyreophorans *Scelidosaurus* (Owen, 1863) and *Scutellosaurus* (Colbert, 1981), either lack marked surface ornamentation or have irregular surfaces marked with numerous pits and canals that give the exterior of the osteoderm a spongy texture (e.g., indeterminate ankylosaurs, BMNH R4299–4311, BMNH R10069 and many others; *Polacanthus*, BMNH R110, BMNH R9293; *Hylaeosaurus*, BMNH R3775; *Euoplocephalus*, BMNH R5161; *Scelidosaurus*, BMNH R1111, BRSMG Ce12785; Figure 7) which is quite distinct from the pustulate texture of the granicones. Many osteoderms from *Scelidosaurus*, *Scutellosaurus* and ankylosaurs possess marked keels on their exterior surfaces (Owen, 1863; Colbert, 1981; Coombs & Maryańska, 1992; see specimens listed above), a feature that is lacking in the granicones. Ankylosaur osteoderms are also much thicker in cross-section than granicones of similar size: the small polygonal osteoderms in the sacral shield of *Polacanthus* (with maximum lengths of around 15–

20 mm; BMNH R9293) have a thickness of around 10 mm, compared with 1 mm or less in the shield-like granicones. These differences in osteoderm morphology suggest that the granicones cannot be referred to the Ankylosauria. It could be argued that the small size of the granicones might indicate that they belonged to a juvenile ankylosaur, and that the immaturity of the specimens could account for the differences in ornamentation, the absence of a keel and the differences in cross-sectional thickness. However, the granicones are comparable to osteoderms of an adult *Polacanthus* (BMNH R9293) in terms of maximum length, but differ in many other aspects of their morphology (see above). Moreover, it has been suggested that juvenile ankylosaurs lacked well-developed osteoderms as they have not been found in association with skeletons of young individuals (Jacobs *et al.*, 1994; Pereda-Suberbiola & Barrett, 1999).

The large, elongate, conical spines and flat, plate-like osteoderms of stegosaurs (e.g., Galton, 1985, 1992) bear little resemblance to either the conical or the shield-like granicones. Smaller dermal ossicles are known from the throat region of *Stegosaurus*, however (Gilmore, 1914; Carpenter, 1998). These are flattened, disk-like structures, with a rounded to sub-hexagonal outline. They lack keels, are pitted and

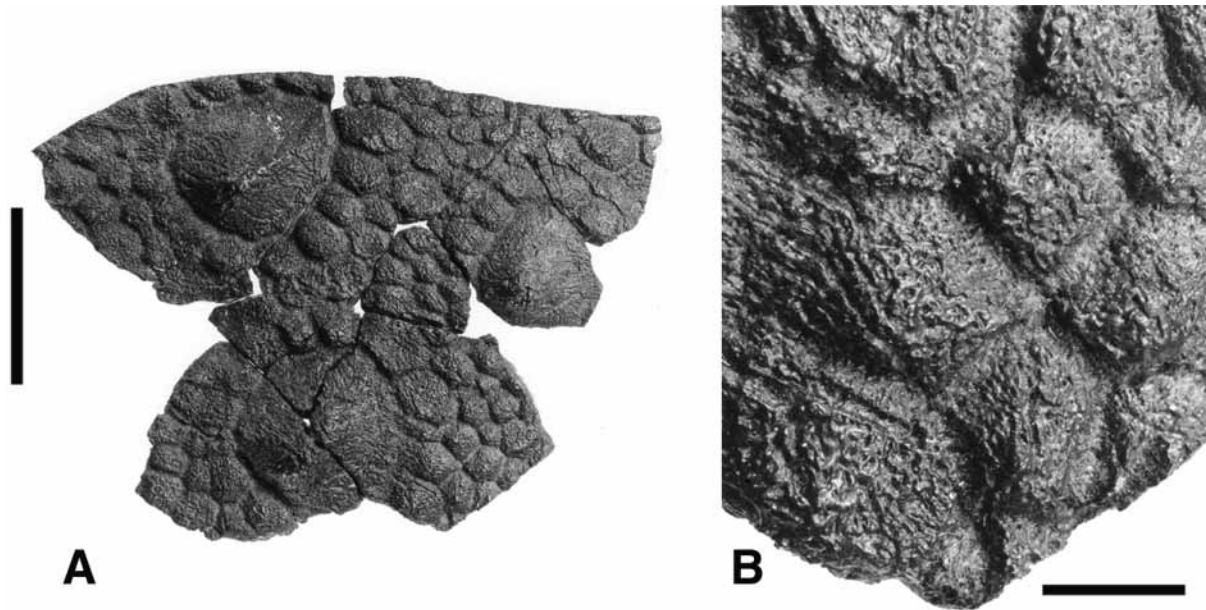


Figure 7. Fused osteoderms from the sacral shield of *Polacanthus foxii* (BMNH R9293) from the Wessex Formation (Barremian) of the Isle of Wight, UK. A, a portion of the sacral shield in dorsolateral view, showing the fusion of numerous small, flattened osteoderms and larger conical osteoderms; scale bar represents 50 mm. B, detail of the sacral shield showing the pitted, irregular surface ornamentation of the individual osteoderms; scale bar represents 10 mm.

grooved on one surface, and reach a maximum diameter of 35 mm (Gilmore, 1914). Nevertheless, they do not resemble the conical granicones and differ from the shield-like granicones in several respects, most notably in their larger size and in their lack of a pustulate texture.

Referral of *Echinodon* to the Heterodontosauridae (Serenó, 1991; Barrett, 1999; Norman & Barrett, *in press*) suggests that the granicones cannot be assigned to this taxon, as no known heterodontosaurid possesses dermal armour (PMB, pers. obs.).

The ceratosaurian theropod *Ceratosaurus* possesses epaxial osteoderms (Madsen & Welles, 2000), but dermal armour is absent in all other known theropod taxa. This observation indicates that the occurrence of osteoderms in the dromaeosaurid theropod *Nuthetes* is extremely unlikely (A. C. Milner, *in press*; Norman & Barrett, *in press*). Moreover, the morphology of the *Ceratosaurus* osteoderms differs considerably from that of the granicones: the former are relatively large (up to 90 mm in length), bear tall midline keels, and have a spongy surface that is criss-crossed by numerous narrow canals (Madsen & Welles, 2000). Conical osteoderms are present in *Ceratosaurus* (Madsen & Welles, 2000), but their large size and spongy surface texture clearly distinguish them from the granicones. Osteoderms are also known in titanosaurid sauropods (e.g., Dodson *et al.*, 1998) and dermal ossifications ('epoccipitals') fuse to the margin of the parieto-

squamosal frill in neoceratopians (Hatcher *et al.*, 1907; Dodson & Currie, 1992). Neither structure resembles the granicones. Titanosaurid osteoderms are thickened dorsoventrally, have a spongy surface texture with many pits and canals, occasionally bear low median ridges on both internal and external surfaces, and are extremely large (reaching a maximum diameter of 280 mm) (Le Loeuff *et al.*, 1994; Dodson *et al.*, 1998). Neoceratopian epoccipitals are usually subconical to subpyramidal in shape and have rugose surfaces marked by numerous vascular canals (Hatcher *et al.*, 1907).

This survey demonstrates that the granicones differ from all known dinosaurian osteoderms in numerous ways; consequently, their referral to the Dinosauria is considered to be highly unlikely.

Turtles

The gross morphology of the granicones clearly indicates that they were not component parts of turtle thecal shell (e.g., Romer, 1956; Zangerl, 1969); they do not resemble any carapace or plastral elements. The smooth, finished base of the granicones demonstrates that they were not fused or sutured to any underlying structures; consequently, they were not attached to either the margins or the dorsal surface of the carapace. Moreover, several differences exist between granicone histology and that of turtle shell (see above).

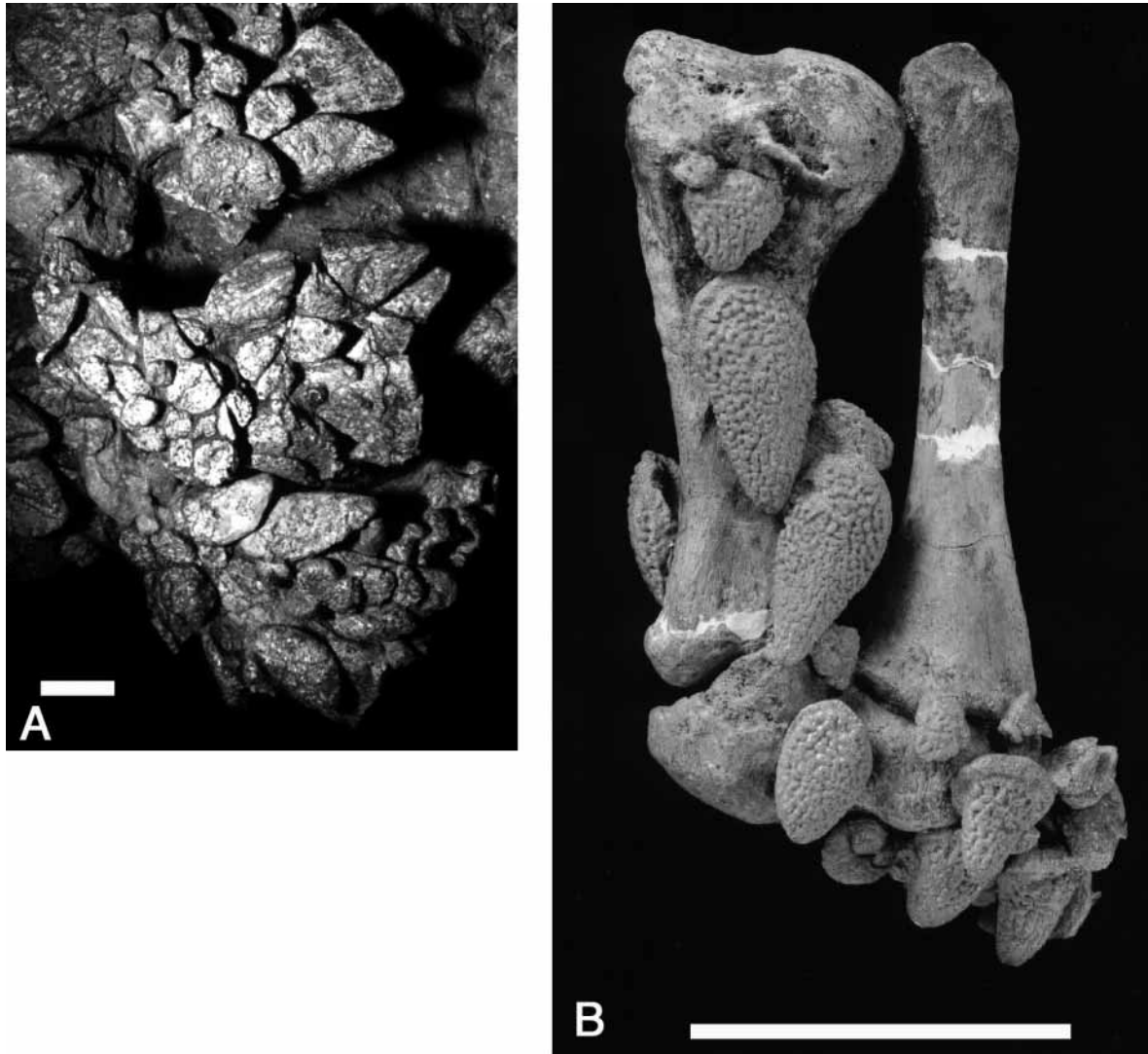


Figure 8. Chelonian osteoderms. A, right forelimb of *Proganochelys quenstedti* in ventral view, showing numerous conical and flattened osteoderms (composite of SMNS 16980 and SMNS 17204); scale bar represents 25 mm. B, articulated right hindlimb of *Naomichelys speciosa* (FMNH PR 273) from the Trinity Group (Aptian–Albian) of Texas, in lateral view; note the strong pustulate ornamentation on the osteoderms; scale bar represents 50 mm.

Osteoderms are known in a variety of chelonian taxa, though they have seldom been described in detail. Among extant forms, testudinids and *Dermochelys* possess dermal ossicles that are embedded in the skin of the limbs and *Chelydra* bears an armoured tail (Romer, 1956). The Late Triassic basal chelonian *Proganochelys* displays a large number of dermal ossifications that are associated with the limbs, neck and tail (Gaffney, 1990; Figure 8A) and the Pleistocene meiolaniids *Meiolania* and *Ninjemys* also bear ossifications on the tail (Gaffney, 1996). The manus and pes of *Meiolania* are associated with osteoderms, though they do not appear to have been present on the proximal limb segments (Gaffney,

1996). An undescribed specimen (FMNH PR 273) from the Lower Cretaceous (Aptian–Albian) Trinity Group of Texas (referred to *Naomichelys*; Hirayama *et al.*, 2000; Figure 8B) has a covering of osteoderms on the dorsal and lateral surfaces of each limb.

The cervical osteoderms of *Proganochelys* are situated on the dorsal surface of the neck. Each osteoderm consists of four vertically inclined conical spines: the central pair of spines is taller than the lateral pair (Gaffney, 1990). Conical osteoderms, arranged in 'triads', form a series of up to six partial rings that cover the dorsal surface of the tail. Distally, these osteoderms co-ossify to form a distinctive tail club. Other conical osteoderms are situated irregularly

along the flanks of the tail. A mixture of small, disc-like osteoderms (ranging in length from 5 to 15 mm) and larger conical osteoderms (averaging approximately 25 mm in length) are arranged along the limbs and several small osteoderms are associated with the manus and pes (Gaffney, 1990; Figure 8A). The conical osteoderms are arranged in rows that extend along the anterior and posterior margins of the limb segments; the disc-like osteoderms are situated in the space between these two rows. The latter are subcircular to subelliptical in shape, have smooth, rounded edges, flat to gently convex external surfaces and lack keels. The conical osteoderms have subcircular to subelliptical bases and their apices are inclined at approximately 45° to the horizontal. All *Proganochelys* osteoderms are smooth and bear no ornament (Figure 8A; E. S. Gaffney, pers. comm. 2001). The manual and pedal osteoderms of *Meiolania* are similar to those of *Proganochelys*, but differ from the latter in having a much more porous surface texture, characterised by the presence of larger, deeper pits on both the internal and external surfaces (cf. Gaffney, 1996). *Meiolania* and *Ninjemyx* possess tail clubs that are similar to that of *Proganochelys*; however, in the former, the tail club consists a series of fused pairs of spines, rather than the fused triads of spines see in *Proganochelys* (Gaffney, 1990, 1996); the ornamentation of the tail osteoderms is similar in all three taxa.

Two solemydid genera possess limb osteoderms. *Naomichelys* (FMNH PR 273; Figure 8B) includes conical and disc-like osteoderms that are somewhat similar to those described for *Proganochelys*. However, the ornamentation on the osteoderms of FMNH PR 273 differs markedly from that of *Proganochelys* and the meiolaniids: it is pustulate, with numerous small tubercles covering the external surfaces of the osteoderms. These tubercles are subcircular to subelliptical in outline and are densely packed, with little space separating them. The conical osteoderms have a well-defined basal region that is expanded relative to the main body of the osteoderm; this region often lacks tubercles. All of the osteoderms lack keels; the main body of the conical osteoderms projects at an angle of approximately 45° relative to the basal region; and the disc-like osteoderms are relatively thin and are ovate, subelliptical or subpolygonal in outline (Figure 8B). Pustulate, disc-like limb osteoderms have also been reported in *Solemys* from the Maastrichtian of France (Lapparent de Broin & Murelaga, 1999).

The combined presence of two osteoderm types (ovate and conical) in several chelonian taxa, the close similarities in gross osteoderm morphology, and the presence of a pustulate surface ornamentation on the

osteoderms of *Naomichelys* (FMNH PR 273) and *Solemys*, strongly suggest that the granicones are isolated chelonian limb or tail osteoderms. Indeed, both the conical and shield-like granicones are almost indistinguishable from the various osteoderms of *Naomichelys*. The arrangement of the osteoderms on the limbs of *Naomichelys* and *Proganochelys* also offers a potential explanation for the greater abundance of conical granicones: in both taxa there are a greater number of conical osteoderms (arranged along the margins of the limbs) than disc-like osteoderms (situated along the axis of the limb).

The carapaces of *Naomichelys* (FMNH PR 273) and *Solemys* bear a pustulate ornamentation (Lapparent de Broin & Murelaga, 1999; Hirayama *et al.*, 2000) that is very similar to that seen on the limb osteoderms; in contrast, the carapace of meiolaniids is traversed by numerous shallow grooves and canals, as are the limb and tail osteoderms (Gaffney, 1996). Thus, it is possible that there is a correlation between carapace and osteoderm ornamentation. If this holds true, then it is probable that the granicones will pertain to a taxon with a pustulate ornament on the carapace.

Many chelonian taxa have been named on the basis of material from the Purbeck Limestone Formation, but the taxonomy of this assemblage is confused and in need of revision. Several authors have restudied this material (Lapparent de Broin & Murelaga, 1999; Hirayama *et al.*, 2000; A. R. Milner, *in press*), but there is currently little consensus on the validity and/or priority of several key genera. Nevertheless, the Purbeck turtle fauna is known to include two taxa with pustulate carapace ornament, both of which are referable to the family Solemydidae: *Helochelydra* (= *Tretosternon*) *anglica* and '*Tretosternon*' *bakewelli* (Lapparent de Broin & Murelaga, 1999; Hirayama *et al.*, 2000; A. R. Milner, *in press*). Indeed, the shared presence of pustulate shell ornamentation in *Helochelydra* (= *Tretosternon*) and *Naomichelys* have led some authors to suggest that these genera are synonymous (Hirayama *et al.*, 2000). Both *H. anglica* and '*T. bakewelli*' are relatively rare components of the Purbeck turtle fauna, but are more abundant in the younger Wealden Group sediments of southeast England and the Isle of Wight (e.g., Owen, 1842; Lydekker, 1889; Lapparent de Broin & Murelaga, 1999; A. R. Milner, pers. comm. 2000). The shared presence of a strong pustulate texture on the carapaces of *Helochelydra anglica* and '*Tretosternon*' *bakewelli* and on the granicones strongly suggests that the latter are referable to one of these two chelonian taxa, a conclusion supported by some taphonomic evidence (see section 4.2).

5. Conclusions

The biological origin of the 'granicones' has been debated since they were first described over 130 years ago. Histological examination confirms that the granicones represent dermal ossifications and detailed comparisons with a wide variety of osteoderms from squamates, crocodylians and dinosaurs demonstrate that they are not referable to any of these taxa (*contra* Owen, 1878a, 1879; Lydekker, 1888; Swinton, 1934; Delair, 1959; Galton, 1981, 1985). Shared similarities in gross morphology and ornamentation indicate that the granicones represent either the limb or tail osteoderms of a chelonian, possibly *Helochelydra* (= *Tretosternon*) *anglica* or '*Tretosternon*' *bakewelli*. This represents the first discovery of a turtle with armoured limbs from the UK and provides an additional character state (pustulate osteoderms) linking the UK forms with *Naomichelys* and *Solemys*. The functions and phylogenetic distribution of osteoderms within Chelonia are currently unknown and are in need of further documentation and study.

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