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THE TURTLES OF THE PURBECK LIMESTONE GROUP OF DORSET, SOUTHERN ENGLAND

by ANDREW R. MILNER

ABSTRACT. The turtles from the Purbeck Limestone are revised and it is concluded that there are four shell-based cryptodire species present, namely *Pleurosternon bullockii*, '*Glyptops*' *typocardium* comb. nov., *Helochelydra anglica* comb. nov., and *Hylaeochelys latiscutata*. There is also one skull-based species, *Dorsetochelys delairi*, which may prove to be the skull of '*Glyptops*', *Hylaeochelys* or an unknown shell-type. All other taxa are junior synonyms except '*Chelone*' *obovata* Owen, 1842 and *Tretosternon punctatum* Owen, 1842 which are *nomina dubia*, the material being unfigured and either lost or incorrectly associated. Other taxonomic conclusions are that (1) because *Tretosternon* is a *nomen dubium*, the next senior name for this Purbeck–Wealden genus is *Helochelydra* Nopcsa, 1928; (2) '*Pleurosternon*' *typocardium* and '*Glyptops*' *ruetimeyeri* are synonymous, the senior combination being '*Glyptops*' *typocardium*; (3) the Purbeck '*Tretosternon*' material is combined with the holotype and only specimen of *Platycheilus*? *anglica* as *Helochelydra anglica* comb. nov.; (4) *Hylaeochelys emarginata* and *H. sollasi* are junior synonyms of *Hylaeochelys latiscutata*; (5) one of Owen's 'lost' syntypes of '*Tretosternon punctatum*' has been recognised and is a plastron of *Hylaeochelys latiscutata*.

KEY WORDS: Cretaceous, cryptodire, reptile, taxonomy.

TURTLES were among the first fossil vertebrates to be recognised and reported from the Purbeck Limestone (Anonymous 1809*a, b*) although systematic description of Purbeck turtle shells did not commence until the 1840s. In his report to the British Association meeting of 1841, Owen described three new taxa of fossil turtle from Purbeck, namely *Platemys bullockii*, which he attributed erroneously to the Eocene London Clay, *Chelone obovata* and *Tretosternon punctatum* (Owen, 1842). The type specimens, all in private collections, were not identified or figured, although they were described fully. Owen later described and fully figured the holotype of *Platemys bullockii* as a London Clay turtle (Owen 1850), but the type specimens of the other taxa were never figured and have been reported as lost from Lydekker 1889*b* onwards. In 1853, Owen described a second series of Purbeck specimens as four new species of the new genus *Pleurosternon*, namely *P. concinnum*, *P. latiscutatum*, *P. emarginatum* and *P. ovatum*, all of these specimens being fully figured and still recognisable. The 1853 paper makes no mention of the 1842 taxa. Seeley (1869) listed and diagnosed briefly four further new species of *Pleurosternon*, each based on a single specimen at the Sedgwick Museum, Cambridge. These species, *P. oweni*, *P. sedgwicki*, *P. typocardium* and *P. vansittarti*, were never figured or fully described. Maack (1869) and Cope (1870) each suggested generic reassignment of some of Owen's species (to *Platemys* and *Digerrhum* respectively) but neither of these taxonomic proposals has endured. Mansell-Pleydell (1888) provided the first overview of the Purbeck turtles but this was rapidly superseded by the series of major revisions undertaken by Richard Lydekker (Lydekker and Boulenger 1887; Lydekker 1889*a, b*). Lydekker and Boulenger (1887) were able to demonstrate that Owen's *Platemys bullockii* was really a Purbeck specimen. They argued that most of Owen's and Seeley's species were synonymous with it under the new combination *Pleurosternon bullocki* (with amended spelling of the species name), although their text suggests that they had not examined Seeley's specimens. Lydekker also showed that Owen's *P. latiscutata* and some *P. emarginata* were distinct and transferred them to *Plesiochelys* (Lydekker and Boulenger 1887) and then to the new *Plesiochelys*-like shell-genus *Hylaeochelys* (Lydekker 1889*a, b*). Lydekker (1889*b*) recognised two rare Purbeck turtles from single incomplete carapaces which he described as *Platycheilus*(?) *anglica* and *Thalassemys ruetimeyeri*. Finally he assigned one Purbeck plastron to the Wealden *Hylaeochelys belli* and

referred new specimens of *Tretosternon* from the Purbeck to *T. punctatum*. This major revision formed the basis for published observations on the Purbeck turtles for the next century. Lydekker's Purbeck turtle taxonomy can be summarised as:

| | |
|-----------------|--|
| AMPHICHELYDIA | |
| Pleurosternidae | <i>Pleurosternum bullocki</i> <i>Platycheles(?) anglica</i> |
| PLEURODIRA | |
| Plesiochelyidae | <i>Hylaeochelys latiscutata</i> <i>Hylaeochelys emarginata</i> <i>Hylaeochelys belli</i> |
| CRYPTODIRA | |
| Chelydridae | <i>Tretosternum punctatum</i> |
| Acichelyidae | <i>Thalassemys ruetimeyeri</i> |

It may be noted that almost nothing of this higher taxonomy has persisted.

Watson (1910*a*) described specimens from Manchester Museum, including new material of *T. ruetimeyeri* that he reassigned to the genus *Glyptops*, described from the contemporaneous Morrison Formation of North America. He later (1910*b*) noted that one of Seeley's species, *P. typocardium*, also represented the same species. Nopcsa (1928) added a fourth species of *Hylaeochelys*, *H. sollasi*, to the Purbeck fauna, based on a carapace at Oxford University Museum. In 1958, Delair reviewed the Purbeck turtles as part of a much larger overview of the Mesozoic reptiles of Dorset. Delair's review was a neutral summary of previous work although he did propose that the Wealden *Tretosternon bakewelli* was also present at Purbeck. He revised the higher systematics in line with contemporary work to give the following situation:

| | |
|-----------------|--|
| AMPHICHELYDIA | |
| Pleurosternidae | <i>Pleurosternum bullocki</i> <i>Tretosternum punctatum</i> <i>Tretosternum bakewelli</i> <i>Platycheles(?) anglica</i> |
| Baenidae | <i>Glyptops ruetimeyeri</i> |
| Plesiochelyidae | <i>Hylaeochelys latiscutata</i> <i>Hylaeochelys emarginata</i> <i>Hylaeochelys sollasi</i> <i>Hylaeochelys belli</i> |

Delair (1966) subsequently recorded several further specimens of Purbeck turtle in regional museum collections. Both Lydekker (1889*b*) and Delair (1958) had mentioned skulls from the Purbeck Limestone and two of these were described by Evans and Kemp in the 1970s, one with some postcranium as *Mesochelys durlstonensis* (Evans and Kemp 1975) and the other isolated skull as *Dorsetochelys delairi* (Evans and Kemp 1976). They did not assign either skull to a shell-taxon, but subsequently Gaffney has treated *Mesochelys* as the skull of *Pleurosternon* and effectively synonymised them (Gaffney and Meylan 1988, followed by Gillham 1994 and de Lapparent de Broin and Murelaga 1999), using this combination to place *Pleurosternon* and *Glyptops* in the same family Pleurosternidae based on the resemblance of the skulls. Little other first-hand work has been carried out on Purbeck turtles since Delair's review, although our understanding of the evolution and higher taxonomy of turtles has changed radically as the result of cladistic analysis. The Amphichelydia is now seen as an undefinable basal grade of turtles (Gaffney 1984) and the Purbeck taxa can all be recognised as cryptodires. Benton and Spencer (1995) summarised the Purbeck turtle fauna, following Delair in most respects, although their review omitted '*Glyptops*'

ruetimeyeri, probably because the holotype had been miscurated in The Natural History Museum in the 1950s and effectively ‘lost’ under the wrong label for 40 years. They also figured (*op. cit.* fig. 9.4F) ‘*Platemys*’ *bullocki* as a London Clay turtle, reviving Owen’s original error. More recently, de Lapparent de Broin and Murelaga (1999) have published revised assessments of some Purbeck *Pleurosternon* and ‘*Tretosternon*’ specimens in their description of the turtle material from the Upper Cretaceous of Laño, Spain. They suggested that the small turtle material from the Beckles Pit at Swanage may include a previously unrecognised small pleurosternid as well as *Pleurosternon*. Finally, Barrett *et al.* (2002) have shown that the enigmatic sculptured ‘granicones’ found on several slabs of Purbeck limestone, particularly from the Beckles Pit, are actually the dermal scales of a turtle, redescribed in the following work as *Helochelydra anglica*.

Remains of turtle shells are among the most frequent vertebrate fossils encountered in the Purbeck Limestone, but first-hand study of them has languished for over a century. The aim of this work is to review the Purbeck turtles with the following objectives: to recheck all associations of specimens to determine the number of definable generic and specific-level taxa present; to place those taxa in a contemporary systematic framework; to provide a simple practical guide to complete and partial carapaces and plastra from the Purbeck Limestone Formation. I have undertaken limited comparative taxonomy with Kimmeridgian material from Solothurn (Rütimeyer 1873; Bräm 1965) and Wealden turtle material (Lydekker 1889*b* and first-hand study). A larger scale comparison of European Jurassic–Cretaceous turtle shells is a necessary exercise in the long term but beyond the scope of this paper. The terminology for the bones and scutes of the carapace and plastron follows that proposed by Zangerl (1969).

Institutional abbreviations and note. BGS, British Geological Survey, Keyworth; BMB, Booth Museum of Natural History, Brighton; BMNH and BMNH R, Department of Palaeontology, The Natural History Museum, London [formerly British Museum (Natural History)]; CAMSM, Sedgwick Museum, Department of Geology, University of Cambridge; DORCM, Dorset County Museum, Dorchester; GLAHM, Hunterian Museum, University of Glasgow; MANCH, Manchester Museum; NMW, Naturhistorisches Museum, Vienna; OUM, Oxford University Museum; UMZC, University Museum of Zoology, University of Cambridge; YPM-PU, Peabody Museum, Yale University, Connecticut (ex Princeton University Collection).

The large collection originally held by the Corfe Castle Museum was transferred to Dorset County Museum in 1894 where the turtle material received DORCM register numbers in the G31–G74 series, some cited by Delair (1958). In 1958, much of the non-type material at Dorchester (including Corfe Castle, Shipp and Cunnington collections) was transferred to The Natural History Museum, London, where it was recatalogued within the serial block BMNH R6862 – BMNH R6921. Where appropriate, BMNH register numbers are given with previous DORCM numbers in parenthesis.

STRATIGRAPHICAL NOTE

Most of the material reviewed in this work was collected in the nineteenth century, and locality and horizon data are imprecise. Many specimens are localised merely as from the ‘Middle Purbeck’ of either Swanage or Langton Matravers. There is potential for using ostracodes to determine the horizons of individual specimens more precisely, but this represents a future focused study. The following observations summarise our present limited knowledge of turtle distribution through the Purbeck succession. Bed names correspond to those used by Clements (1993) and the DB-numbering is that used by Clements for the type section in Durlston Bay. Turtles are found in the Mammal Bed (DB 83) at the base of the Middle Purbeck Beds (near top of Lulworth Formation) up to the Crocodile Bed (DB 221) above the base of the Upper Purbeck Beds (in Upper Durlston Formation), and parallel the distribution of crocodiles in this respect (Salisbury 2002).

Mammal Bed (DB 83). A carbonaceous calcareous shale and clay (Clements 1993) believed to be the principal productive horizon in the ‘Mammal Pit’ (also known as the ‘Beckles Pit’) excavated by Samuel Beckles on the hillside near the ‘Zig-Zag Path’ in Durlston Bay. Salisbury (2002) discussed this horizon and its possible relationship to Beckles’ Residuary Marls as described by Owen. These marls may have derived from one or more of several beds between DB 83 and DB108. Most of the small *Pleurosternon*

material and the smaller *Helochelydra* specimens appear to have originated from either the ‘Mammal Pit’ or the residuary marls along with the lizards, mammals and small crocodiles but, as noted by Salisbury (2002), the precise horizon of any given specimen is not self-evident and requires further investigation.

Cinder Member (DB 111). This is a shell bank set in a matrix of light grey calcareous mudstone and muddy micrite in the lower part of the Middle Purbeck Beds (Clements 1993). A right hypoplastron of *Pleurosternon bullockii* was collected from this horizon by Henry Willett and is now in the collection of the Booth Museum, Brighton.

Intermarine Member (DB 112–145). The Intermarine Member or Upper Building Stones is an extensive complex of limestones and shales including several hard and massive limestones in the middle of the Middle Purbeck Beds. These limestones, the ‘Building Stones’, were quarried extensively in the nineteenth century in a series of quarries between Swanage and Worth Matravers. The majority of large *Pleurosternon*, ‘*Glyptops*’ and *Hylaeochelys* specimens were collected then from these quarries, were attributed to the Middle Purbeck Beds, and are in blocks of hard and massive limestones. The range of matrices and colours of the preserved bone suggest that more than one productive horizon was the source of this material, but there is no precise documentation with any of the type or figured specimens. Again, further investigation will be required to ascertain if it is possible to place these specimens more precisely within the Middle Purbeck Beds.

Crocodile Bed (DB221). Described by Clements (1993) as a richly fossiliferous complex of rough limestones, clays and shales within the Unio Member of the Upper Purbeck Beds. The Crocodile Bed *sensu stricto* is a light grey biosparite at the top of DB 221 and there are calcareous clays and shales below it. Clements (1993, fig. 2) recorded turtle material in this horizon. In 1978, Dr A. C. Milner and I collected *Pleurosternon* shell elements from both the Crocodile Bed and the underlying clays at Peveril Point at the north end of Durlston Bay.

OWEN’S LOST TYPES AND THE PROBLEM OF *TRETOSTERNON*

Owen (1842) initially described three Purbeck turtle taxa (*Platemys bullockii*, *Chelone obovata* and *Tretosternon punctatum*) from four specimens (*T. punctatum* had two syntypes). All were in private collections, none was figured or identified with a catalogue number, but they were described in some detail. Of these four specimens, the holotype of *Pleurosternon* (‘*Platemys*’) *bullockii* survives with a continuous history of recognition and presents no taxonomic problems. The other three types were not referred to subsequently by Owen and were stated by Lydekker (1889*b*) to be lost, a conclusion followed by all later workers. I have relocated one (the Bowerbank specimen of ‘*T. punctatum*’) as described below. Consideration of all of Owen’s ‘lost types’ will form a later study.

‘*Chelone*’ *obovata* has not been used as a binomen since Owen’s time and can be treated as a *nomen dubium* without creating any taxonomic complications. It will only raise such complications if the holotype is rediscovered and proves it to be a senior species to one of the taxa other than *P. bullockii*.

Tretosternon punctatum with two lost syntypes, is much more problematic for several reasons. Firstly, Owen created the genus with two Purbeck specimens forming the type species *punctatum* and then referred Mantell’s senior Wealden *bakewelli* material to this genus, despite the fact that the descriptions show few points of resemblance. Secondly, Lydekker (1889*b*), having noted the loss of the two syntypes, proceeded to refer several other *bakewelli*-like Purbeck specimens to *T. punctatum* and these have acted as surrogates for the types subsequently, although they do not match Owen’s description. Thus, there is a Purbeck–Wealden turtle with characteristic pustulate ornament on the carapace, generally called *Tretosternon*, with a Purbeck species *punctatum* and a Wealden species *bakewelli*, with the names *Tretosternon* and *punctatum* based on unfigured, supposedly lost types, which lack the generally accepted characters of the genus. Careful reading of Owen’s description (Owen 1842, p. 165) of the dermal pitting and striations on the first (Egerton collection) syntype indicates that it might be a partial carapace of *Pleurosternon bullockii* but is certainly not like Mantell’s *bakewelli*.

The relocated second (Bowerbank Collection) syntype is BMNH 39457 (Text-figs 1–2) which is actually a half plastron of *Hylaeochelys laticutata*. It was catalogued by Lydekker (1889*b*, p. 194) as a specimen of *Hylaeochelys belli* and it is clear that Lydekker was unaware of its original systematic status. It can be recognised as one of Owen's syntypes on the following basis:

1. Much of the Bowerbank Collection was purchased by auction by the British Museum (Natural History) in 1865 (Cleevely 1983), and therefore Owen's Bowerbank syntype could be expected to be in that collection.
2. BMNH 39457 is the only Purbeck turtle specimen recorded as from the Bowerbank Collection.
3. Like Owen's syntype, BMNH 39457 is an almost complete left plastron in ventral aspect with a damaged posterior xiphiplastron, and a small semicircular half-fontanelle on the midline.
4. BMNH 39457 is dimensionally identical to Owen's syntype.
5. The sutures and scute margins described by Owen can all be matched on the specimen including a non-standard undulation at the distal edge of the suture between the hypoplastron and xiphiplastron.

The conclusion that one of the syntypes of *Tretosternon punctatum* is actually a specimen of *Hylaeochelys laticutata* is potentially highly destabilising for both genus and species. Because the Bowerbank specimen was the second syntype described, I propose that the Egerton specimen (which has page priority) becomes the lectotype for *Tretosternon punctatum* leaving the taxon as a *nomen dubium*, while the Bowerbank specimen loses its type status and is simply transferred to the hypodigm of *Hylaeochelys laticutata*. That is followed here. Given that the name *Tretosternon* is senior to *Pleurosternon* and *Hylaeochelys*, it may be least confusing to have it suppressed rather than have it become the senior name for a taxon with which it has never been associated. In the meantime it seems safest to continue to treat *T. punctatum* as a *nomen dubium* with a lost lectotype. The replacement generic name for this material has been determined by De Lapparent de Broin and Murelaga (1999) who showed that the next published synonym that unequivocally applies here is *Helochelydra* Nopcsa (1928), created for an Isle of Wight Wealden '*Tretosternon*' specimen. An unfortunate feature of Nopcsa's paper was that he created the new genus *Helochelydra* without naming a species to fall within it. This is now unacceptable taxonomic practice, but can be valid for genera named before 1931 [Article 69 of the ICZN code (International Commission on Zoological Nomenclature 1999)]. De Lapparent de Broin and Murelaga (1999) created the species name *nopcsai* for Nopcsa's *Helochelydra* material, and proposed that this generic name replace *Tretosternon* for some of the British material with pustulate shells.

SYSTEMATIC PALAEOLOGY

Order TESTUDINES Linnaeus, 1758

Infraorder CRYPTODIRA Cope, 1868

Capaxorder SELMACRYPTODIRA Gaffney, Hutchinson, Jenkins and Meeker, 1987

Hyperorder PLEUROSTERNOIDEA Hay, 1930 (p. 69 as -oidae)

Family PLEUROSTERNIDAE Cope, 1868

[= GLYPTOPIDAE Marsh, 1890 (as -OPSIDAE)]

Included genera. *Pleurosternon* (= *Mesochelys*), *Glyptops*, *Compsemys*, *Dinochelys*, *Desmemys*.

Diagnosis (after Gaffney and Meylan 1988). Primitive cryptodires sharing one synapomorphy, namely pterygoids separated by anteriorly elongate basisphenoid.

Genus PLEUROSTERNON Owen, 1853

[= DIGERRHUM Cope, 1870, PLEUROSTERNUM Lydekker, 1889*b*,

MESOCHELYS Evans and Kemp, 1975]

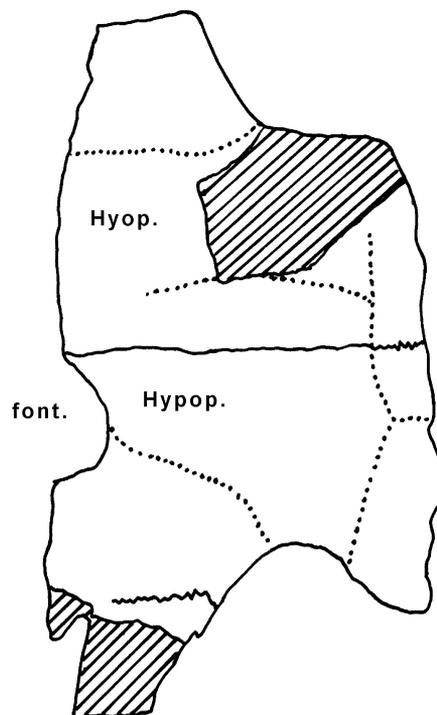
Type species. *Platemys bullockii* Owen, 1842.



TEXT-FIG. 1. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH 39457, left plastron in ventral aspect. The small plastral fontanelle is represented by the semicircular indentation on the midline sutural line, two-thirds of the way along the length of the specimen. Specimen originally in the Bowerbank Collection and one of the syntypes of '*Tretosternon punctatum*' Owen 1842; $\times 0.5$.

Diagnosis. Carapace extremely depressed, oval in shape with almost no nuchal emargination in the adult (more pronounced in juveniles). Posterolateral peripheral bones normally not emarginated (emargination in a few specimens may represent healed damage). Eight neurals and two suprapygals, the first suprapygals a slightly elongate rectangle, expanded posteriorly. Neural 8 and suprapygals 1 occasionally replaced by a single element. Pygal indented posteriorly. Costal 1 is an irregular rhomboid, slightly less than twice as long as wide. Outer costal outline oval, roughly matching carapace outline. Costals 6–7 show slight curvature in posterolateral direction. Mesoplastrals present, extending to midline. Xiphiplastrals with a

TEXT-FIG. 2. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH 39457, left plastron in ventral aspect. Explanatory figure for Text-fig. 1. Sutures indicated as solid lines, scute boundaries as dotted lines, damage as diagonal shading. Abbreviations: font., Fontanelle; other abbreviations as in Text-figure 6.



broad V-shaped notch posteriorly. No cervical scute visible dorsally, first marginal scutes meeting in the midline along the anterior half of the nuchal bone. Vertebral scutes about one-third width of carapace with vertebral 1 almost as large as vertebral 2. Pleural scutes barely overlapping peripheral bones with only slight overlap anterolaterally. Carapace and plastron outer surfaces smooth and shiny, mostly covered in regular, clearly defined pitting, with plate margins bearing fine linear striations perpendicular to the margins. Growing to carapace length of 0.56 m (CAMSM J5328).

Pleurosternon bullockii (Owen) Lydekker and Boulenger, 1887

Text-figs 3–4, 5A, 6, 7A

- 1842 *Platemys bullockii* Owen, p. 164.
- 1850 *Platemys bullockii* Owen, p. 62, pl. 21.
- 1853 *Pleurosternon concinnum* Owen, p. 3, pls 2–3.
- 1853 *Pleurosternon emarginatum* Owen, p. 6, *partim* pls 5–6 (*non* pl. 4).
- 1853 *Pleurosternon ovatum* Owen, p. 8, pl. 7.
- 1869 *Pleurosternon sedgwicki* Seeley, p. 86.
- 1869 *Pleurosternon vansittarti* Seeley, p. 86.
- 1869 *Pleurosternon oweni* Seeley, p. 87.
- 1869 *Platemys concinna* (Owen) Maack, p. 288.
- 1869 *Platemys ovata* (Owen) Maack, p. 293.
- 1870 *Digerrhum bullocki* (Owen) Cope, p. 156.
- 1887 *Pleurosternon bullocki* (Owen); Lydekker and Boulenger, p. 272.
- 1889a *Pleurosternon bullocki* (Owen); Lydekker, p. 516, figs 3–4.
- 1889b *Pleurosternum bullocki* (Owen); Lydekker, p. 206, figs 45–46.
- 1910a *Glyptops ruetimeyeri* (Lydekker); Watson, *partim* fig. 1, (*non* Lydekker 1889b).
- 1958 *Pleurosternum bullocki* (Owen); Delair, p. 48.



TEXT-FIG. 3. *Pleurosternon bullockii* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH R911, the holotype plastron in ventral aspect; $\times 0.25$.

- 1958 *Hylaeochelys* sp. Delair, p. 53 (*non* Lydekker 1889*b*).
- 1966 *Pleurosternon bullocki* (Owen); Delair, p. 60.
- 1975 *Mesochelys durlstonensis* Evans and Kemp, p. 26, pls 4–5, text-figs 1–9.
- 1979 *Mesochelys durlstonensis* (Evans and Kemp); Gaffney, figs 26*B*, 27*B*, 28*B*.
- 1988 *Pleurosternon* (Owen); Gaffney and Meylan, p. 173.
- 1999 *Pleurosternon bullockii* (Owen); de Lapparent de Broin and Murelaga, p. 189.

Holotype. BMNH R911, a large complete plastron (Text-fig. 3), previously figured by Owen (1850, pl. 21).

Locality and horizon. Purbeck, Dorset; Purbeck Limestone Group. The type specimen was originally erroneously described by Owen (1842, 1850) as from the London Clay of Sheppey. It was correctly localised by Lydekker and Boulenger (1887) but there are no precise locality details. Most other specimens are simply localised to ‘Swanage’ but some are identified as having been collected from Durlston Bay, Langton Matravers and Herston.

Diagnosis. Species of *Pleurosternon* in which entoplastron is wider than long, and intergular shield is shield-shaped with five straight edges (contra the Portlandian *P. portlandicum* in which entoplastron width equals length and intergular shield is pyriform and narrow posteriorly).

Referred large Purbeck material with taxonomic or figured status. BMNH 28433, plastron figured by Lydekker (1889*b*, fig. 46); BMNH 28618 (Text-fig. 5A), holotype carapace of *P. ovatum* figured Owen (1853, pl. 7); BMNH 46317, syntype carapace and plastron of *P. emarginatum* figured Owen (1853, pls 5–6); BMNH R1524, plastron figured Lydekker (1889*a*, fig. 4); BMNH R3413, a complete carapace (Text-fig. 4); CAMSM J5326 (Seeley No. 1), holotype carapace of *P. sedgwicki*; CAMSM J5327 (Seeley No. 2), holotype carapace of *P. vansittarti*; CAMSM J5328 (Seeley No. 3), holotype carapace of *P. oweni*; [Note that CAMSM J5329 (Seeley No. 4), the holotype carapace of *P. typocardium* Seeley has been removed from this synonymy and forms the type of ‘*Glyptops*’ *typocardium* q.v.]; DORCM G.17, holotype juvenile carapace and plastron of *P. concinnum* figured Owen (1853, pls 2–3); MANCH L9520, carapace with marginals and plastron from the Middle Purbeck Cap/Feather Bed in a quarry two miles (1.3 km) west of Swanage, figured by Watson (1910*a*, fig. 2) as *Glyptops ruetimeyeri*; UMZC T1041, the holotype of *Mesochelys durlstonensis*, a skull and partial postcranial skeleton collected by Mr John Evans and described and figured by Evans and Kemp (1975).

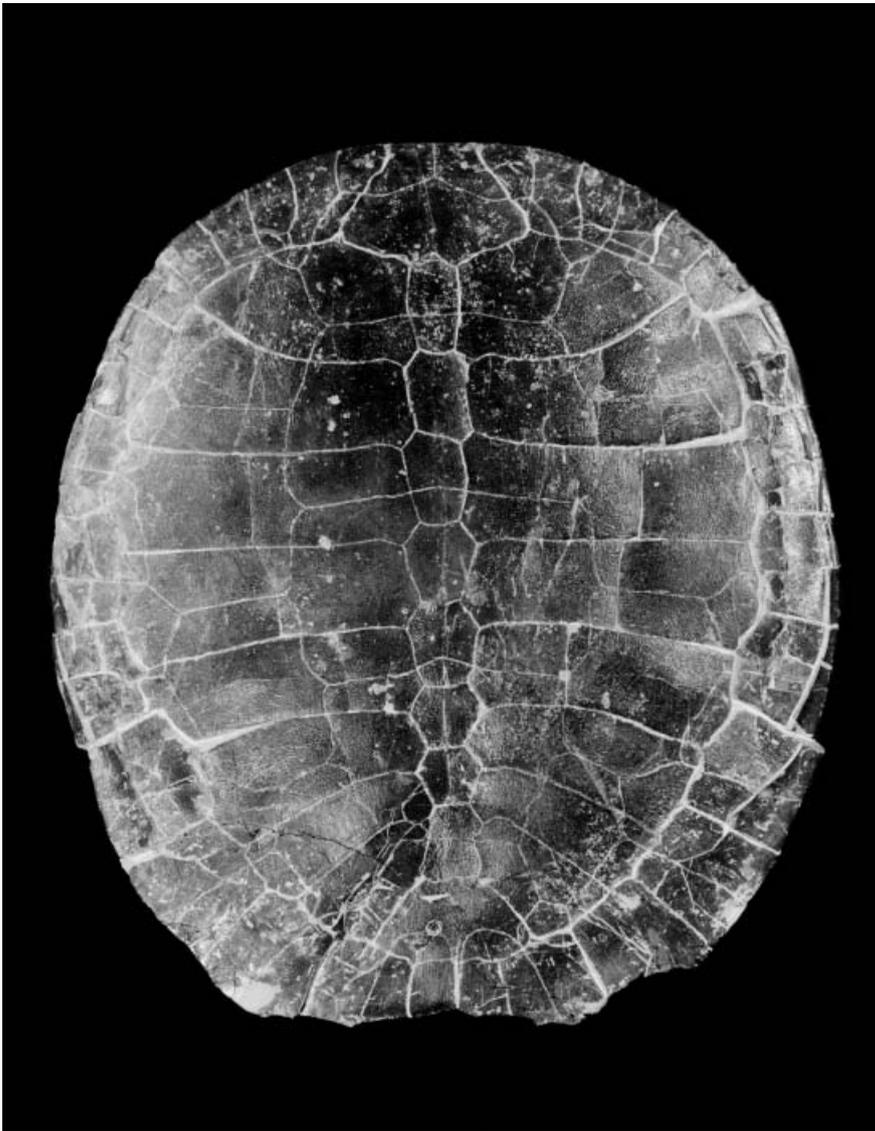
Other referred large material. Lydekker (1889*b*, pp. 206–215) listed a further 40 specimens of this taxon, many from the Cunnington, Willcox and Beckles’ collections. Significant specimens currently in the BMNH collection include the following carapaces: BMNH 21351, 24298 (internal), 35574, 38733, 43621, R1891, R5486; complete shells: BMNH R1889 and R3727; and several plastra: BMNH 35772, 40646, R4317. The following BMNH specimens were acquired in 1958 and are ex Dorset County Museum collection. The Dorset collection number is given after the BMNH number: R6868 (G64), R6869 (G45), R6876 (G46), R6879 (G41), R6880 (G59), R6883 (G31), R6887 (G37), R6888 (G65), R6891 (G32), R6895 (G33), R6896 (G34) [incorrectly mentioned by Delair 1958, p. 53 as a possible new species of *Hylaeochelys*], R6897 (G36), R6912 (G35), R6913 (G170). Material from other institutions includes BGS 58053, partial carapace; BGS 92123–6, a carapace; BMB 001790 a right hypoplastron from the Durlston Bay Cinder Bed (DB 111); BMB 001795–1797 [Willett Collection]; CAMSM J5330–5331; CAMSM J5333–5336; DORCM G15; DORCM G179; DORCM G6262 and one uncatalogued carapace; GLAHM V.914, scute noted by Delair (1966); MANCH L9521, L11346; OUM J13793, partial carapace lacking most marginals; OUM J13794 partial carapace (internal); OUM J13797 plastron (internal) [J. Parker Coll.]; YPM-PU 3363, large carapace; YPM-PU 3364, partial carapace lacking most marginals.

Referred small material of uncertain taxonomic status. The following specimens are all of small individuals (carapace length 150 mm or less) collected from the assemblage of small vertebrates in Beckles’ ‘Mammal Pit’. They are treated here as juveniles of *Pleurosternon bullockii*, but Lapparent de Broin and Murelaga (1999, p. 189) have suggested that some may represent a new genus of small pleurosternid, and future study by Lapparent de Broin may demonstrate this. The only figured specimen is BMNH 48262, carapace and plastron (Text-fig. 6) previously figured by Lydekker (1889*a*, fig. 3). Unfigured specimens include BMNH 48263, carapace; BMNH 48263*a*, *c*, *e*, three carapaces; BMNH 48264, interior of carapace; BMNH 48343–48344, plastra; BMNH 48347, partial plastron; BMNH 48353–48354, carapaces.

Remarks. Much of the above synonymy was established by Lydekker and Boulenger (1887) and Lydekker (1889*a*), and the content of *Pleurosternon bullockii* has remained relatively stable since then. Only a few significant assignments and removals merit further comment. Lydekker (1889*b*) implied that all four of Seeley’s (1869) *Pleurosternon* species belong here but one, *P. typocardium*, is assigned to another genus below, as noted by Watson (1910*b*).

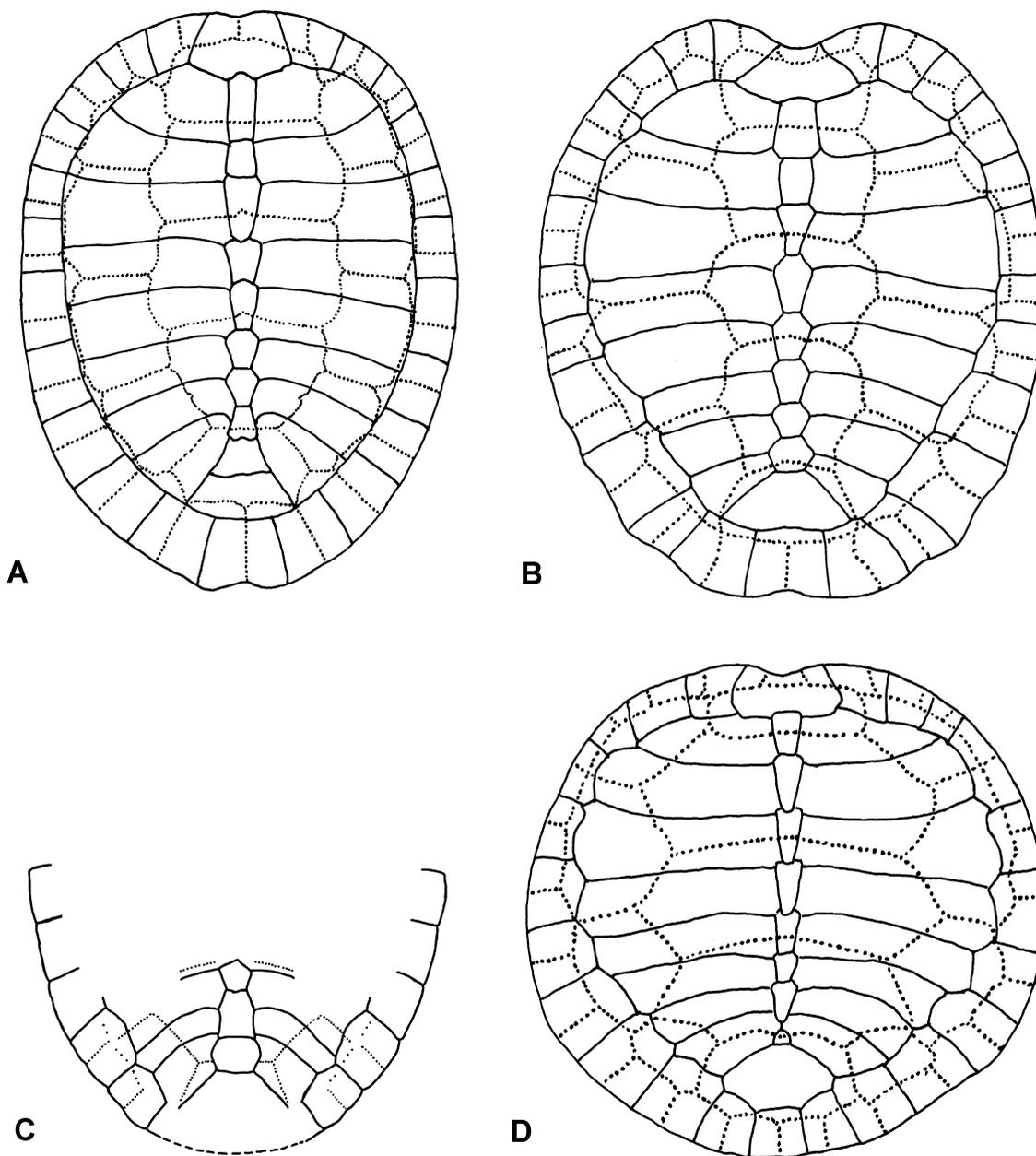
Watson (1910*a*) reported several small Purbeck shell specimens in the collections of Manchester Museum as *Glyptops ruetimeyeri*, but only two carapaces in that collection (MANCH L7017 and L11347) actually represent the same taxon as Lydekker’s type. MANCH L9520, the specimen figured by Watson (1910*a*, fig. 2) as the only plastron of *G. ruetimeyeri*, has the smooth shell surface with light even pitting and marginal parallel striations characteristic of *P. bullockii*. It is associated with a carapace with no significant nuchal emargination and with backwardly recurved costals 6 and 7, both features of *P. bullockii*. Its possession of a mesoplastron and a divided xiphoplastron simply confirms the presence these features in *P. bullockii*. The plastron of ‘*Glyptops*’ *typocardium* is unknown and these features may or may not be shared with that taxon.

The skull and associated postcranium, described as *Mesochelys durlstonensis* by Evans and Kemp



TEXT-FIG. 4. *Pleurosternon bullockii* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH R3413, a well-preserved carapace in dorsal aspect with sutures and scute margins inked in; $\times 0.25$.

(1975), was assigned here by Gaffney and Meylan (1988) and is now usually treated as a junior synonym of *P. bullockii*, although to my knowledge, the precise arguments for this association, which must be based solely on the associated carapace fragments, have not been set out fully. The carapace fragment illustrated by Evans and Kemp (1975, pl. 5, figs 1–2) comprises left costals 7 and 8, left peripheral 10, neural 8, and fragments of left costal 6 and suprapygal 2. All bear the characteristic smooth surface with even shallow pitting and marginal parallel striations. The only possible alternative assignment might be to '*Glyptops*' *typocardium*, but the '*Mesochelys*' carapace fragment has a backwardly curved costal 6 bearing scute grooves along its outer edge where supramarginal scute 4 meets marginal scutes 9 and 10. In '*Glyptops*' *typocardium*, costal 6 is straight and laterally directed and the scute margin grooves do not impinge on its



TEXT-FIG. 5. Reconstructions of carapaces of Purbeck turtles in dorsal aspect. A, *Pleurosternon bullockii* (BMNH 28618). B, '*Glyptops*' *typocardium* (composite from CAMSM J5329 and BMNH 40676). C, *Helochelydra anglica* (posterior carapace only, composite from BMNH 48357 and MANCH L9522). D, *Hylaeochelys laticutata* (OUM J.13796). Sutures indicated as solid lines, scute boundaries as dotted lines.

surface. Furthermore, the slot for the absent suprapygal 1 shows it to be a nearly rectangular rhomboid, longer than wide with some posterior widening as in *P. bullockii*. In '*Glyptops*' *typocardium*, suprapygal 1 is a very wide triangular structure. The plastron associated with '*Mesochelys*' bears the posteriorly divided xiphiplastron that typifies *Pleurosternon bullockii*, although, as noted above, the situation in '*Glyptops*'



TEXT-FIG. 6. Small pleurosternid specimen, BMNH 48262, a left carapace and right plastron in dorsal aspect; $\times 0.5$. This may be a juvenile of *Pleurosternon bullockii* or represent a new genus of small pleurosternid (Lapparent de Broin and Murelaga 1999).

typocardium is unknown. The emarginate peripheral element in '*Mesochelys*' is probably not significant as occasional emarginate posterior peripherals are found in most taxa and appear to be healed injuries. In conclusion, the fragments of shell associated with the '*Mesochelys*' skull are consistent only with attribution to *Pleurosternon* and this synonymy seems robust.

A large number of small *Pleurosternon* specimens were collected from the Beckles Pit. Most have not been described or figured although Lydekker (1889a, fig. 3) figured one individual and listed many of the others (Lydekker 1889b) as juveniles of *Pleurosternon bullockii*. This attribution is followed here, but it should be noted that De Lapparent de Broin and Murelaga (1999, p. 189) have suggested that some of this material represents a new genus of small pleurosternid. Until a full ontogenetic sequence of *Pleurosternon* shells can be established from Purbeck material, it remains to be demonstrated whether the characteristics of these small forms represent taxonomically significant features or part of the normal ontogeny of *Pleurosternon*.

Genus GLYPTOPS Marsh, 1890

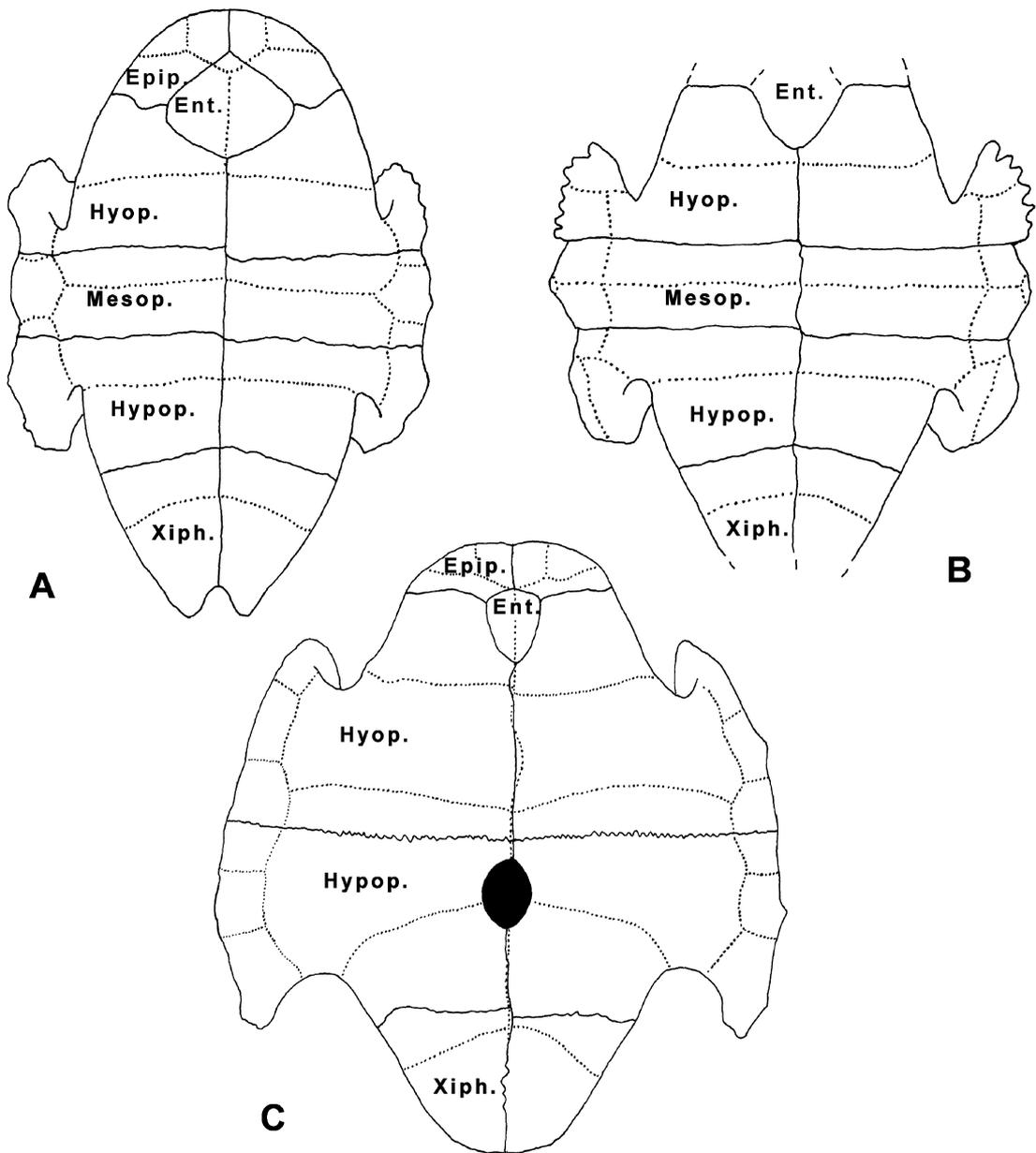
Type species. *Compsemys plicatulus* Cope, 1877, from the Morrison Formation, Colorado.

Taxonomic note. The genus *Glyptops* only certainly applies to *G. plicatulus* from the Morrison Formation and is critically diagnosed on cranial features. The following Purbeck material has been regularly treated as a glyptopid and was referred to *Glyptops* by Watson (1910a). In the absence of a skull, it is here retained as '*Glyptops*' and not assigned to a new genus. If the skull of *Dorsetochelys* proved to belong with this material, that would become the senior generic name, but the skull of *Dorsetochelys* is not that of a *Glyptops*-like form and the resulting taxon would then have to be removed from the Pleurosternidae (= Glyptopidae).

'*Glyptops*' *typocardium* (Seeley) comb. nov.

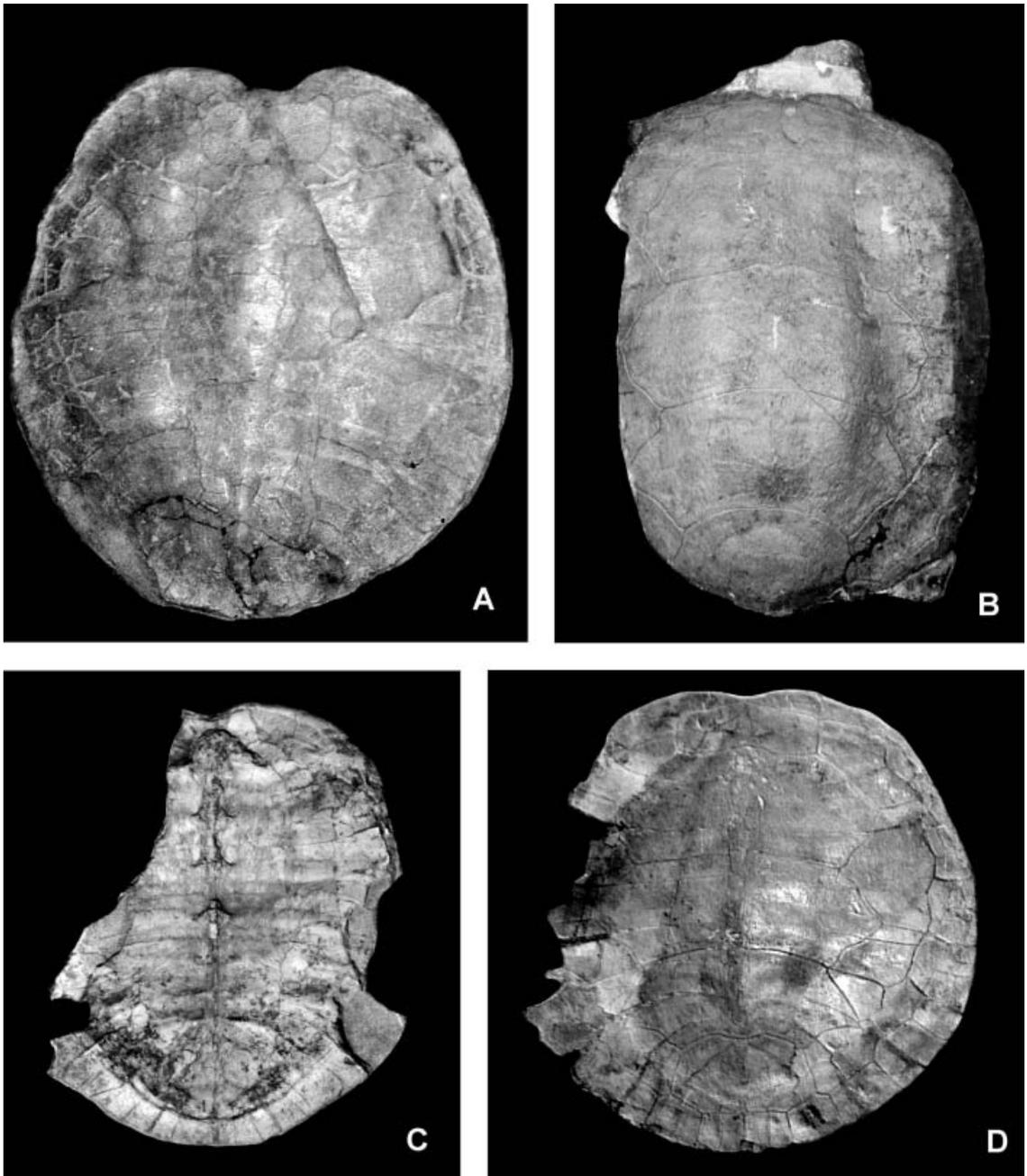
Text-figs 5B, 8A, 9

- 1869 *Pleurosternon typocardium* Seeley, p. 87.
- 1887 *Eurysternum* sp. Lydekker and Boulenger, p. 274.
- 1889b *Thalassemys ruetimeyeri* Lydekker, p. 149, fig. 36.
- 1910a *Glyptops ruetimeyeri* (Lydekker); Watson, p. 311, figs 1–2.



TEXT-FIG. 7. Reconstructions of plastra of Purbeck turtles in ventral aspect. A, *Pleurosternon bullockii* (BMNH R911). B, *Helocheyledra anglica* (hyoplastron from BMNH 46325, posterior plastron from MANCH L9522). C, *Hylaeochelys latiscutata* (NMW unnumbered specimen). Sutures indicated as solid lines, scute boundaries as dotted lines. Abbreviations: Ent., Entoplastron; Epip., Epiplastron; Hyop., Hyoplastron; Hypop., Hypoplastron; Mesop., Mesoplastron; Xiph., Xiphiplastron.

- 1910b *Glyptops ruetimeyeri* (Lydekker); Watson, p. 381.
 1958 *Glyptops ruetimeyeri* (sic) (Lydekker); Delair, p. 51.
 1979 '*Glyptops*' *ruetimeyeri* (Lydekker); Gaffney, p. 108.
 1999 '*Thalassemys*' *ruetimeyeri* (Lydekker); De Lapparent de Broin and Murelaga, p. 192.



TEXT-FIG. 8. Purbeck turtle carapaces. A. '*Glyptops*' *typocardium* (Seeley) comb. nov., Purbeck Limestone Group, near Swanage, precise locality unknown. CAMSM J5329 (Seeley No. 4), the holotype of '*Pleurosternon*' *typocardium* Seeley, 1869 in dorsal aspect; $\times 0.27$. B. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. DORCM G.20, the holotype in dorsal aspect; $\times 0.21$. C. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. DORCM G.16 the holotype of *Hylaeochelys emarginata* in ventral aspect; $\times 0.18$. D. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. OUM J.13796, holotype of *Hylaeochelys sollasi* Nopcsa 1928, in dorsal aspect; $\times 0.125$.

Holotype. CAMSM J5329 (Seeley No. 4) (Text-fig. 8A), holotype of *P. typocardium*, a complete carapace in dorsal aspect, mentioned as a glyptopid by Watson (1910b).

Locality and horizon. Purbeck, Purbeck Limestone Group.

Diagnosis. Carapace depressed with a midline ‘hump’, basically oval in shape but with very pronounced nuchal emargination, the nuchal element itself being highly concave. Posterolateral peripheral bones normally not emarginated (emargination in one specimen may represent healed damage). Eight neurals and two suprapygals, the first suprapygals a wide rhomboid, twice as wide as long and with posterior width over twice the anterior width. Costal 1 is an irregular rhomboid, slightly less than twice as long as wide. Outer costal outline heart-shaped, narrowing posteriorly in contrast to oval carapace outline. Small rectangular cervical scute separates first marginal scutes over anterior half of nuchal bone. Vertebral scutes about one-quarter width of carapace with vertebral 1 almost as large as vertebral 2. Pleural scutes overlapping peripheral bones and covering about a quarter of their area. Carapace outer surface is smooth and mostly covered in poorly defined or coarse pitting. Growing to at least an estimated carapace length of 0.3 m (BMNH 40676 and CAMSM J5329).

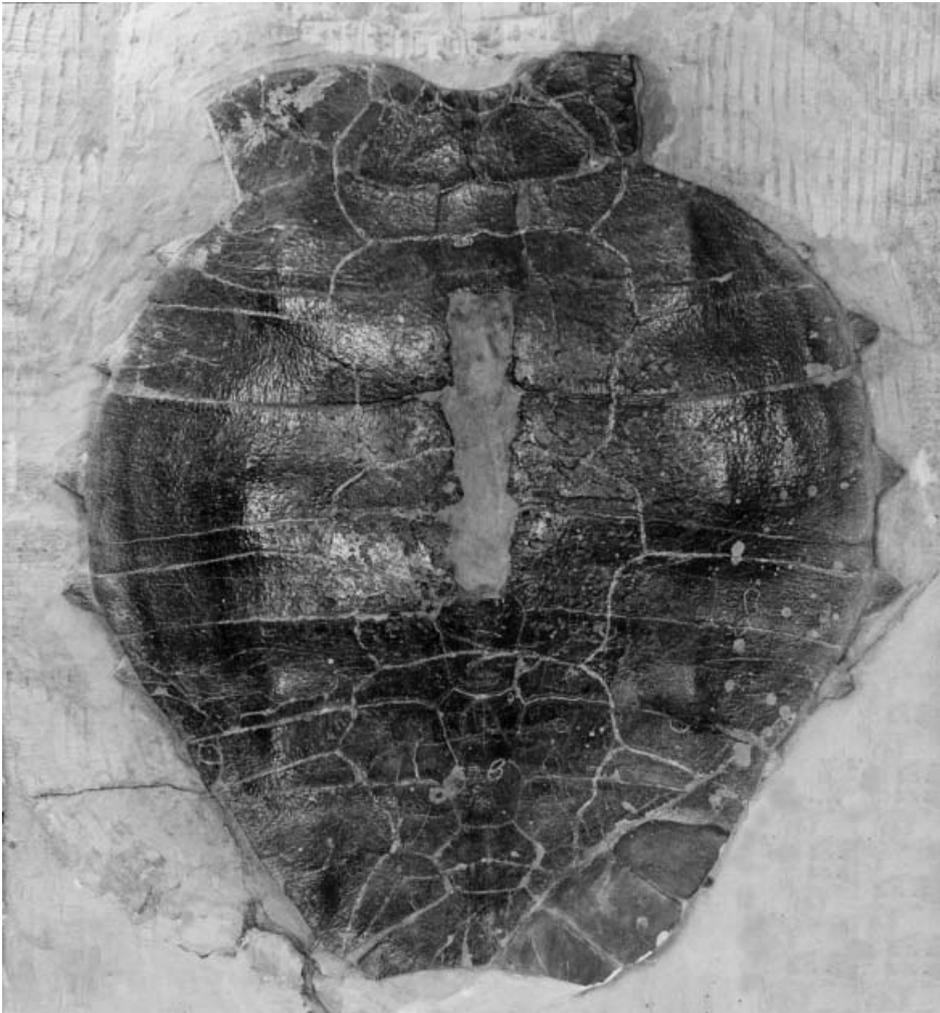
Referred material. BMNH 40676, the holotype of ‘*Glyptops*’ *ruetimeyeri* (Text-fig. 9) a carapace in dorsal aspect lacking most marginals, figured by Lydekker (1889b, fig. 36); BMNH R1522, large highly emarginate nuchal in ventral aspect listed by Lydekker (1889b, p. 189) as a specimen of *Hylaeochelys emarginata*; MANCH L7017, carapace lacking marginals from the Middle Purbeck Cap/Feather Bed at Swanage, figured by Watson (1910a, fig. 1); MANCH L11347, a fragment of a small carapace.

Remarks. This taxon comprises the most novel combination of previously named taxa in this work and deserves more explanation. The core material in the previous literature was BMNH 40676, Lydekker’s *ruetimeyeri* holotype carapace, and MANCH L7017, one of the Manchester Museum carapaces referred here by Watson (1910a). Because of the double use of the catalogue number BMNH 40676 in Lydekker 1889b (p. 149 for this specimen and p. 209 for a *Pleurosternon* carapace), this specimen was miscatalogued in the 1950s, and remained unrecognised, hidden under an incorrect label (see Text-fig. 9) in the wrong cupboard until I reidentified it in 1997. Gaffney (1979, p. 108) appears not to have examined either it or the Manchester material, and De Lapparent de Broin and Murelaga (1999, p. 192) also reported it missing. Watson’s principal Manchester specimen, MANCH L7017, is a smaller but otherwise very similar carapace.

These two specimens share the combination of moderate flattening, pronounced nuchal emargination, shiny dermal surface with poorly defined punctuations but no striations, squarish vertebral scutes, costals combining to have a heart-shaped outline (Text-figs 5B, 9); costal 3 expanded laterally, costal 6 straight and laterally directed; and suprapygals rhomboidal almost triangular and very wide posteriorly. Recognition of the association of these specimens and their characteristics led me to the same conclusion as Watson (1910b, p. 381), namely that the holotype of Seeley’s *Pleurosternon typocardium* had the same carapace characteristics. This carapace (Text-fig. 8A) has not previously been figured, but Seeley (1869) did name it, assign it a number (Specimen 4) and give a brief description that constitutes an indication under ICZN regulations. The species name is treated as valid and the resulting shell-taxon carries the senior species name *typocardium*.

Watson (1910a) referred a second Manchester Museum specimen, MANCH L7020, here, but that specimen is a small shell of *Pleurosternon bullockii* as discussed under that taxon. It retains a mesoplastron and has a notched xiphoplastron, and Watson attributed these characteristics to ‘*G. ruetimeyeri*’ on the basis of this specimen. These characteristics are those of *P. bullockii*, and the condition in *G. ruetimeyeri* is unknown, as no plastron is known that can be unambiguously referred here. MANCH L7017 is a partial posterior carapace that matches BMNH 40676 in the relationships of plates and scutes.

The dermal sculpture of ‘*Glyptops*’ *typocardium* is most similar to that of *P. bullockii* in that the basic shell surface is shiny but the pitting is coarser. Although complete carapaces are clearly distinct, the identity of fragmentary or poorly preserved specimens is not so easy to establish and there may be further specimens of this taxon in amongst the many poor specimens identified as *P. bullockii*.



TEXT-FIG. 9. '*Glyptops*' *typocardium* (Seeley) comb. nov., Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH 40676, the holotype of '*Thalassemys*' *ruetimeyeri* Lydekker, 1889*b* in dorsal aspect; $\times 0.63$.

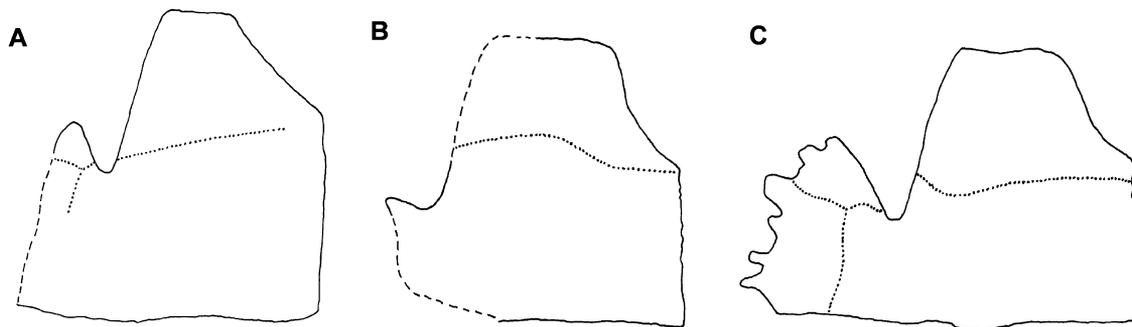
Family SOLEMYDIDAE de Lapparent de Broin and Murelaga, 1996

Included genera (after de Lapparent de Broin and Murelaga 1999). *Solemys*, *Naomichelys*, *Helochelydra*.

Genus HELOCHELYDRA Nopcsa, 1928

Type species (designated by de Lapparent de Broin and Murelaga 1999). *Helochelydra nopcsai* de Lapparent de Broin and Murelaga, 1999 (see notes below).

Diagnosis (after de Lapparent de Broin and Murelaga 1999). Solemydid with shell decorated completely with separate raised tubercles, thin pustules about 1 mm in diameter forming vermiculate ridges towards the medial parts of the pleurals, entoplastral scute possibly oval/rounded and situated towards the anterior of the entoplastron.



TEXT-FIG. 10. Hyoplastra of *Helochelydra* species in ventral aspect. A, *H. nopcsai*, based on hyoplastra of BMNH R171 from the Wealden of the Isle of Wight. B, *H. bakewelli*, composite based on hyoplastra BMNH 2276 from the Wealden of Cuckfield and BMNH R658 from the Wealden of Battle. C, *H. anglica*, based on BMNH 46325, a right hyoplastron from Purbeck. Sutures indicated as solid lines, scute boundaries as dotted lines.

Other features relevant to recognition of material at Purbeck include: posterior neurals bearing distinct midline ridge and weaker parallel ridges, posterior costals bearing radiating ridge system underlying the pustular decoration, xiphiplastrals lack midline posterior notch, mesoplastrals retained.

Helochelydra nopcsai de Lapparent de Broin and Murelaga, 1999

Text-figure 10A

Diagnosis. Species of *Heleochelydra* in which the hyoplastron has the following characters (see Text-fig. 10A): ventral surface covered with prominent raised discrete tubercles; border with entoplastron is straight, suture with epiplastron is angled with its distal end anterior to its medial end; suture with entoplastron occupies half of width of anterior ramus of hyoplastron; medial border between humeral and pectoral scutes not visible.

Helochelydra bakewelli (Mantell) comb. nov.

Text-figure 10B

Synonymy of type and other Wealden material.

- 1827 unnamed specimen, Mantell, p. 60, pl. 6, figs 1, 3.
- 1833 *Trionyx bakewelli* Mantell, p. 255, unnumbered figure.
- 1842 *Tretosternon bakewelli* (Mantell) Owen, p. 167.
- 1851 *Tretosternon bakewelli* (Mantell); Mantell, p. 157, pl. 34.
- 1888 *Tretosternon punctatum* (Owen); Mansell-Pleydell, p. 5, *non* Owen.
- 1889b *Tretosternum bakewelli* (Mantell); Lydekker, pp. 138–140.
- 1889b *Tretosternum punctatum* Owen, Lydekker, p. 141, *non* Owen.
- 1958 *Tretosternum bakewelli* (Mantell), Delair, p. 50.

Holotype. BMNH 2265 a costal bone in dorsal aspect from the Wealden of Cuckfield, originally in the Mantell collection.

Diagnosis. Species of *Helochelydra* in which the hyoplastron has the following characters: ventral surface covered with low tubercles tending to coalesce into groups of 2–3; border with entoplastron is concave, suture with epiplastron is perpendicular to antero-posterior axis; suture with entoplastron occupies one-third of width of anterior ramus of hyoplastron; border between humeral and pectoral scutes gently curves

posteromedially to midline and touches posterior end of entoplastron. Most of the above characteristics distinguish it from *H. nopcsai*, but the coalescing tubercles and the margin between the humeral and pectoral scutes also distinguish it from *H. anglica* from Purbeck.

Remarks. The above diagnosis is based on two hyoplastra from the Lower Wealden of Sussex, namely BMNH 2276, a right element from Cuckfield (also figured by Lydekker 1889*b*, fig. 33), and BMNH R658, an incomplete left element from Battle. The composite reconstruction in Text-figure 11B is based on these two specimens.

Referred Purbeck material. *H. bakewelli sensu stricto* (as *Tretosternon*) was not reported from Purbeck until Delair (1958, p. 50) noted 'additional and more perfect specimens' from Durlston Bay, but did not elaborate on their institutional location. None of the specimens transferred from Dorset County Museum to the Natural History Museum belongs here or is recorded as ever having been identified as such. The only Purbeck specimens that I have seen that were labelled as '*Tretosternon bakewelli*' are two carapaces remaining at Dorset County Museum [DORCM G6262 (ex Corfe Castle collection) and uncatalogued] and these may have formed the basis of Delair's observation. They are in fact both carapaces of *Pleurosternon bullockii* with prominent pitting on the dermal surface.

Helochelydra anglica (Lydekker) comb. nov.

Text-figures 5c, 7b, 8c, 11

- 1887 *Tretosternum punctatum* Owen; Lydekker and Boulenger, p. 273, *non* Owen.
- 1888 *Tretosternum punctatum* Owen; Mansell-Pleydell, p. 5, *non* Owen.
- 1889*b* *Tretosternum punctatum* (Owen); Lydekker, p. 141, *non* Owen.
- 1889*b* *Platychelys*(?) *anglica* Lydekker, p. 217, fig 49.
- 1958 *Tretosternum punctatum* (Owen); Delair, p. 50, *non* Owen.
- 1958 *Tretosternum bakewelli* (Mantell); Delair, p. 50.
- 1958 *Platychelys*(?) *anglica* Lydekker; Delair, p. 50.
- 1999 Undefined form, De Lapparent de Broin and Murelaga, p. 190.

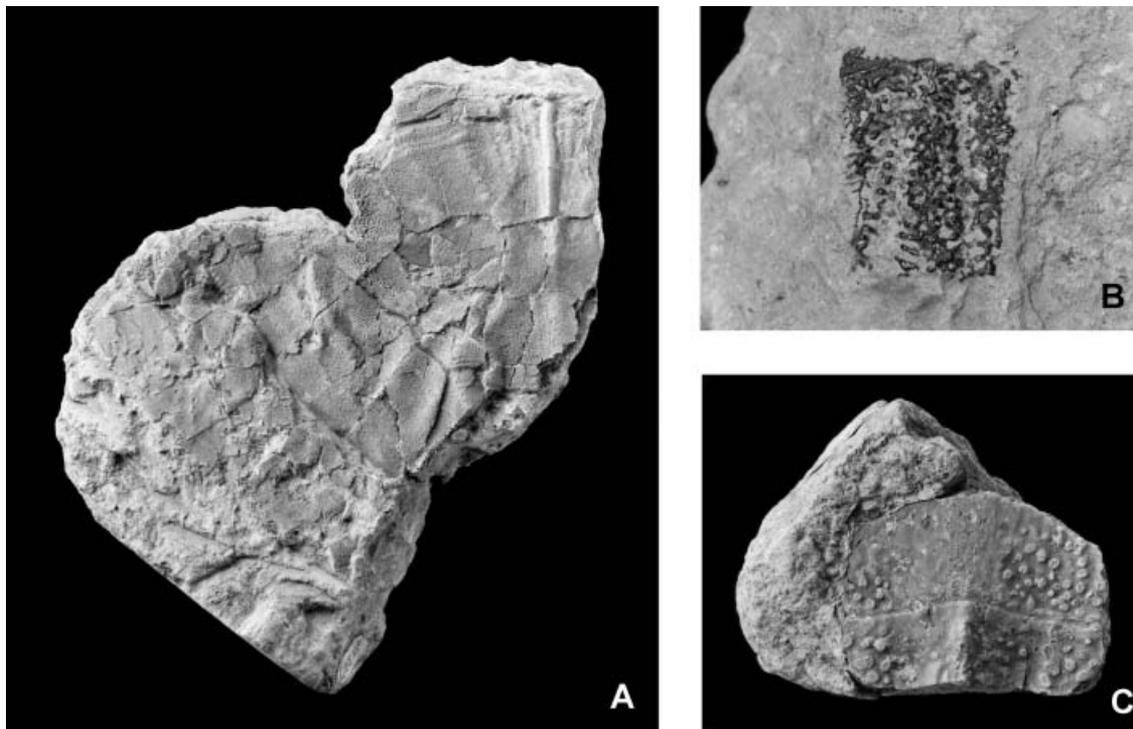
Holotype. BMNH 48357, the holotype of *Platychelys*(?) *anglica* (Text-fig. 11A), a partial posterior carapace from the Beckles Collection figured by Lydekker (1889*b*, fig. 49).

Locality and horizon. Purbeck; Purbeck Limestone Group.

Diagnosis. Purbeck material growing to carapace length of 0.33 m. Species of *Helochelydra* in which the hyoplastron has the following characters: ventral surface covered with low discrete tubercles; border with entoplastron is concave, suture with epiplastron is perpendicular to antero-posterior axis; suture with entoplastron occupies one-third of width of anterior ramus of hyoplastron; medial border between humeral and pectoral scutes is perpendicular to midline and passes about 8 mm behind posterior end of entoplastron.

Referred material. BMNH 46325, partial plastron (Text-fig. 10c) originally in the Cunnington Collection from Swanage reported by Lydekker and Boulenger (1887, p. 273); BMNH 48349, fragmentary specimen from Durlston Bay mentioned by Lydekker and Boulenger (1887, p. 274); BMNH 48352, block number for assorted costal plates (Text-fig. 11B–C) from the Beckles Pit, Durlston Bay; MANCH L9522, partial posterior plastron and underside of carapace of a small specimen. Barrett *et al.* (2002) have demonstrated that the so-called 'granicones', found on several slabs from Purbeck, are sculptured dermal scales of *Helochelydra anglica*, on which basis, all granicone-bearing slabs recorded by Barrett *et al.* include material referable to this taxon. I have not incorporated these in the synonymy for this form, which is restricted to carapace- and plastron-based specimens.

Systematic remarks. '*Platychelys*(?) *anglica*' was described by Lydekker on the basis of a single crushed posterior carapace from the Beckles Pit (Text-fig. 11A). It belonged to a small individual, probably with a carapace length of about 0.2 m. and may well have been a juvenile, many juvenile *Pleurosternon* specimens being present in the Beckles Pit material. Lydekker described it as a primitive platychelyid with



TEXT-FIG. 11. *Helochelydra anglica* (Mantell) comb. nov., Purbeck Limestone Group, Swanage. A, BMNH 38457, posterior left carapace in dorsal aspect. Previously the holotype and only specimen of *Platycheilus(?) anglica* Lydekker, 1889b; $\times 0.7$. B–C, BMNH 38452, isolated neural plates showing pustulate ornament and midline ridge. B, anterior-middle neural, $\times 1.15$. C, neural 8 bearing scute edge groove; $\times 0.8$.

a ridge extending along the posterior neurals, low prominences on the posterior costals and posterior marginals not emarginated. Lydekker's figure of this specimen is almost a diagram of a very crushed specimen in which some sutures and cracks are difficult to distinguish. The surface is covered with fine vermiculate ornament and the possibility that this is a juvenile *Helochelydra* is one that has not previously been considered. Bräm (1965) redescribed the type *Platycheilus oberndorfi* material (making no mention of '*P.(?) anglica*') and comparison of this specimen with his account of the type species reveals very few similarities. The carapace of *P. oberndorfi* is deep and has radiating sculpture ridges on the bones corresponding to the shields, radiating ridges along the midline but no continuous midline ridge on the neurals, highly emarginate marginals, and no fine surface sculpture. The carapace of *P.(?) anglica* does not appear to have been significantly deep; there are radiating ridge patterns like those in *Platycheilus*, the only resemblance to it, a midline ridge on the neurals, broad non-emarginate marginals and vermiculate sculpture on the bones. It differs from *Platycheilus* in all but one feature and other identities must be considered. The neurals are not slender as in *Hylaeochelys* and the sculpturing precludes relationship to all but *Helochelydra*.

Comparisons are rendered difficult by the fact that there is no *Helochelydra* specimen with a good posterior carapace and the best fragmentary material belongs to carapaces of 0.5–0.6 m length whereas this specimen was at most 0.2 m in length. Isolated small *Helochelydra* elements have vermiculate sculpture like '*P.(?) anglica*'. Fragmentary carapaces from Purbeck such as BMNH 48349 show the marginals to have been non-emarginate. Two large isolated neurals (BMNH 48352, Text-fig. 11B–C) from the Beckles collection combine pustulate sculpture with a pronounced midline ridge, and one has two

parallel lateral ridges as well. This ridge is thus a feature of the Purbeck *Helochelydra*, as indeed was noted by Delair (1958). It is not found in any of the other taxa. The search for costal plates bearing traces of radiating ridges was less successful and these are not visible in large *Helochelydra*. However, BMNH 3528, a Mantell specimen from the Wealden of Cuckfield, is a seventh right costal of a small *Helochelydra bakewelli* combining pustulate sculpture with a clear ridge extending along its length. The bone is a mirror for the left seventh costal of '*P.(?) anglica*' which bears a corresponding ridge along its length. This suggests that small *Helochelydra* specimens did bear some of the same ridges as '*Platycheilus(?) anglica*' and it is possible that they became less prominent during growth.

In conclusion, *Helochelydra* specimens show most of the characteristic features of *Platycheilus(?) anglica* and I propose to synonymise the latter with the Purbeck *Helochelydra* as having characteristics consistent with it being a juvenile of this taxon. Because *anglica* is the only species name uniquely applied to the Purbeck *Helochelydra*, it becomes the valid name for that species and the specimen becomes the holotype.

Mantell and Owen had maintained the Wealden '*T. bakewelli*' and Purbeck '*T. punctatum*' as separate species, but later authors had some difficulty justifying this separation and Lydekker and Boulenger (1887) and Mansel-Pleydell (1888) suggested lumping them as one species. However, Lydekker later (1889b) re-established the two species. '*T. bakewelli*', defined by a distally expanded first costal and vermiculate dermal sculpture, was used for the mainland Wealden material, while '*T. punctatum*', defined by a non-expanded first costal and pustulate sculpture was applied not only to (non-type) Purbeck material but also to new specimens from the Upper Wealden of the Isle of Wight. This distinction has largely persisted although Delair (1958, p. 50) reported complete specimens of the vermiculate '*T. bakewelli*' from Purbeck (see note above).

First-hand examination of *Helochelydra* material suggests that the sculpture distinctions can only be used where direct comparisons of individual elements can be made. Pustulate and vermiculate sculpture demonstrably occur on the same elements. BMNH R9706, a costal plate from the Wealden of Hastings, shows vermiculate sculpture at one end and pustulate at the other. Other carapace fragments from Purbeck show vermiculate sculpture on the marginals and pustulate sculpture on the costals. In general, it appears that vermiculate sculpture predominates on fragments of smaller individuals and pustulate sculpture replaces it on larger specimens, but that replacement is not uniform, vermiculate patterning being retained in areas of continuing remodelling such as the edges of the marginals. Comparisons of the hyoplastra of Purbeck, and Sussex and Isle of Wight Wealden specimens does show consistent differences in the sculpture on the hyoplastra together with the shapes of these elements and the relationships of the scute patterns to the bones. For this reason I have felt able to diagnose the three sets of *Helochelydra* as separate species.

Hyperorder DAIOCRYPTODIRA

Parvorder EUCRYPTODIRA Gaffney, 1975

Family PLESIOCHELYIDAE Rüttimeyer, 1873

Included genera. *Plesiochelys*, *Portlandemys*, *Thalassemys* on skull characters (Gaffney and Meylan 1988), *Hylaeochelys*.

Diagnosis. Gaffney (1975b, p. 5) provided an extensive cranial diagnosis for this family based on *Plesiochelys* and *Portlandemys*, and Gaffney and Meylan later assigned *Thalassemys* here on cranial characters as well. Gaffney (1975b, p. 6) also provided a diagnosis, albeit gradistic, of the shell of *Plesiochelys*, and the shell of *Hylaeochelys* corresponds to this in most respects except for the uniquely wide vertebral scutes. For this reason, I have included *Hylaeochelys* in the Plesiochelyidae.

Genus HYLAEOCHELYS Lydekker, 1889a

Type species. *Pleurosternon latiscutatum* Owen, 1853.



TEXT-FIG. 12. *Hylaeochelys latiscutata* (Owen), Purbeck Limestone Group, near Swanage, precise locality unknown. BMNH R1640, immature carapace in dorsal aspect. Most peripheral plates are missing and the costal plates have not completely overgrown the ribs distally. The vertebral scute margins appear as four dark lines extending across the specimen. Vertebral-pleural scute margins are visible only at the edges of costals 3 and 5; $\times 0.41$.

Diagnosis. Carapace roughly circular with length and breadth subequal. Shallow cervical emargination and no pygal emargination. Carapace characterised by elongate narrow neurals, with neurals 2–4 at least twice as long as wide. Eight neurals and two suprapygals, the first suprapygals a wide rhomboid, three times as wide as long and with posterior width about three times the anterior width. Costal 1 is a rectangle more than twice as long as wide. Costals 3–4 up to four times as wide as long. Mesoplastrals absent. Xiphiplastral not notched. Plastron with plastral fontanelle of varying size. Very short wide cervical scute completely separates first marginals over anterior quarter of the nuchal bone. Vertebral scutes at least twice as wide as they are long and over half the width of the carapace, contra *Plesiochelys* (e.g. *P. etalloni*, *P. brodiei*) in which vertebral scutes are less than twice as wide as they are long. Vertebral scute 1 about

half the size of vertebral 2. Vertebral scute 4 extending laterally to reach the ninth marginal bones. Pleural scutes correspondingly reduced, but extending substantially over peripheral plates to cover about one-third of their area. Shell surface is plain or striated bone with no suggestion of smoothness, pitting or pustulation.

Included species. *H. latiscutata* (Owen), *H. belli* (Mantell), *H. lata* (Owen).

Hylaeochelys latiscutata (Owen) Lydekker, 1889a

Text-figures 1, 2, 5D, 7C, 8B–D, 12

- 1853 *Pleurosternon latiscutatum* Owen, p. 9, pl. 1.
 1853 *Pleurosternon emarginatum* Owen, p. 6, pl. 4. *non* pls 5–6 (*partim* Lydekker and Boulenger 1887).
 1869 *Platemys emarginata* (Owen); Maack, p. 293.
 1869 *Platemys latiscutata* (Owen); Maack, p. 295.
 1887 *Plesiochelys emarginata* (Owen); Lydekker and Boulenger, p. 272.
 1887 *Plesiochelys latiscutata* (Owen); Lydekker and Boulenger, p. 272.
 1889a *Hylaeochelys latiscutata* (Owen); Lydekker, p. 513.
 1889b *Hylaeochelys latiscutata* (Owen); Lydekker, p. 185.
 1889b *Hylaeochelys emarginata* (Owen); Lydekker, p. 189.
 1928 *Hylaeochelys sollasi* Nopsca, p. 50, fig. 9 (as *solassi, sic*).
 1958 *Hylaeochelys latiscutata* (Owen); Delair, p. 52.
 1958 *Hylaeochelys emarginata* (Owen); Delair, p. 52.
 1958 *Hylaeochelys belli* (Mantell); Delair, p. 53, *non* Mantell.
 1958 *Hylaeochelys sollasi* Nopsca; Delair, p. 53.

Holotype. DORCM G.20, large carapace visible in external aspect (Text-fig. 8B), originally in the collection of C. Willcox of Swanage, figured by Owen (1853, pl. 1).

Locality and horizon. Purbeck; Purbeck Limestone Group.

Diagnosis. As for the genus. This material may or may not be distinct from the Wealden *H. belli* that requires restudy. Growing to a carapace length of at least 0.44 m.

Referred material. BMB 001798, an eroded partial carapace; BMNH R1640 (Text-fig. 12), central portion of an immature carapace referred to *H. latiscutata* by Lydekker (1889b, p. 187); BMNH 45937, half plastron with large fontanelle, associated with some *latiscutata*-type costal plates; BMNH 39457 (Text-figs 1–2), a similar half plastron with smaller fontanelle, from the Bowerbank Collection, referred to *H. belli* by Lydekker (1889b, p. 194), but also one of the syntypes of '*Tretosternon punctatum*' Owen, 1842; BMNH R3480, a costal plate; BMNH R6866 (DORCM G52), a costal plate; BMNH R6867 (DORCM G53), a costal plate; BMNH R6878 (DORCM G56), a costal plate; BMNH R6882 (DORCM G168), a right plastron, BMNH R6885 (DORCM G47), a right hypoplastron from Langton Matravers; BMNH R6889 (DORCM G42), a right xiphiplastron; BMNH R6900 (DORCM G39), a costal plate; CAMSM J35319, anterior portion of very large carapace; DORCM G.16 (lectotype of *H. emarginata*) (Text-fig. 8c), carapace visible in internal aspect with some areas visible as a mould of the external surface, figured by Owen (1853, pl. 4), DORCM G152, a posterior carapace in dorsal aspect; NMW unnumbered specimen, large complete plastron (Text-fig. 7c); OUM J.13796 (holotype of *H. sollasi*) (Text-fig. 8D), a carapace in external aspect in the J. Parker Collection figured by Nopsca (1928, fig. 9).

Remarks. In the context of the Purbeck fauna, this taxon is most readily recognised by the smooth unornamented dermal shell surface and the extreme width of the vertebral scutes, more than twice as wide as they are long. This is shown clearly in the holotype carapace DORCM G.20 (Text-fig. 8B). The holotype of *H. sollasi* (Text-fig. 8D) is also a large carapace, OUM J.13796, described by Nopsca in 1928. As figured, it appears to be wider than the type of *H. latiscutata* but this is because DORCM G.20 is slightly laterally compressed (Owen's engraving is a perspective dorsal view) whereas OUM J.13796 is extremely flattened. The two carapaces would have been very similar in size and proportions in life. The type of *H. latiscutata* has neurals 7 and 8 in sutural contact whereas in *H. sollasi*, they are separated by a short contact

by costals 8. However, this feature is variable within species and is not of itself of taxonomic significance. Nopcsa (1928, p. 49) reported that *H. sollasi* was characterised by the extreme width of vertebral scute 4 which extended as far as the peripheral plate 9. However, the type of *H. latiscutata* shows the same condition although Owen's figure does not depict this and implies that the peripherals are missing. The posterolateral right peripherals are partly present and their relationship to the scutes is identical to that in *H. sollasi*. None of Nopcsa's diagnostic characters for *H. sollasi* separates it from the type of *H. latiscutata* and the two are synonymised here.

DORCM G16, the type of *Hylaeochelys emarginata*, has proved to be one of the most difficult specimens to place as it comprises only an internal face of the carapace with some imprints of the dorsal surface where bone has exfoliated (Text-fig. 8c). The scute pattern is thus not determinable and there is only an incomplete representation of the carapace elements, plus some indication of the dermal bone surface along the marginal edges and on the impression. The dermal surface is not pitted or sculptured, suggesting that it is not *Pleurosternon*, *Helochelydra* or '*Glyptops*'. The prominent cervical emargination also eliminates *Pleurosternon* but would be consistent with '*Glyptops*' or *Hylaeochelys*. The carapace must have been relatively rounded rather than oval and this, together with the lack of dermal sculpture, places this specimen in the genus *Hylaeochelys*.

The plastron of *H. latiscutata*, with its characteristic plastral fontanelle, can be recognised through association in BMNH 45937 in which a plastron with a large fontanelle (length about three times width) is associated with *H. latiscutata* carapace elements. *Hylaeochelys belli* is based on Wealden material but Lydekker (1889b, p. 194) attributed one Purbeck plastron BMNH 39457 (Text-figs 1–2) to *H. belli* and was followed in this by Delair (1958, p. 53). As most of the criteria used by Lydekker to discriminate *H. belli* from *H. latiscutata* related to the carapace, it appears that the assignment of BMNH 39457 to *H. belli* was based on the presence of a different shape of plastral fontanelle. BMNH 39457 has a smaller shorter plastral fontanelle (length equals width) but is otherwise identical to BMNH 45937. It demonstrates that the fontanelle is variable in size in a single population but does not demonstrate taxonomic distinction as this is believed to be a variable feature in other plesiochelyid species. It seems likely that the degree of closure of the fontanelle during ontogeny is variable within a single species as discussed by Gaffney in relation to the closely related *Plesiochelys etalloni* material from Solothurn (Gaffney 1975, p. 11).

Although *Hylaeochelys latiscutata* is the genotype species, the genus includes the senior *H. belli* (Mantell) based on assorted fragments from the Wealden of Sussex. This species requires revision and the many fragments have not been assembled and described comparatively to the complete carapaces of *H. latiscutata*. Some of the past distinctions are based on misidentifications of individual elements. The holotype of *H. belli*, BMNH 36529, is a single element from the Wealden of Cuckfield described as the distal extremity of the left costal 2 (e.g. Lydekker 1889b, pp. 190–191) but the highly asymmetrical scute margin pattern identifies it as the distal extremity of the more robust costal 6. BMNH 2266, also from Cuckfield, was identified as the left costal 2 (e.g. Lydekker 1889b, p. 192) but is clearly the right costal 2 by comparison with the Purbeck material. These elements appear to be identical to their correctly recognised counterparts on the carapace of *H. latiscutata*. It is beyond the scope of this work to revise this material but it clearly requires revision prior to any published conclusion concerning its synonymy or non-synonymy with *H. latiscutata*.

Family *incertae sedis*

Genus DORSETOCHELYS Evans and Kemp, 1976

Type and only species. Dorsetochelys delairi Evans and Kemp, 1976

Dorsetochelys delairi Evans and Kemp, 1976

- 1909 *Pleurosternum* sp. Woodward, p. 144.
- 1958 *Pleurosternum* sp. Delair, p. 49.
- 1976 *Dorsetochelys delairi* Evans and Kemp 1976, p. 318, text-figs 1–2.
- 1979 *Dorsetochelys delairi* Evans and Kemp; Gaffney, figs 27c, 28c.

Holotype skull. DORCM G.23, a complete skull, presented by Sir Charles Richardson in 1908 and prepared by Jeanne Evans; figured by Evans and Kemp (1976, figs 1–2).

Locality and horizon. Swanage; Purbeck Limestone Group.

Diagnosis (after Evans and Kemp 1976 and Gaffney 1979). Turtle skull with the following features: dorsal prefrontal lappets large but not meeting medially; broad parietal-squamosal contact associated with very shallow skull emarginations; broad, wedge-shaped, supraoccipital dorsal exposure between parietals; palatine extends onto triturating surface; pterygoids contact medially, not separated by basisphenoid; posterior foramen of the internal carotid canal midway along basisphenoid; short pterygoid-basioccipital contact.

Referred skull. DORCM G.10715, a partly prepared skull visible in palatal aspect collected by D. Costain from a fallen block on the beach near the Zig-Zag Path in Durlston Bay in 1985. The palate of this specimen corresponds to that of *Dorsetochelys* in shape, size and several structural details. The palatines contribute to the triturating surface, the pterygoids meet anteriorly ahead of the foreshortened basisphenoid and there is an abbreviated pterygoid-basisphenoid contact.

Systematic position of Dorsetochelys. In considering the possible association of the *Dorsetochelys* skull with postcranial material, some alternatives can be immediately eliminated. The association of the *Mesochelys* skull with *Pleurosternon* precludes the *Dorsetochelys* skull type being assigned to that genus. The first skull of *Helochelydra* has recently been collected from the Wealden of the Isle of Wight and is currently being studied by Professor R. Moody, Ms. S. D. Chapman and Mr C. A. Walker (S. Chapman, pers. comm. 2002). It is clearly distinct from *Dorsetochelys* and bears the same pustulate sculpture as the shell of *Helochelydra*. *Dorsetochelys* might be the skull of a cryptodire taxon unrepresented by shells at Purbeck but it does seem very unlikely that a Purbeck turtle taxon comprising two out of four recorded skulls should not be represented by shells in such a large assemblage.

Thus we are left with ‘*Glyptops*’ and *Hylaeochelys* as possible shell-genera to which the *Dorsetochelys* skull type might be assignable. In *Dorsetochelys*, the prefrontals do not meet and the internal carotid canals lie between the pterygoids and the basisphenoid. These are more primitive conditions than those found in *Plesiochelys sensu stricto* (prefrontals meet and carotid foramina in pterygoids) and suggest that *Dorsetochelys* is unlikely to be the skull of *Hylaeochelys*, the shell of which is very similar to *Plesiochelys* in all features other than the dorsal scute width. It is, of course, possible that *Hylaeochelys* and *Plesiochelys* shells represent a broad grade of organisation within which significant cranial evolution occurred, so association cannot be firmly excluded. *Dorsetochelys* would seem more likely to be the skull of ‘*Glyptops*’ *typocardium*. The large skull of *Dorsetochelys* corresponds to the large cervical emargination of ‘*Glyptops*’ *typocardium*, and it is possible but unprovable that *Dorsetochelys* is the skull of that taxon. If so, ‘*Glyptops*’ *typocardium* may not be pleurosternid and would certainly not be assignable to *Glyptops*. *Dorsetochelys* lacks the sole pleurosternid synapomorphy recognised by Gaffney and Meylan (1988), namely basisphenoid extending between the pterygoids, so that association of these specimens would place the resulting combination outside the family as presently defined. However, the association is as yet undemonstrated and *Dorsetochelys* is retained here as a skull of uncertain association.

UNDESCRIBED CRANIAL MATERIAL

A skull preserved in dorsal view was held in the collections of the Royal College of Surgeons Museum and was mentioned by Lydekker (1889*b*, p. 204). Casts include BMNH R463 and R2966. It was still in the inventory in 1904 (B. Davis, pers. comm. 1999) but is now lost and appears to have been destroyed, along with a significant fraction of the RCS collections, by bombing during the 1939–45 war. The casts are not of good fidelity but the skull was distinct from those of *Pleurosternon* (‘*Mesochelys*’) and *Dorsetochelys*. It was highly emarginated posteriorly with a long supraoccipital crest. The anterior region resembled that of *Pleurosternon* with an abbreviated snout and large closely space orbits. No sutures are visible. It must remain an enigma but might have been the skull of ‘*Glyptops*’ or *Hylaeochelys*.

Two good sets of undescribed mandibles were mentioned by Lydekker (1889*b*, p. 204), namely BMNH 21974*x*, an unprepared mandible in dorsal aspect from Swanage purchased in 1848; and BMNH 44815, a mandible from Swanage presented by B. Bright in 1873 and fully prepared out by A. Rixon in 1952. These merit further study but are beyond the scope of this work and I have not attempted to identify them.

REJECTED NAMES

Tretosternon punctatum Owen, 1842 *nomen dubium*

Syntypes. The two syntypes of *T. punctatum* were described by Owen in 1842 (p. 165). One was a posterior carapace in the Egerton Collection, untraceable by 1889 (Lydekker 1889*b*, p. 141); the other a partial left plastron in the Bowerbank Collection that I have recently relocated (Text-figs 1–2).

Remarks. As noted in an earlier section, I am treating this taxon as a *nomen dubium*, pending further research on the status of the Egerton syntype, given lectotype status earlier in this paper.

Chelone obovata Owen, 1842 *nomen dubium*

Holotype. A slab bearing a separate carapace and plastron, both in ventral aspect plus hind limb elements, described by Owen (1842, p. 170) but never figured.

Remarks. When described, the specimen formed part of the Channing Pearce Collection. The only later reference was by Woodward (1909) who used this species name for specimens in the Corfe Castle Museum collections now at BMNH and DORCM. No specimen in these collections corresponds to Owen's description and none with full histories is attributable to the Channing Pearce Collection. Nothing resembling this slab is now known. Delair (1958, p. 49) noted that Owen's description accords with that of *Pleurosternon bullocki*, the commonest species at Purbeck. However, Owen described the costal outline as narrowing posteriorly, which is the condition in '*G.*' *typocardium*. As the type specimen is both lost and unfigured, the species must continue to be treated as a *nomen dubium* unless the holotype is relocated.

DISCUSSION

Wider systematics

This revision has largely concentrated on the intrinsic taxonomy of the Purbeck material without much reference to related forms from elsewhere. Comparison with similar Wealden taxa is obviously a priority and it may be that some of the nomenclature established here will be overturned after comparison with Wealden forms.

Relative numbers and distribution

With this revision, it becomes possible to consider the relative numbers of the turtle shell-taxa in the Purbeck Limestone. *Pleurosternon bullockii* is clearly the only abundant form. Sixty-two large specimens are listed here but there are many more in the BMNH collections, either listed by Lydekker or not published, and at least 150 specimens exist, if the small Beckles' Pit specimens are counted as juveniles. '*Glyptops*' *typocardium* and *Helochelydra anglica* are recognised here from five and six specimens respectively, and *Hylaeochelys latiscutata* is recognised from 18 specimens, five of which are isolated costal plates. These approximations suggest that *Pleurosternon* comprises about 84 per cent of the turtles in the Purbeck Limestone with *Hylaeochelys* represented by ten per cent and *Helochelydra* and '*Glyptops*' at three per cent each. The obvious conclusion is that *Pleurosternon bullockii* was the predominant endemic turtle in the water bodies that gave rise to the upper horizons of the Purbeck Limestone, while the other genera were either rare elements in the fauna or transported transients/erratics. They may have been local in occurrence within the Purbeck Limestone. Several of the *Hylaeochelys* specimens are isolated costal plates, suggesting that some of this material was from a specific horizon where transport and

break-up of the carapaces had occurred. Some of the *Helochelydra* material was collected by Beckles and appears to have come from the Beckles Pit so may also have been local in origin.

Future research

This revision has concentrated on the systematic essentials, and there is much more work that could be undertaken on the Purbeck turtles. There are many isolated and associated skeletal elements that merit further study. There is sufficient material of *Pleurosternon* to permit study of ontogenetic change and biological variation. There is also the potential for much of the material to be localised to horizon to establish its origins and perhaps the circumstances of its burial.

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ANDREW R. MILNER

School of Biological and Chemical Sciences
Birkbeck College, Malet Street
London WC1E 7HX, UK
e-mail a.milner@biology.bbk.ac.uk

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