THE CRANIAL MORPHOLOGY OF A NEW LOWER CRETACEOUS TURTLE FROM SOUTHERN ENGLAND

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ABSTRACT. A new turtle *Mesochelys durlstonensis* gen. et sp. nov. is described from an almost complete skull and partial postcranial skeleton found at Durlston Bay, Dorset (Purbeckian, basal Cretaceous). Its closest relative is *Glyptops plicatulus* from the Morrison Formation of North America and, together, these two constitute the most primitive cryptodire family Glyptopidae. The structure of the basicranial axis, the pterygoid, and the roofing bones indicate that *Mesochelys* is the most primitive post-Triassic chelonian yet described.

IN December of 1971 Mr. John Evans collected an extremely well-preserved skull and partial postcranial skeleton of a turtle, contained in a large block of limestone on the foreshore of Durlston Bay, Swanage, Dorset. The matrix, a hard, dark limestone possibly from the Upper Building Stone, responded well to the acetic-acid method of preparation. A 10% solution of acid was used and the exposed bone was strengthened by 'Vinalak' (polybutyl methacrylate) in methylethyl ketone. The matrix has been completely removed.

The skull is slightly crushed dorso-ventrally, just separating the sutures sufficiently for them to be clearly determined. The palatines, basioccipital, and exoccipitals are missing, as are the squamosal and quadratojugal of the left side. There is no lower jaw, and the postcranial bones preserved are one cervical vertebra, several caudal vertebrae, the left ilium, pubis and femur, several foot bones, and a very incomplete shell.

SYSTEMATIC POSITION

The great majority of Mesozoic turtles are known only from their shells and it is upon this feature, therefore, that the taxonomy is primarily based (Delair 1958). Even then, several genera have been established on very incomplete specimens, while such phenomena as the degree of individual variation and possible sexual dimorphism have never been investigated. The remains of the shell of the present specimen are insufficient for a positive identification to be made, although enough is known to remove certain genera from consideration, particularly those with distinctive types of shell ornamentation. The general nature of the shell points towards the genera *Pleurosternon* Owen and *Hylaeochelys* Lydekker. The notched xiphiplastral bone is suggestive of the former genus whilst the presence of an emarginate marginal bone suggests the latter.

Skull structure is well known for three Upper Jurassic turtles, of which *Glyptops plicatulus* of the Morrison Formation of North America is the only one with associated postcranial skeleton. The other two were described in detail by Parsons and Williams

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(1961), one from Portland (possibly the same as *Stegochelys planiceps* Owen) and the other from Solnhofen. A fourth kind of chelonian skull, from the Purbeck of Swanage, is currently being described by ourselves. Of these four kinds, the present specimen is very like *Glyptops plicatulus* (Baur 1891; Gaffney 1972*a* and pers. comm.) and must be placed in the same family as that form. Shells referred to *Glyptops ruetimeyeri* are known from the Purbeckian (Watson 1910) although, as indicated above, the shell of our specimen is inadequate for comparison. We have elected to create a new genus for our Dorset form on the basis of several marked differences from *Glyptops*, despite the possibility that it belongs to an existing genus known only from the shell. It seems to us likely that skull structure is eventually going to provide a far more reliable guide than the shell to the taxonomic and phyletic relationships of early turtles, and it is important therefore that one of the most primitive and best known of the Mesozoic kinds should be appropriately named and diagnosed.

Suborder CRYPTODIRA
Family GLYPTOPIDAE

Diagnosis. Primitive cryptodiran turtles with the basisphenoid completely separating the pterygoids; foramen posterior canalis carotici interni lying half-way along the basisphenoid-pterygoid suture. Pterygoid not completely flooring the cavum acusticojugulare. Epipterygoid present. Prefrontals with moderate dorsal exposures but not meeting one another. Triturating surfaces narrow and not expanding posteriorly.

Genus MESOCHELYS gen. nov.

Diagnosis. Glyptopid turtles with the skull only moderately elongated. Frontal making a long, oblique suture with the nasal. Maxillae well separated from one another. Jugal just entering the orbital margin. Triturating surfaces relatively wide. Carapace with at least one emarginate marginal bone. Xiphiplastron bone notched.

Mesochelys durlstonensis sp. nov.

Diagnosis. As for genus.

Holotype. Cambridge University Museum of Zoology. **T** 1041. Skull and partial postcranial skeleton.

Locality. Durlston Bay, Dorset.

Horizon. Purbeckian, possibly Durlston Formation (Lower Cretaceous, Casey 1973).

Nomenclature of cranial structures used throughout this paper is that of Gaffney (1972*b*) as developed from Parsons and Williams (1961).

Abbreviations used in text-figures

ad. can. stap-temp.—aditus canalis stapediotemporalis
ant. postot.—antrum postoticum
bpt. art.—basipterygoid articulation
bpt. pr.—basipterygoid process
BSP—basisphenoid
can. cav.—canalis cavernosus
cond.—condyle
dor. sel.—dorsum sellae
EPT—epipterygoid
F—frontal
for. alv. sup.—foramen alveolare superius
for. car. post.—foramen posterior canalis carotici interni
for. n. abd.—foramen nervi abducentis
for. n. trig.—foramen nervi trigemini

for. pal. post.—foramen palatinum posterius
for. prepal.—foramen praepalatinum
for. stap-temp.—foramen stapedio-temporale
for. supramx.—foramen supramaxillare
fossa acust-fac.—fossa acustico-facialis
hiatus acust.—hiatus acusticus
IL—ilium
in. col. aur.—incisura columellae auris
ISCH—ischium
J—jugal
MX—maxilla
N—nasal
OPIS—opisthotic
opis. sut.—sutural surface for the opisthotic
P—parietal
PMX—premaxilla
PO—postorbital
PRO—prootic
pro. sut.—sutural surface for the prootic
PRF—prefrontal
PT—pterygoid
pt. sut.—sutural surface for the pterygoid
pt. w. q.—pterygoid wing of the quadrate
PUB—pubis
Q—quadrate
QJ—quadratojugal
qj. sut.—sutural surface for the quadratojugal
Q (opis)—sutural surface of quadrate for the opisthotic
rec. lab. pro.—recessus labyrinthicus prooticus
rec. lab. so.—recessus labyrinthicus supraoccipitalis
rost. bsp.—rostrum basisphenoidale
sel. tur.—sella turcica
SO—supraoccipital
SQ—squamosal
sq. sut.—sutural surface for the squamosal
V—vomer

Description: skull

General features

The skull is wedge-shaped when seen from above, and low in lateral view. The face is short with circular dorso-laterally directed orbits, and a small, narrow snout. The external nares are confluent. There is only slight emargination of the posterior edge of the skull roof and the crista supraoccipitalis is not well developed. The ventro-lateral margin of the skull in the region of the jugal and quadratojugal bones is distinctly emarginated.

The palatal surface lacks all trace of a secondary palate and the triturating surfaces of the maxillae are only slightly expanded posteriorly and bear sharp labial ridges but no tomial ridges. The paired premaxillae project downwards as a small serrated beak. The posterior surface of the palate is flat and the processus pterygoideus externus of each pterygoid is relatively well developed. The quadrate is stout and curved, and the cavum tympani is developed just as in typical modern turtles. The incisura columellae auris is barely open posteriorly and the antrum postoticum is prominently developed.

In posterior view there is a large fenestra postotica.

The external surfaces of the skull are lightly sculptured and pitted with small nutritive foramina.

Bones of the skull roof

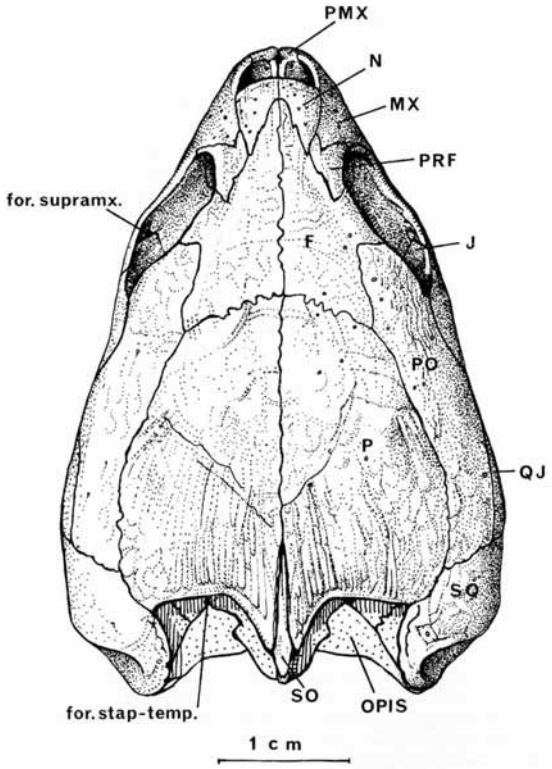
Parietal. The form and large size of the parietal is clear from the figures. The posterior edge is somewhat emarginated between the posteriorly directed spur which runs alongside the supraoccipital and the short contact with the squamosal bone laterally. The processus inferior parietalis (text-fig. 3*b*) is large and descends in a parasagittal plane to contact the small epipterygoid antero-ventrally and the prootic postero-ventrally, these three bones forming the foramen nervi trigeminalis (although in the specimen slight distortion on both sides has rather obscured the foramen). Above the level of the prootic, the parietal forms a very extensive overlapping contact with the external surface of the supraoccipital.

Frontal. The shape of the frontal is rather unusual in being triangular with a pointed anterior process extending, in contact with its fellow, between the nasals. A distinct lateral lappet of the frontal forms a small part of the dorsal margin of the orbit.

A well-developed ventral ridge just lateral to and parallel with the mid-line marks the limit of the sulcus olfactorius.

Nasal. A pair of small nasals are present which contact the frontals and also the prefrontals externally. From side to side the nasals are slightly convex.

Prefrontal. The dorsal exposure of the prefrontal is limited to a small rectangle forming the antero-dorsal corner of the orbital margin. A descending process curves down from the anterior end, medial to and in



TEXT-FIG. 1. *Mesochelys durlstonensis*. Skull, slightly restored, in dorsal view.

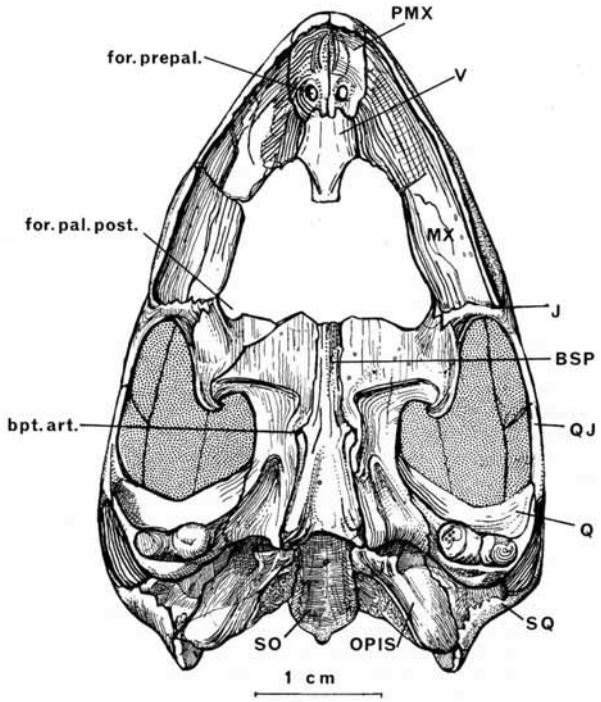
sutural contact with the dorsal process of the maxilla, and so forms the anterior wall of the orbit. The ventral end of the process contacts the vomer.

Postorbital. The anterior end of the postorbital is thickened to form the hind wall of the orbit, but otherwise the bone is thin and makes simple sutures with the adjacent bones.

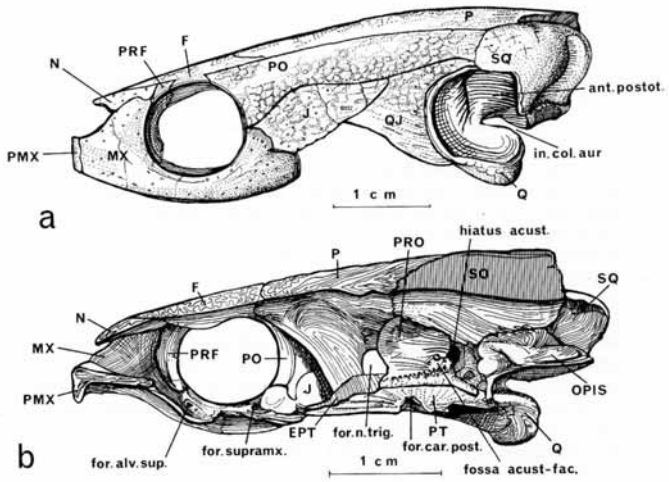
Jugal. The small jugal is greatly thickened anteriorly, where it forms a short portion of the posterior wall of the orbit (text-fig. 3*b*) between the postorbital and the maxilla. However, it barely enters the orbital margin as seen in lateral view (text-fig. 3*a*) because of a superficial extension of the maxilla towards the postorbital. It has a short, stout postero-medial process contacting the pterygoid and behind this region it forms a thin sheet.

Quadratojugal. The quadratojugal is a thin, simple bone of characteristic chelonian form, curving postero-dorsally in contact with the lateral edge of the quadrate.

Squamosal. As in typical advanced chelonians, the squamosal has a ventral extension behind the quadrate forming the posterior wall of the antrum postoticum, and bearing a broad, shallow groove on its posterior face for the depressor mandibuli muscle. The medial part of the squamosal extends inwards a short way, capping the medial extension of the quadrate, and it also makes an edge-to-edge contact with the opisthotic along the dorso-lateral part of that bone.



TEXT-FIG. 2. *Mesochelys durlstonensis.* Skull, slightly restored, in ventral view.



TEXT-FIG. 3. *Mesochelys durlstonensis. a*, skull, slightly restored, in lateral view. *b*, internal view of skull from mid-sagittal view.

Bones of the palate

Premaxilla. The premaxillae are small, paired bones completely lacking an internarial process and together forming a serrated continuation of the labial ridges of the maxillae. The foramen praepalatinum in the palatal surface is towards the posterior edge of the premaxilla, and on the dorsal surface at the anterior edge there is a single, median pit.

Maxilla. The facial exposure of the maxilla is extensive and forms some two-thirds of the external orbital margin, although this bone contributes only the floor of the fossa orbitonasalis. The foramen supramaxillare opens into the posterior part of the floor of the fossa just in front of the suture of the maxilla with the jugal, while the foramen alveolare superius opens into the anterior end of the floor immediately below the descending process of the prefrontal.

The triturating surface of the maxilla is narrow and is only slightly expanded posteriorly. The labial ridge is sharp and well developed along the lateral edge but medially the tomial ridge is negligible.

Vomer. Only the anterior part of the vomer is preserved, as a small median bone with a concave ventral surface and a dorsal surface divided by the medial sulcus vomeri on either side of which is a small boss for contact with the descending process of the prefrontal.

Palatine. Both palatines are missing. However, the position of the apertura narium interna between the palatine, maxilla, and vomer can be inferred from the edges of it on the latter two bones; and similarly, part of the margin of the foramen palatinum posterius between the palatine and the pterygoid remains preserved on the latter. The sizes of these two respective apertures cannot, however, be ascertained with any accuracy.

Pterygoid. The basisphenoid completely separates the paired pterygoids from one another. Each pterygoid is in sutural contact with the full length of the basisphenoid and the sutural faces are oblique, so that the dorsal surface of the basisphenoid is wider than the ventral surface (text-fig. 5). Two points are of particular interest. First, the anterior part of the contact is very much narrower dorso-ventrally than the posterior part, and indeed is no more than an edge-to-edge contact at the very front. Second, the remnant of the primitive basipterygoid articulation can be discerned at about mid-length along the ventral surface of the basisphenoid, where a small lateral spur, the basipterygoid process, fits into a distinct pit (text-fig. 3) in the ventro-medial edge of the pterygoid.

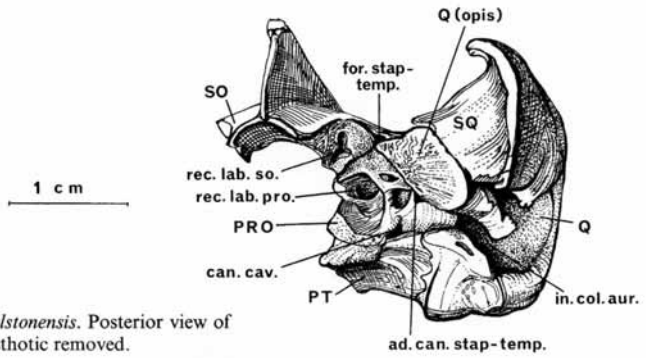
The processus pterygoideus externus is well developed and bears a slight ridge (text-fig. 2) parallel to its posterior edge, presumably marking the anterior limit of origin of pterygoideus muscle fibres. The ridge turns posteriorly alongside the medial edge of the pterygoid and terminates at the level of the basipterygoid articulation.

The antero-lateral part of the pterygoid bears a large, antero-laterally facing pit into which fits the palatal process of the jugal. The maxilla also contacts the pterygoid in this region. The dorsal surface of the pterygoid meets the small, thin epipterygoid anteriorly and has a long horizontal suture with the prootic posteriorly (text-fig. 3*b*). Posteriorly the pterygoid rises up slightly to overlap the outer face of the prootic a little.

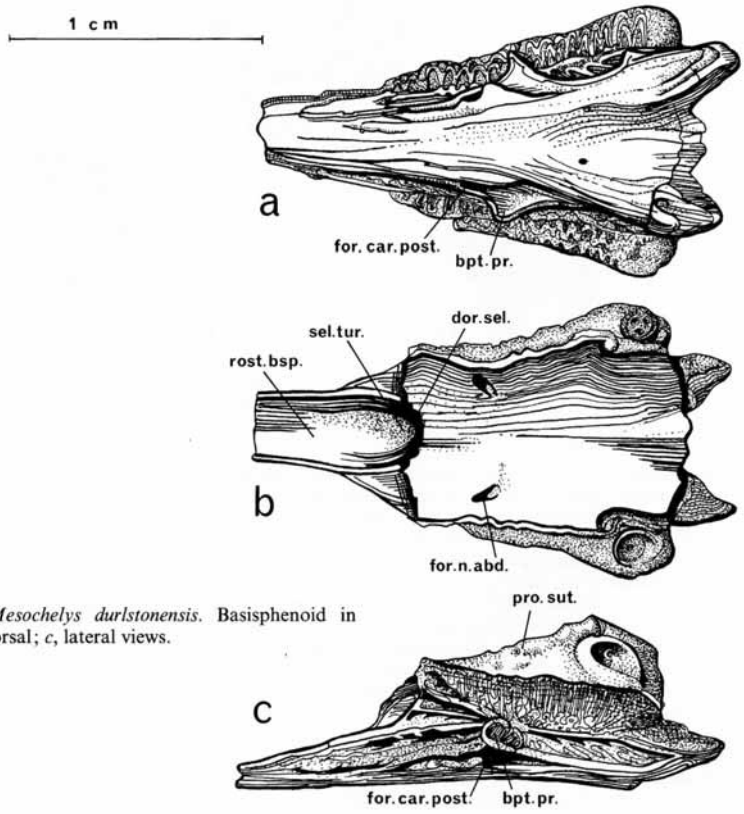
The quadrate ramus of the pterygoid expands ventro-medially to form a horizontal process which partially floors the cavum acustico-jugularis, although much less extensively than in typical modern chelonians. The lateral side of the quadrate ramus is deeper and is completely overlapped by the lower part of the antero-medial wing of the quadrate.

The dorsal surface of the pterygoid shows the typical chelonian form. It has a broad sulcus cavernosus running backwards just lateral to the basisphenoid and becoming the canalis cavernosus where it is roofed over by the prootic. The canal emerges posteriorly into the cavum acustico-jugulare (text-fig. 4). A small ventral foramen lies just behind and lateral to the basipterygoid articulation, and is presumably the foramen pro ramo nervi vidiani which would lead through the pterygoid into the canalis cavernosus, although this cannot be positively confirmed in the specimen. A second foramen opens into the pit for reception of the basipterygoid process. It leads anteriorly and is probably therefore the posterior opening of the canalis nervi vidiani; the anterior opening of this canal lies on the dorsal surface of the pterygoid, lateral to the sulcus cavernosus and towards the anterior end.

Epipterygoid. Both the epipterygoids are damaged slightly. Each is a low, thin plate lying immediately lateral to the sulcus cavernosus of the pterygoid and connecting that bone to the parietal, as noted earlier (text-fig. 3*b*).



TEXT-FIG. 4. *Mesochelys durlstonensis*. Posterior view of right side of skull, with opisthotic removed.

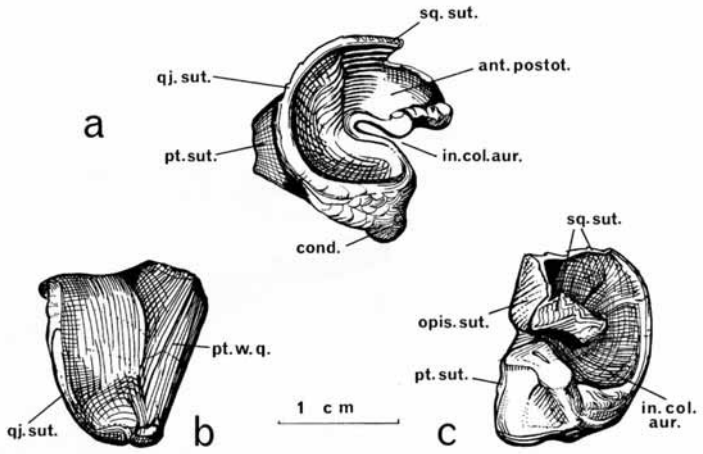


TEXT-FIG. 5. *Mesochelys durlstonensis*. Basisphenoid in *a*, ventral; *b*, dorsal; *c*, lateral views.

Quadrate. The quadrate (text-fig. 6) resembles that of typical modern chelonians. It is very stout and strongly curved to form a deeply concave cavum tympani. The dorsal part continues the curve backwards and downwards to make a prominent antrum postoticum and to reduce the incisura columellae auris to a narrow slit. The articulating condyle is short from front to back and is double, the convex medial part being slightly better developed than the almost flat lateral part.

The curved antero-lateral edge sutures with the thin quadratojugal while the whole width of the dorsal part is capped by the squamosal. Again as in modern forms, the medial part of the quadrate forms a high vertical wing sutured to the pterygoid below, to the prootic antero-dorsally, and by a postero-laterally running suture to the opisthotic behind.

Two canals leading into the cavum acustico-jugulare are formed in part by the quadrate. The canalis stapedio-temporalis runs between the quadrate and the prootic from the roof of the braincase in the temporal fossa into the dorso-lateral part of the cavum; and quadrate forms the dorso-lateral wall of the canalis cavernosis where it emerges into the ventro-lateral region of the cavum.



TEXT-FIG. 6. *Mesochelys durlstonensis*. Left quadrate in *a*, lateral; *b*, anterior; *c*, posterior views.

Bones of the braincase

Basioccipital and exoccipital. These are completely missing. The existing sutural surfaces indicate that the basioccipital met the basisphenoid in a more or less transverse suture, and furthermore that it barely made contact with the pterygoid or otic bones. The exoccipital met the opisthotic by an extensive postero-laterally inclined suture and it also made a much more limited attachment to the supraoccipital.

Supraoccipital. The supraoccipital has a high but thin median keel which abruptly flares out below as the broad braincase roof (text-fig. 4). The crista supraoccipitalis is not developed posterior to the parietal although this could be a result of breakage during preservation. The paired parietals completely cover the anterior one-third of the supraoccipital. The normal series of lateral sutures between the supraoccipital and the prootic, opisthotic, and exoccipital respectively are present.

The middle region of the lateral edge forms the dorsal edge of the unossified hiatus acusticus and the notch which represents the foramen aquaducti vestibuli is perfectly preserved on the left side of the specimen (text-fig. 3*b*). There is a well-developed recessus labyrinthicus supraoccipitalis (text-fig. 4) showing the union of the anterior semicircular canal, most of which is in the prootic, with the posterior semicircular canal of the opisthotic.

Basisphenoid (text-fig. 5). In this account no attempt to distinguish a parasphenoid from a basisphenoid is made since the two are in fact indistinguishable.

The important relationship between the basisphenoid and the pterygoids has been described earlier. There is a transverse suture face extended posteriorly by a pair of ventral spurs for attachment of the (missing) basioccipital. The prootic contacts the basisphenoid along a horizontal line in the postero-dorsal region, behind which is a short facet for contact with the opisthotic.

The dorsal surface is quite strongly concave from side to side and is in two distinct parts. The broader posterior part terminates as the feebly developed dorsum sellae in front of which is the sella turcica at a lower level. The side walls of the sella peter out anteriorly leaving the rostrum of the basisphenoid as a thin process, slightly concave from side to side.

The foramen posterior canalis carotici interni is on the ventro-lateral margin of the basisphenoid at about mid-length, alongside the basipterygoid process. The corresponding anterior foramen lies at the base of the sella turcica. A pair of small anterior foramina nervi abducens enter the dorsal surface of the basisphenoid a little behind the dorsum sellae and the canals emerge alongside the sella turcica.

Prootic. The prootic rises more or less vertically from its horizontal suture with the dorsal surface of the pterygoid to its contacts with the parietal, which overlaps it laterally, and with the supraoccipital (text-fig. 3*b*). The free anterior edge of the prootic is smoothly rounded, forming the posterior margin of the foramen nervi trigemini, and a depression in the lower part of the medial face is the fossa acustico-facialis bearing three foramina, a large anterior one for the facial nerve and a large dorsal one plus a small ventral one for two branches of the acustic nerve.

The posterior part of the prootic is expanded and houses the recessus labyrinthicus prooticus in typical chelonian fashion, freely confluent with the more lateral cavum acustico-jugulare (text-fig. 4).

The dorsal and lateral surfaces of the prootic suture with the quadrate; the contact with the opisthotic is restricted to the upper part of the posterior face of the prootic, the fenestra ovalis laterally and the hiatus acusticus medially separating these two bones.

Opisthotic. The stout paroccipital process runs postero-laterally in broad contact with the quadrate anteriorly, and also just touching the free medial edge of the squamosal. The dorsal surface is in the form of a deep trough and the medial surface bears an extensive sutural facet for the (missing) exoccipital.

The medial part of the opisthotic is expanded, sutures with the supraoccipital above, the prootic anteriorly and just with the pterygoid ventrally, and it carries the recessus labyrinthicus opisthoticus of normal chelonian form. The position of the foramen jugulare anterius is indicated by a smooth groove just in front of the facet for the exoccipital and thus the foramen must have lain between these two bones.

Postcranial skeleton

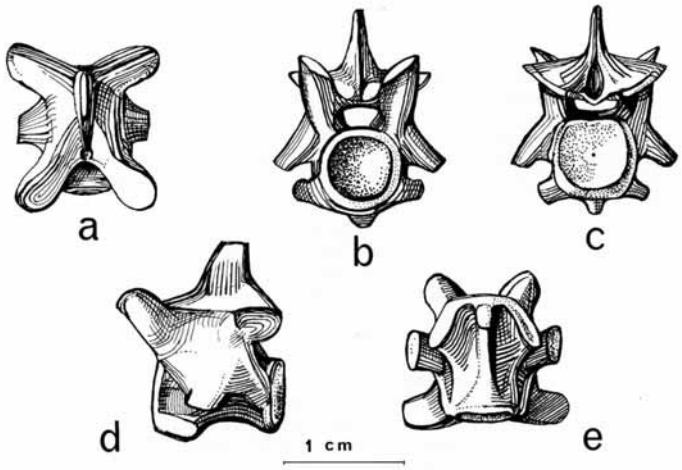
A very incomplete postcranial skeleton is associated with the skull, consisting of parts of the shell, one cervical and a few caudal vertebrae, a radius, an ulna, the left ilium and pubis, the left femur and tibia, and a number of indeterminate phalanges.

Shell (Pl. 5). The over-all form of the shell is flattened. Both the carapace and the plastron are very incomplete but, nevertheless, a number of useful features are to be seen. Of the carapace, a fairly substantial piece remains showing part of the margin including a more or less complete marginal bone. This is important because it shows a characteristic emargination of the edge of the bone itself, a character not present in many Upper Jurassic and Purbeck turtles. The ornamentation of the dorsal surface is very fine, consisting of very small pits at the centre of the scutes and more elongated, almost imperceptible markings towards the edges. The lines indicating the positions of the horny scutes are narrow, very shallow grooves.

Of the plastron, only the incomplete left xiphiplastron bone is recognizable. It does, however, show a characteristic form. The lateral margin is almost straight to the posterior corner, where it turns sharply medially. The posterior edge is markedly concave. The ornamentation of this region of the plastron is very similar to that of the carapace bones.

For the rest, the shell consists of broken, indeterminate fragments of both carapace and plastron, which add no further details of taxonomic value.

Vertebrae. A single cervical vertebra (text-fig. 7) is preserved. The neural arch is broad and rather flat and the respective pre- and postzygapophyses are widely spaced. The neural spine is small and posteriorly placed and the transverse process, also short, points ventro-laterally. The whole of the neural arch is attached to the centrum by an unfused suture. The centrum is circular in section with a mid-ventral keel developed along the anterior half. The anterior face of the centrum is concave, but not notochordal, while



TEXT-FIG. 7. *Mesochelys durlstonensis.* Cervical vertebra in *a*, dorsal; *b*, anterior; *c*, posterior; *d*, lateral; *e*, ventral views.

the posterior face is almost flat. The lower lateral part of the anterior face is produced postero-laterally as a smooth facet presumably for the reception of a free cervical rib.

About five caudal vertebrae remain but all are badly damaged. In general they are small and elongated.

A single very small haemal arch is present.

Forelimb. The only identifiable remains are the right radius and the left ulna. The radius has a strongly flattened head which expands medially. The lower end is only slightly expanded.

The ulna is of about the same thickness as the radius. Its head is less expanded and it bears a small olecranon process. Its distal end is a convex roller shape.

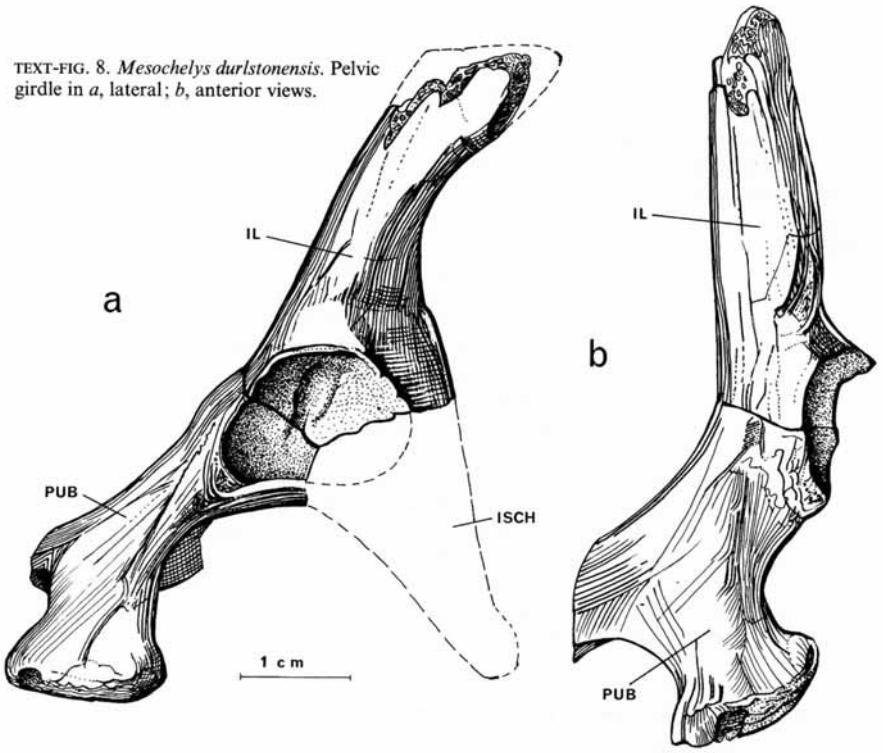
Pelvic girdle. The ilium and the pubis of the left side are almost complete but the ischium is absent except for a possible fragment (text-fig. 8). The general structure is very like that described by Hay (1908) for *Glyptops plicatulus.* The ilium is a narrow process inclined strongly postero-dorsally and more or less circular in cross-section. The distal tip is damaged. The ventral end expands to form the dorsal part of the acetabulum and to make broad buttressing sutures with the ventral pelvic bones.

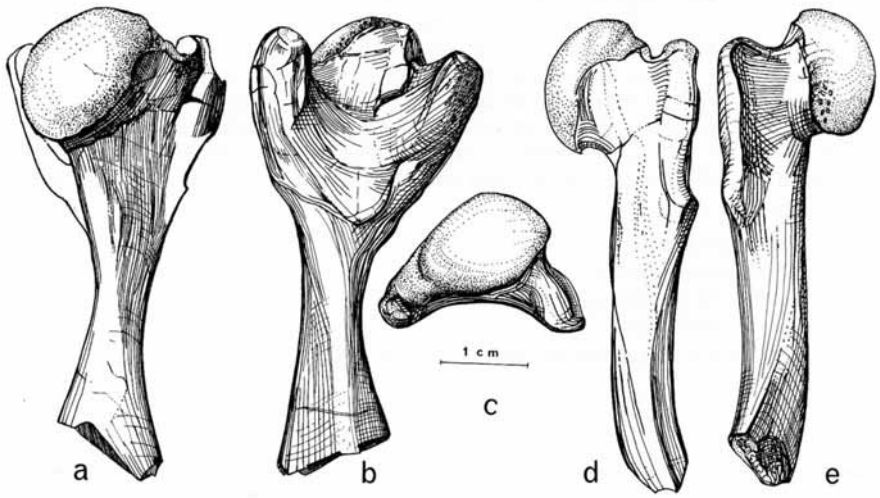
The pubis is stout and consists of a thick dorsal part, triangular in section, forming the anterior part of the acetabulum and carrying a stout, plate-like lateral process ending in a rugose cap that presumably made a ligamentous connection with the plastron. The medially directed process of the pubis is a thin, flat plate which lies at an approximate right angle to the lateral process. The medial part of the process is damaged but presumably formed a pubic symphysis with its fellow, and the posterior edge is finished in a manner indicating the presence of a large thyroid fenestra.

Hindlimb. Only the femur (text-fig. 9) and tibia of the left side are preserved. The femur has the very characteristic chelonian form of a large hemispherical head set to face dorsally. The anterior and posterior trochanters are also very large and developed to about the same extent as one another. Between them, on the ventral surface, is a broad fossa. The shaft narrows rather abruptly distal to the trochanters and then starts to widen again towards the distal end.

The tibia is not well preserved. Its head is expanded and flattened, and bears a well-developed cnemial crest on its mid-dorsal surface. The distal end is an incipiently double convex roller surface.

TEXT-FIG. 8. *Mesochelys durlstonensis*. Pelvic girdle in *a*, lateral; *b*, anterior views.





TEXT-FIG. 9. *Mesochelys durlstonensis*. Left femur in *a*, dorsal; *b*, ventral; *c*, proximal; *d*, posterior; *e*, anterior views.

DISCUSSION

In 1889 Lydekker erected a suborder Amphichelydia for those turtles which had not developed the distinctive features of either of the two living suborders, Cryptodira and Pleurodira. In more recent years it has become widely accepted that the Amphichelydia is an artificial taxon for generally primitive, mainly Mesozoic turtles which cannot as yet be allotted to their true respective phylogenetic places as primitive cryptodires, primitive pleurodires, or short-lived sidelines of chelonian evolution. The work of interpreting the amphichelydians in a more sophisticated way, work which must involve increasing knowledge of skull structure, has commenced largely as a result of two papers. Parsons and Williams (1961) studied the cranial anatomy of two Upper Jurassic forms from Portland and Solnhofen respectively and compared them with the extremely primitive Upper Triassic turtle *Proganochelys*. They concluded that the Upper Jurassic forms were essentially modern in skull structure and indeed they were unable to demonstrate a single character that was not represented in at least some of the extant turtles. This contrasted with the very primitive nature of the skull of *Proganochelys* and illustrated the imbalance of associating the Upper Jurassic forms with *Proganochelys* in a single sub-Order Amphichelydia to the exclusion of all the modern species. Parsons and Williams also noted that, to judge from the differences between their two forms, the Chelonia had already undergone a significant radiation by Upper Jurassic times.

The second important contribution to amphichelydian study was that of Gaffney (1972*a*) on the baenids, a group appearing in the Lower Cretaceous and hitherto regarded as relatively advanced amphichelydians. Quoting from his unpublished thesis (Gaffney, E. S. 1969, 'The North American Baenoidea and the cryptodire–pleurodire dichotomy', Ph.D. thesis, Columbia University, New York) Gaffney concluded that the Cryptodira can be distinguished from the Pleurodira on a number of very marked skull characters which appear to indicate a fundamental and presumably early dichotomy between the two groups, and that on these criteria the baenids must be regarded as members of the Cryptodira, despite their lack of the specializations of the postcranial skeleton found in living cryptodires. Furthermore, Gaffney showed that the Upper Jurassic form *Glyptops plicatulus* has a cryptodiran skull too. His taxonomic conclusion was that *Glyptops* and the baenids should be removed from the Amphichelydia and placed as the most primitive superfamily of the Cryptodira viz.

Suborder: CRYPTODIRA
  Superfamily: BAENOIDEA
    Families: GLYPTOPIDAE
              BAENIDAE.

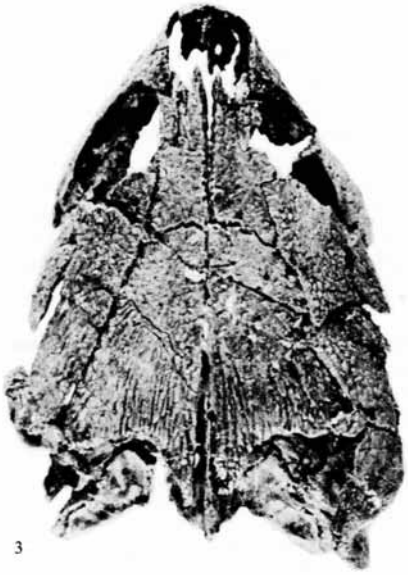
Glyptops is seen as the direct ancestor of the baenids.

EXPLANATION OF PLATE 4

Figs. 1–4. *Mesochelys durlstonensis* gen. et sp. nov. Skull of holotype. Cambridge University, Museum of Zoology, **T** 1041. 1, left lateral view. 2, right lateral view. 3, dorsal view. 4, ventral view, × 1·5.

1

2



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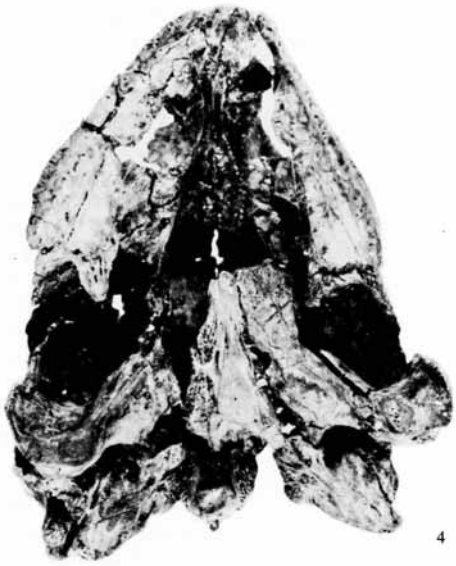


4

EVANS and KEMP, *Mesochelys*

The skull structure of *Mesochelys durlstonensis* indicates that it, too, is a cryptodire, that it is closely related to *Glyptops* and can thus be accommodated in the family Glyptopidae, and that it is, in fact, the most primitive turtle known subsequent to *Proganochelys*.

Of the diagnostic characters of the Cryptodira used by Gaffney (1972*a*), the following can be positively demonstrated in *Mesochelys*.

1. The position of the trochlea for the cartlago transiliens (sliding cartilage of the adductor tendon) is on the anterior edge of the otic chamber and not on a process of the pterygoid.
2. The pterygoid extends posteriorly between the quadrate and the braincase.
3. There is no canal separate from the canalis cavernosus whereby the hyomandibular branch of the facial nerve crosses the equivalent of the cranio-quadrate space. (In Gaffney (1972*a*, p. 249) this character is mis-stated. 'Hyomandibular nerve in its own canal . . .' should presumably read 'Hyomandibular nerve *not* in its own canal . . .' (Gaffney, pers. comm.).
4. Ossified epipterygoid present.
5. Foramen palatinus posterius is in the floor of the fossa orbitalis.
6. Canal for the vidian nerve ends just behind the foramen palatinum posterius.
7. Foramen supramaxillare present.
8. Descending process of the prefrontal meeting the vomer ventro-medially present.
9. Only the position of the mandibular artery and features of the lower jaw are indeterminate in the skull of *Mesochelys*.

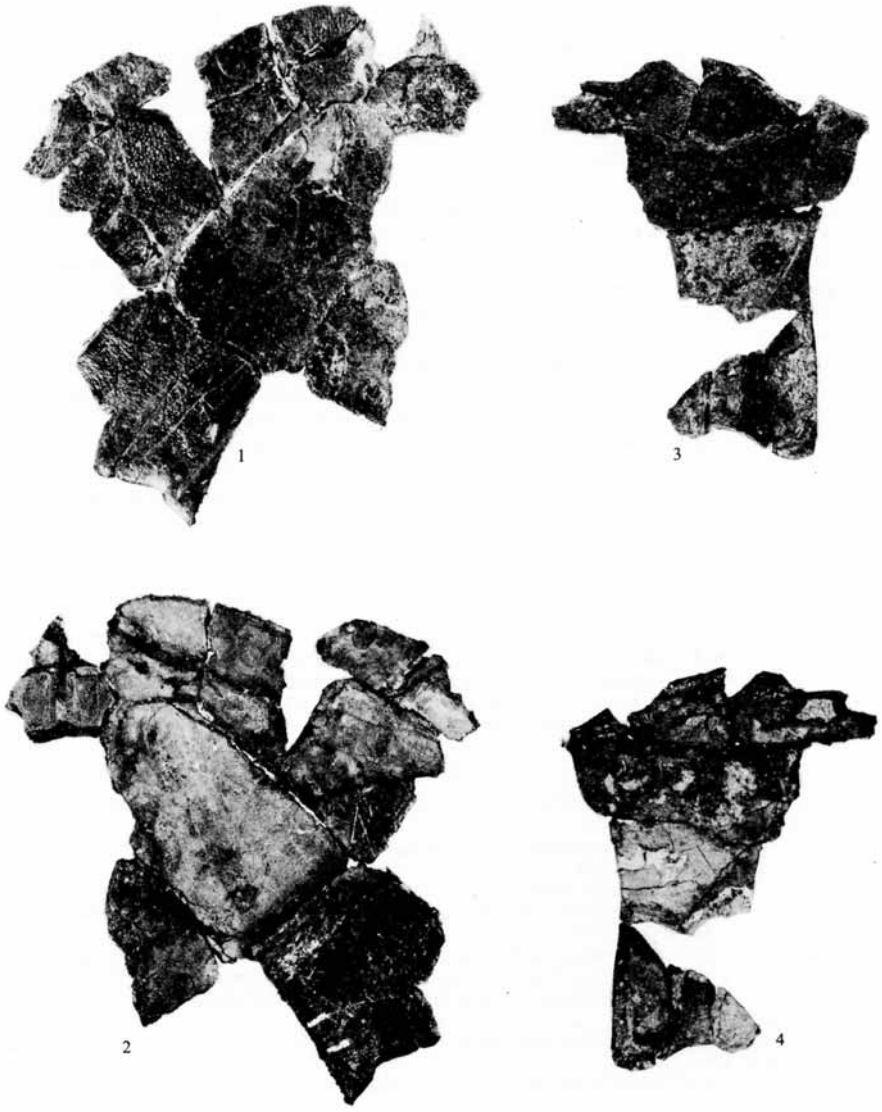
The features of the skull of *Mesochelys* which are probably primitive include particularly the organization of the basicranial axis. The basisphenoid completely separates the two pterygoids. At about mid-length along the suture, the basipterygoid articulation can be recognized in the form of a small spur of the lateral face of the basisphenoid fitting into a distinct pit in the medial face of the pterygoid. Anterior to this, the connection between the basisphenoid and each pterygoid is a very thin contact suggesting the relatively recent closure of an interpterygoid vacuity of the basic reptilian type noted in *Proganochelys* by Parsons and Williams (1961). The position of the foramen posterior canalis carotici interni at the level of the basipterygoid articulation is also a primitive reptilian character. Thus, although the nature of the suturing of the basicranial axis to the pterygoid is unquestionably chelonian in nature, the structure of this region in *Mesochelys* shows a greater similarity to the reptilian condition than in other turtles apart from *Proganochelys*. *Glyptops plicatulus*, however, appears to have a similar condition because although not known in detail yet, the basisphenoid does separate the pterygoids completely, and the position of the foramen posterior canalis carotic interni is about half-way down the length of that bone (Gaffney 1972*a* and pers. comm.).

A second primitive feature of *Mesochelys* which is shared by *Glyptops* is the failure of the pterygoid completely to floor the cavum acustico-jugularis, correlated with an extremely limited contact between the pterygoid and the basioccipital bone.

Thirdly, the pattern of roofing bones of the skull of *Mesochelys* is primitive in so far as it has certain basic reptilian features not found in combination in other turtles.

EXPLANATION OF PLATE 5

Figs. 1–4. *Mesochelys durlstonensis* gen. et sp. nov. Shell fragments of holotype. 1, fragment of carapace in external view. 2, same in internal view. 3, left xiphisternal region of plastron in external view. 4, same in internal view, ×0·8.



EVANS and KEMP, *Mesochelys*

A pair of nasal bones are present which make extensive contact with the frontals, and the dorsal exposure of each prefrontal is moderate, neither expanding to meet its fellow in the mid-line as in Parsons and Williams's Portland skull, nor being reduced as in typical baenids (Gaffney 1972*a*). The skull of *Glyptops* is slightly more specialized in that its maxillae meet medially and thus prevent the nasals from meeting the frontals (Gaffney manuscript). The prefrontal of *Glyptops*, however, is similar to that of *Mesochelys*.

These three primitive characters are not yet known in Jurassic or later turtles outside *Mesochelys* and *Glyptops* and, together with ossified epipterygoids, the narrow triturating surfaces (both probably primitive chelonian characters but which can be found in members of some later groups) relate the two genera in a family, Glyptopidae which is the most archaic family within the Cryptodira. Of the two, *Glyptops* is the more specialized, with a rather longer, narrower skull than *Mesochelys* and with the maxillae meeting in a brief contact mid-dorsally. The jugal is excluded from the orbital margin by a substantial contact between the postorbital and maxilla bones on the side of the skull. The most significant difference from *Mesochelys*, however, according to Gaffney's (manuscript and pers. comm.) account, is the shape of the quadrate bone. *Glyptops* is shown as lacking a postero-ventral extension of its quadrate so that an antrum postoticum is not developed. This is in marked contrast to the typical chelonian type of quadrate of *Mesochelys*. However, Gaffney notes that this region of his *Glyptops* material is badly damaged and so, in the light of the close correspondence of skull structure in these two forms in all other respects, it does seem likely that the appearance of the *Glyptops* quadrate is a result of this damage.

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