Memoirs of the Queensland Museum | **Nature 55(1)**

NOTE

Revision of *Flindersichthys denmeadi* Longman 1932, a marine teleost from the Lower Cretaceous of the Great Artesian Basin, Queensland

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ABSTRACT

Prepared and naturally exposed specimens of the large, fossil teleost, *Flindersichthys denmeadi* Longman, 1932, in the collections of the Queensland Museum, form the basis of a revision of this relatively common, carnivorous, Lower Cretaceous (latest mid to late Albian) marine fish. Originally described from a single specimen, this larger sample has enabled the skeletal morphology of the taxon to be amplified and, where necessary, clarified. *Flindersichthys* has been referred to the Order Elopiformes within the Superorder Elopomorpha but is considered *incertae sedis* at familial level. Nearly all referred specimens have been derived from marine sediments of the Toolebuc and Allaru Formations in the northern part of the Eromanga Basin, part of the Great Artesian Basin but rare occurrences are recorded from the Normanton Formation in the Carpentaria Basin. The morphological description remains incomplete, especially in the post-cranial area, with the material studied being almost exclusively cranial or from the very anterior of the body. □ *Teleostei, Elopomorpha, Elopiformes, Flindersichthys denmeadi; Lower Cretaceous (latest mid to late Albian); Great Artesian, Eromanga and Carpentaria Basins; Toolebuc, Allaru and Normanton Formations; Euroka Arch.*

Lower Cretaceous (latest mid to late Albian) marine sediments of the Great Artesian Basin in central Queensland, Australia, have long been the source of a rich suite of fossil vertebrates and invertebrates. The earliest described vertebrate taxa were identified in Etheridge (1872) and the fauna is now known to include a range of marine fishes comprising both chondrichthyans and osteichthyan actinopterygians, together with numerous marine reptiles and even terrestrial vertebrates that were washed or carried out into the epeiric sea or which died and were preserved in littoral or deeper water situations. Among the actinopterygians already recorded, Bartholomai (1969) has revised the pachyrhizodontid teleost, *Pachyrhizodus marathonensis* (Etheridge Jnr. 1905) and later (Bartholomai 2004) he revised the aspidorhynchid, *Richmondichthys sweeti* (Etheridge Jnr. & Smith Woodward 1891). The ichthyodectiform, *Cooyoo australis* (Smith Woodward 1894) was revised by Lees & Bartholomai (1987), while a probable neoteleost, *Dugaldia emmelta,* was described by Lees (1990). Kear (2007) added the pachycormid, *Australopachycormus hurleyi* Kear from the Toolebuc Formation near Boulia in the northwest of the Eromanga Basin portion of the Great Artesian Basin.

The current study represents a continuation of work on this latest mid to late Albian fish fauna. It is almost exclusively based on a review of exposed and acetic acid prepared specimens in the collections of the Queensland Museum, mostly those added over the last few decades

through field work by the author, his research assistant Ms Tempe Lees (retired), other staff of the institution, especially Mr Terry Tebble, Senior Preparator (retired) and through donations by members of the public,.

Almost all the fossil fish referable to *Flindersichthys denmeadi* have been derived from the marine Toolebuc Formation (with less from the Allaru Formation) in the northern Eromanga Basin, the largest part of the Artesian Basin. Indeed, no material referable to *Flindersichthys* has yet been discovered from the Eromanga Basin away from the inflow area across and below the basement Euroka Arch south of the current Gulf of Carpentaria and in the nearby Hughenden- Richmond area of north-central Queensland. Rare occurrences do occur further north of the Euroka Arch, within the Carpentaria Basin, from near Weipa, Cape York and at the Little Bynoe River crossing, in marine sediments interpreted as the Normanton Formation. Dating of the Toolebuc Formation as latest mid to late Albian is based on its correlation with the *Pseudoceratium ludbrookiae* dinoflagellate zone and the upper *Coptospora paradoxa- Phimopollenites pannosus zone* (Moore et al. 1986; McMinn & Burger 1986). A more refined age of early Late Albian for the Toolebuc has been suggested by Henderson (2004), based on ammonite and nannofossil biostratigraphy, with the Formation being no older than the upper *Prediscosphyraera columnata* zone and no younger than the *Mortoniceras inflatum* zone. However, the less precise age has been applied in the current work. The Toolebuc contributes only some 5-35 m of the total ca.2 km thickness of Lower Cretaceous marine sediment in the Eromanga Basin. The Allaru Formation deposited conformably on the Toolebuc is much thicker than the Toolebuc but is also considered to be of Late Albian age, again within the *P. pannosus* zone (Burger 1986). The Normanton Formation is generally regarded as having been deposited during the early Cretaceous.

Marine incursions into the Great Artesian Basin during the Lower Cretaceous were relatively short lived. Surface expression of the sedimentary deposits is extensive but poor because of extremely shallow dips and low topographic elevation. These physical characteristics have resulted in deep weathering and limited exposures through erosion of the predominant Toolebuc facies, viz. coquinite and organic-rich shale (Henderson 2004). Fortunately, many of the fossils found at the surface exist as the nucleus around which calcium carbonate was deposited within the sediments, creating hardened calcareous concretions. These appear to be related to the coquinite units and are often exposed on the surface by deflation or are concentrated in such gullies and streams as are rarely encountered. More complete teleost skeletons, not covered by concretionary structures, have been discovered in the coquinite units during recent excavations by the Kronosaurus Korner Museum, Richmond (Stumkat, *pers. comm.*).

The fossil fish remains in the current study are therefore predominately of cranial specimens preserved in concretions, occasionally including partial skeletons that are mostly of the anterior of the body. Scattered, disarticulated material is present and there are very rare instances where more complete skeletons have been encountered. Most species, including *F. denmeadi,* are represented by large to very large individuals. The occasional presence of more complete skeletons and identification of new taxa, regardless of the completeness of the material, encourages the continuation of further exploration, as does the presence of masses of disarticulated bones of very small individuals that are occasionally found in the coquinites at the surface. Small actinopterygians have also been encountered rarely in cores recovered from depth in the sequence (e.g. Parfrey, 1990).

The fossil fish fauna in general has come from the arc of sediments stretching from near Hughenden, in the northeast of the Eromanga Basin westwards through and above Richmond and Julia Creek and then down to beyond Boulia, in the northwest of the Eromanga Basin. The age attributed to the fauna suggests it has the potential to add to a better understanding of early teleost radiation in the oceanic and near-oceanic waters off the dispersing Gondwanaland tectonic plates. Unfortunately, Lower Cretaceous (Aptian) sediments from within the Great Artesian Basin have limited fossil fish records. Specimens from above and close to the Euroka Arch duringthe later Toolebuc-Allaru times must have had ready access to tidal, oceanic waters from the north, with the majority of fish finds continuing around the north and northwest of the Eromanga Basin, in keeping with a suggested anti-clockwise current flow within the epeiric sea. Glikson & Taylor (1986) concluded that the Euroka Arch intermittently restricted the area south of the Gulf of Carpentaria and that facies changes show that the eastern side of the entry strait across the Arch, from which a concentration of fossil fishes has been located, was shallow for a greater distance from land than usual. The entry was partially blocked by the N-S St. Elmo Structure towards the west. Depositional conditions in both Toolebuc and Allaru times are discussed in Wade (1993), as well as in Henderson (2004).

ABBREVIATIONS USED IN TEXT FIGURES

ace . . . . . . anterior ceratohyal
ang . . . . . . angular
ao . . . . antorbital
apal. . . . . . autopalatine
art . . . . articular
asp . . . . . . autosphenotic
bh . . . . basihyal
boc . . . . . . basioccipital
brr . . . . branchiostegal ray
bsp . . . . . . basisphenoid
cl . . . . cleithrum
de . . . . dermethmoid
den . . . . . . dentary
df. . . . . dilatator fossa
dhh . . . . . . dorsal hypohyal
dpal. . . . . . dermopalatine
d.pl . . . . . . dental plate
ecp . . . . . . ectopterygoid
enp . . . . . . endopterygoid
epo . . . . . . epiotic
exo . . . . . . exoccipital
fahm . . . . . hyomandibular facet
fica . . . . . . foramen for internal carotid artery
fm . . . . foramen magnum
foa . . . . foramen for orbital artery
fr . . . . frontal
fsp . . . . foramen for occipital nerve
fuv. . . . . . . fused vertebral centrum
hm. . . . . . . hyomandibular
ic . . . . intercalary
io . . . . infraorbital (1-5)
iop. . . . . . . interoperculum
l.e . . . . lateral ethmoid
mes . . . . . mesethmoid
mpt . . . . . metapterygoid
m.s.c . . . . . mandibular sensory canal
mx. . . . . . . maxilla
op . . . . operculum
ors . . . . orbitosphenoid
ot.s.c . . . . . otic sensory canal
pa . . . . parietal
par. . . . . . . parasphenoid
part.p . . . . postarticular process
pce . . . . . . posterior ceratohyal
pcl . . . . postcleithrum
pec f . . . . . pectoral fin
pmx. . . . . . premaxilla
pop . . . . . . preoperculum
pro . . . . . . prootic

pro.ic . . . . prootic-intercalar bridge
psp . . . . . . pterosphenoid
ptf . . . . post-temporal fossa
pto. . . . . . . pterotic
ptfc . . . . . posterior opening of pars jugularis
ptt . . . . post-temporal
qu . . . . quadrate
rart . . . . . . retroarticular
scl . . . . supracleithrum
sc pl. . . . . . sclerotic plate
smx . . . . . . supramaxilla (1-2)
so. . . . . supraorbital
soc. . . . . . . supraoccipital
soc sp . . . . supraoccipital spine
sop . . . . . . suboperculum
so.s.c. . . . . supraorbital sensory canal
stt . . . . supratemporal
sy. . . . . symplectic
tpbh . . . . . basihyal tooth plate
vhh . . . . . . ventral hypohyal
vo . . . . vomer
I . . . . foramen for olfactory tract
II . . . . foramen for optic tract
VIIhm . . . . foramen for hyomandibular trunk of facial
VIIot . . . . . foramen for otic branch of facial
IX. . . . . foramen for glossopharangeal
X . . . . foramen for vagus

SYSTEMATIC DESCRIPTIONS
AND DISCUSSIONS

Division Teleostei

Superorder Elopomorpha

Order Elopiformes

Family *incertae sedis*

Discussion. Reference of fossil taxa within an acceptable Linnean classification is problem-atical in most instances for those that, in the fauna are shown to possess generalised elopomorph characters. Forey et al. (1996) indicate that the elopomorph fishes, including those referable to the Order Elopiformes, have a rich but patchy fossil record extending back to the Lower Cretaceous (Valanginian) and even to the Upper Jurassic (Kimmeridgian) where *Anaethalion* is concerned (see Forey 1973), considerably earlier than the marine Lower Cretaceous (Albian) sediments from which *Flindersichthys* has been recorded. However, these authors acknowledge the generalised features of many elopomorph fossils that result in their relegation as *incertae sedis* at various ranks and conclude that a number of older taxa traditionally referred to the Elopiformes should be regarded as Elopomorpha *incertae sedis.* Nonetheless, it has been considered reasonable to adopt a less conservative position in regard to the present taxon (see below).

It has been felt prudent to maintain an *incertae sedis* status for *Flindersichthys,* at the familial level, rather than to refer it to the Family Megalopidae, action taken by Taverne (1999) in regard to the somewhat similar elopiform, *Arratiaelops,* from the Lower Cretaceous Wealdon of England and Belgium.

Flindersichthys Longman, 1932

Flindersichthys Longman, 1932: 89; Taverne, 1999: 91-3.

Generic Diagnosis (emended). A very large elopiform with prognathous lower jaw, reaching in excess of 1.25 metres in total estimated body length. Neurocranial roof moderately broad, slightly depressed posteromedially. Maximum depth of neurocranium at occipital region. Orbit relatively small. Dermethmoid laterally with prominent, elongated, posteroventral processes and broad, medial, dorsal ridge, terminating in elevated opening above anterior of elongate, interfrontal fontenelle. Rostral absent. Outer margin of olfactory capsule defined anteriorly by dermethmoid process and posteriorly by

lateral ethmoid below and by rarely preserved, relatively small supraorbital above. Antorbital present. Nasal plate-like. Parietal subovate but sometimes squarer anteriorly, longer than broad. Supraoccipital with strong posterior spine. Dilatator fossa elongate, anteriorly deep, shallow, partially roofed along its entire length by the pterotic, reduced posteriorly by prominent, curved ridge forming roof of hyomandibular facet. Strong, subparallel ridges occur longitudinally on the pterotic, parietal and the back of the frontal. Exoccipital excluded from margin of post-temporal fossa. Intercalar contributes significant-ly to the prootic-intercalar bridge. Autosphenotic spine extended posteroventrally into stout, lateral ridge. Descending lamina of frontal 'V' shaped, large, dished and deeply plicated longitudinally meeting anterodorsal margins of autosphenotic and pterosphenoid and posterodorsal margin of orbitosphenoid. Orbitosphenoid very large, extended dorsoventrally and anteriorly by ossified interorbital septum reaching to parasphenoid, with large, prominently walled foramen posteroventrally. Parasphenoid near planar, deepening into inverted 'Y' shape anteriorly, ventrolaterally supported to below orbit by posteriorly tapering vomerine processes. Vomer with small, multiserial, villiform teeth. Dermopalatine with larger teeth. Endo-pterygoid and metapterygoid very large. Maxilla extends posteriorly well beyond level of orbit. Sclerotic plates present. Circumorbital series incomplete above orbit. Jaws massive, with dentary shallower anteriorly and with relatively low coronoid process. Retroarticular not fused. A relatively extensive external part of the angular anteriorly meets the dentary and posteriorly joins with the retroarticular to produce prominent postarticular process. Mandibular sensory canal opens medially. Ang-ular and articular contribute to articulatory cup internally, separated by prominent fissure. Gular elongate but narrow. Dentition on premaxilla, maxilla and dentary of very small, multiserial, villiform, conical teeth represented mainly by

hollow, circular bases, set on expanded oral plates that often extend beyond the buccal margins. Occasional slightly larger, slightly recurved teeth occur internally. Hyomandibular with elongate process strengthened by strong, medial, angular ridge. Anterior ceratohyal very large, posteriorly deep, fenestrated towards dorsal margin. At least 14 pairs of branchiostegal rays present. Operculum and suboperculum large. Supratemporal extremely large. Ganoine present. Pectoral splint and at least 15 pectoral fin rays present. Vertebrae large, cylindrical, much shorter than high, laterally with numerous, fine, longitudinal striae.

Type and only species. *Flindersichthys denmeadi* Longman, 1932.

Flindersichthys denmeadi Longman, 1932
(Figs 1-8).

Flindersichthys denmeadi Longman, 1932: 69-97; Taverne, 1999: 91-3.

Specific diagnosis (emended). As for the genus.

Holotype. QMF2210, nearly complete skull, Flinders River, one mile east of Richmond, NCQ., from sedi-ments now interpreted as Toolebuc Formation.

Material examined. QMF2388, partial posterior of skull and anterior of body, Hughenden district, NCQ. QMF5780, partial skull, crushed dorsoventrally, Stewart Creek, Hughenden, NCQ. QMF5798, partial skull, 'Boree Park' Station, west of Richmond, NCQ. QMF11042, posterior of neurocraium, Little Bynoe River crossing, NCQ. QMF12878, incomplete skull and body, 'Toronto Park' Station, 3 km. east of homestead in gully on ridge above creek, Toolebuc Fm., NCQ. QMF13735, QMF13736, QMF13769, QMF13797, QMF13800, QMF13804, QMF13809, QMF13811, QMF13848, QMF13888, partial skeletons, 'Dunraven' Station, nr. Hughenden, banks of unnamed branch of Stewart Creek, NCQ. QMF13720, nearly complete skull, 'Dunraven' Station, nr. Hughenden, unnamed tributary of Stewart Creek, NCQ. QMF13714, partial skull, 'Dunraven' Station, nr. Hughenden, Stewart Creek, west of Pelican Bore, NCQ. QMF13743, QMF13755, QMF13813, partial skeletons, 'Dunraven' Station, nr. Hughenden, Stewart Creek, downstream from Pelican Bore, NCQ. QMF13707, QMF13715, QMF52273, partial skull, 'Dunraven' Station, nr. Hughenden, cobble

bed nr. Pelican Bore, NCQ. QMF13719, QMF13737, QMF13807, partial skeleton, 'Dunraven' Station, nr. Hughenden, Stewart Creek, upstream from junction with Soda Creek, NCQ. QMF13808, partial skeleton, 'Dunraven' Station, nr. Hughenden, Stewart Creek, upstream from Pelican Bore, NCQ. QMF15215, partial skull, 'Dunraven' Station, nr. Hughenden, NCQ. QMF13601, posterior of skull and anterior of body, 'Dunraven' Station, nr. Hughenden, at Pelican Bore, NCQ. QMF15986, partial skeleton, 'Alderley' Station, via. Hughenden, NCQ. QMF18916, skull and partial body, upper tributary of Myall Creek, 'York Downs' Station, nr. Weipa, Cape York, at 12º 40'S and 142º 22'E, mapped as undifferentiated Rolling Downs Group but most probably Normanton Fm. based on BMR Weipa 1 drill core, of Albian age, Carpentaria Basin (see Smart *et al.,* 1980). QMF52274, almost complete skull, 'Dunraven' Station, steep gully of Stewart Creek, at 20º 29.98´ S, 148º 55.5´ E, NCQ.

Formations and Age. Marine Toolebuc and Allaru Formations of Lower Cretaceous (latest mid to late Albian) age and Normanton Formation of Early Cretaceous age.

Description. A very large species with an estimated length exceeding 1.25metres and with an estimated body depth of more than 30 cm.

Neurocranium. The neurocranium is slightly less than three times as long as deep. Width of the neurocranium is often difficult to assess accurately because of distortion that is usual during preservation. However, it appears that maximum width across the occipital region, is only slightly more than across the area of the autosphenotic ridges. Maximum depth is in the occipital area. The orbit is relatively small and comprises about 17 % of the total length of the neurocranium.

The dermethmoid is a thin element forming the anterior end of the neurocranial roof. The bone is elongate, anteriorly narrow and broadest posteriorly and is constricted in dorsal view about one-third its length from the front. It is broadly 'V'-shaped anteriorly in dorsal view and anteriorly possesses a low, broad, median swelling becoming a well-defined ridge running longitudinally; this opens posteriorly through a large, slightly elevated and anteriorly directed pit at the anterior of an interfrontal fontenelle. A poorly developed groove parallels the lateral margin of the anterior point. No ethmoid commissure appears present. The front of the ethmoid area slopes posteroventrally and is sometimes separated by an unossified area from the mesethmoid below. The mesethmoid bears a maxillary facet on each side, behind the broadly pointed tip. It is possible that a further facet exists along each of the converging surfaces of the anterior point to accommodate the dorsal wing of the premaxilla. Ventral to the maxillary facet, the mesethmoid carries an articulating surface for contact with the autopalatine head. Internally, the ethmoid area appears largely cartilaginous posteriorly in some specimens. The anterior of the mesethmoid is narrowly dumbbell-shaped above the anterior of the vomer and appears to then expand posteriorly to broadly support the upper surface of that bone. A prominent, elongate, lateral process of the dermethmoid curves posteroventrally from near the middle of the dorsal margin, delimiting the anterior and anteroventral parts of the olfactory capsule. The lateral process is, in turn, sutured to the supraorbital and lateral ethmoid, towards the back and also below the lateral and posterior margins of the olfactory capsule. The dorsal surface of the dermethmoid in front of the anterodorsal margin of the olfactory capsule is shallowly indented to accommodate the front of the nasal.

The frontals make up the major part of the skull roof. Each frontal meets that of the other side along a medial, longitudinal suture that becomes interdigitated posteriorly. The lateral margin progressively widens above the lateral ethmoid. Anterior to this, the dorsal surface of the frontal is pointed to above the front of the olfactory capsule where it meets the back of the dermethmoid. It also provides the margin of the unossified, interfrontal fontenelle that variably separates the frontals anteriorly. Above the
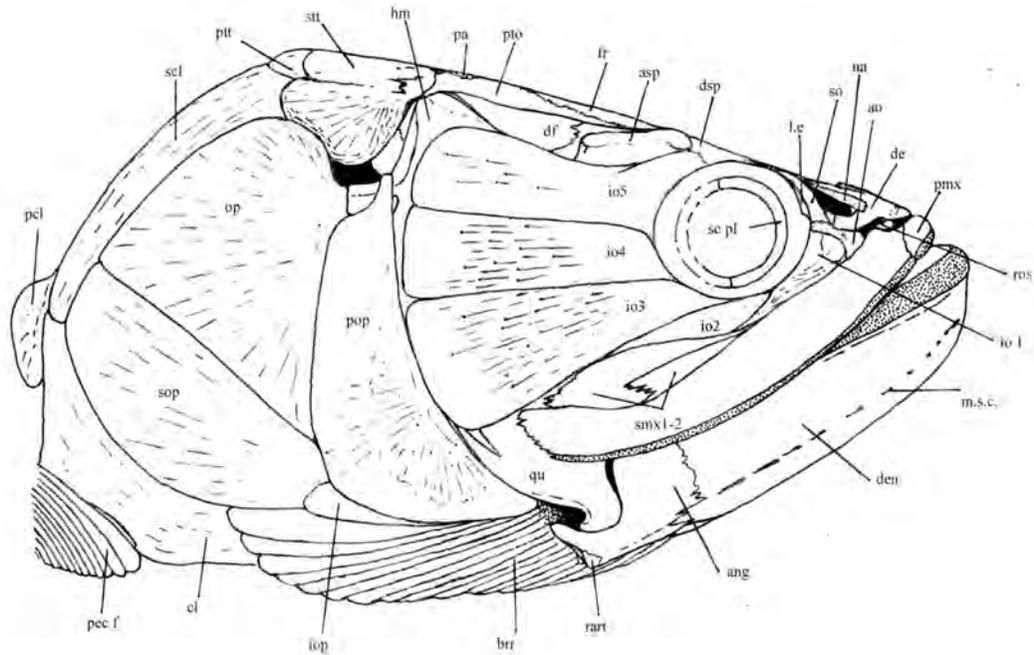
FIG. 1. *Flindersichthys denmeadi* Longman. Composite reconstruction of cranium in right lateral view; length ca. 31.8 cm.

orbit the lateral margin again expands before being gently concave for a relatively short distance, reflecting the presence of a relatively small eye. Greatest width of the frontal occurs above the autosphenotic. The frontal then narrows posteriorly to its junction with the parietal. The dorsal surface of the cranium along the medial suture is shallowly depressed in the posterior moiety but this is often accentuated by lateral or dorsoventral crushing during preservation. The supraorbital sensory canal is roofed and lies within a longitudinal ridge that extends from near the anterolateral margin behind the nasal, continuing back to the surface of the parietal. Strong subparallel, near longitudinal, subsidiary ridges emanate from above the middle of the autosphenotic and the main ridge onto the parietal while others

pass posterolaterally onto the pterotic. Pores associated with the supraorbital sensory canal system occur irregularly towards the inner ends of some of the shallow grooves between the subsidiary ridges, especially posterolaterally and on the parietal. Ventrally, below the orbit, the frontal has a prominent, dished, 'V'-shaped descending lamina that is characterised by numerous, deep, longitudinal placations that often separate variable small to very small foramina. The lamina meets the dorsal part of the autosphenotic within the orbit, as well as the pterosphenoid and orbitosphenoid along its raised rims.

The nasal is rarely preserved and is only known from its anterior moiety. It is a thin, plate-like bone and carries the supraorbital sensory
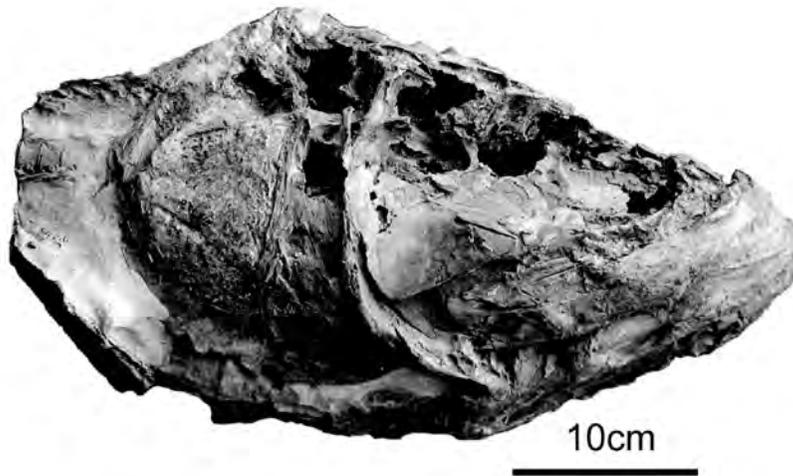
FIG. 2. *Flindersichtyys denmeadi* Longman. QMF13720, view of right side of incomplete skull (prepared by acetic acid treatment), unnamed tributary of Stewart Creek, 'Dunraven' Station, nr. Hughenden, NCQ., length 48 cm.

canal and would have covered much of the dorsomedial margin of the olfactory capsule.

No rostral element has been identified.

The parietal is a relatively small, irregularly ovate bone that is sometimes more squared anteriorly in some specimens. It is longer than broad and meets its counterpart along the midline except for a short distance posteriorly where the supraoccipital intrudes onto the dorsal surface for a short distance. The dorsal surface is ornamented by the extension of the main ridge of the supraorbital sensory canal and subsidiary ridges that are subparallel with the midline.

The posterolateral part of the skull roof is formed by the dorsal portion of the prominent pterotic. This forms the bulk of the roof of the post-temporal fossa. The posteromedial margin meets the dorsal part of the epiotic along a sinuous junction. The dilatator fossa is moderately elongate, anteriorly deep and shallow and is contributed to and partially roofed along its length by the lateral margin of the pterotic, which extends anteriorly to above the middle of the autosphenotic ridge. The dilatator fossa is limited posteriorly by a strong, obliquely anteroventrally curving ridge that excludes the fossa from the posterolateral corner of the neurocranium and forms the upper rim of the hyomandibular facet. The lower rim of the hyomandibular facet provides the roof of the relatively shallow sub-temporal fossa. Medially, the pterotic contributes to the lateral wall of the post-temporal fossa. Posteriorly, it contributes only relatively minimally to the dorsolateral margin of the post-temporal fossa external to its junction with the epiotic and above the dorsally extended intercalar. The dorsal surface of the pterotic is ornamented by continuations of the relatively strong, subparallel, subsidiary ridges, slightly angled away from the main supraorbital sensory canal ridge and pit lines from the supraorbital sensory canal are present posterolaterally.
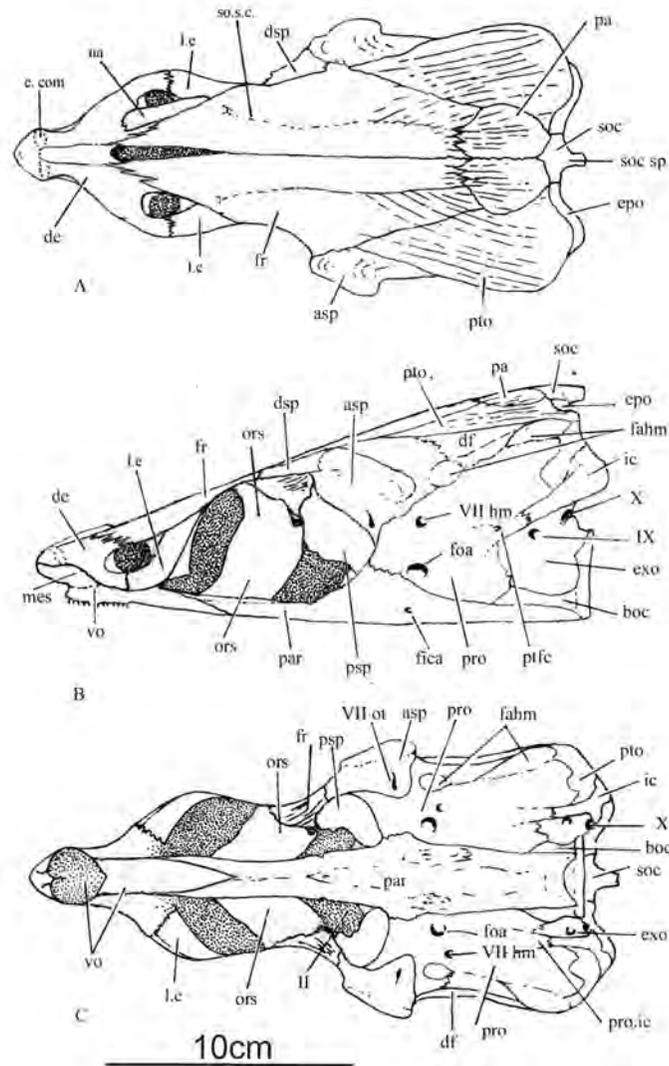
FIG. 3. *Flindersichthys denmeadi* Longman. Composite reconstructions of neurocranium. A, dorsal view; B, left lateral view; C, ventral view.

The epiotic is visible posteriorly and dorsally, the latter comprising a minor expansion along the posterodorsal margin of the neurocranial roof, together with a knob-like epiotic process development. The epiotic also forms almost all the medial margin of the opening of the post-temporal fossa and contributes to its medial wall but joins with the intercalar in excluding the exoccipital from the ventromesial margin of the post-temporal fossa. It is slightly dished across the posterior surface but not to the extent of forming a subepiotic fossa.

The supraoccipital is a relatively small bone which, posteriorly lies between the epiotics and posterodorsally extends onto the dorsal surface between the back of the parietals. It is shield-shaped in posterior view and possesses a stout, dorsomedial spine, directed posteriorly from the upper part of the posterior surface (2.7 cm long in the holotype). The bone is slightly dished across the posterior surface.

The exoccipital is excluded from contributing to the margin of the opening of the post-temporal fossa by the epiotic and intercalar. It meets its counterpart in a vertical junction above the foramen magnum but does not appear to meet below this foramen. It is dished inwards in posterior view but not developed into a definable subepiotic fossa. A small foramen is present for the occipital nerve, close to the foramen magnum. The exoccipital has a short junction with the intercalar posterolaterally and a much longer junction with the epiotic posterodorsally. The back of the lateral face of the exoccipital is not well preserved. However, a large foramen for the vagus nerve is present. Anteroventrally to this is a slightly smaller foramen for the glossopharangeal nerve. Ventrally, the exoccipital curves deeply over the dorsal surface of the basioccipital and then curves sharply anterodorsally towards and then below the anterior base of the intercalar-prootic bridge.

The intercalar forms a large cap over the posteroventral corner of the base of the opening of the post-temporal fossa. It is particularly well developed between its junctions with the exoccipital, epiotic and pterotic within the fossa. The posteroventral corner of the post-temporal fossa margin is extended backwards to form an angled knob on the intercalar to support the ventral limb of the post-temporal bone. Although the full extent of the anterior extension of the intercalar on the lateral face of the neurocranium has not been observed, a strong base for an anterior ridge is present as a significant contribution to the prootic-intercalar bridge standing clear of the neurocranial wall below the subtemporal fossa.

The basioccipital is broadly 'W'-shaped in posterior view with the central part contributing the posterior myodome. The posterior portion of the basioccipital extends dorsally to meet the exoccipital and is firmly united with a thin vertebral centrum that is often difficult to recognise as discrete in adult specimens. In younger individuals, the vertebra tapers dorsally in lateral view. Dorsally there is a short autogenous neural arch and spine but there are no pits developed to accommodate these on the dorsal surface of the attached vertebra. In lateral view, the basioccipital extends to the prootic along a near 45°, posterodorsally angled junction that reaches the anterior base of the exoccipital. The longitudinal junction with the exoccipital is broadly convex ventrally.

The prootic is imperfectly preserved anteriorly in all specimens and this may reflect poor ossification of this element. It is a relatively large bone. The lateral face is extended posteriorly into the anterior moiety of the prootic-intercalar bridge and contributes the bulk of the anterior of the relatively deep, subtemporal fossa. Foramina for the hyomandibular trunk of the facial nerve and for the orbital artery are well developed towards the anterior of the lateral face of the prootic and many small foramina

are present immediately anterior to the base of the prootic-intercalar bridge. Above the base of the bridge, the junction of the prootic and exoccipital is penetrated by a foramen, believed to be for the jugular vein.

The autosphenotic is large and has an expanded anteroventral face that descends medially from a longitudinally elongated, 'ridge-like' autosphenotic spine, curving broadly then flattening below the frontal and then recurving to meet the posterolateral part of the pterosphenoid. The opening for the otic branch of the facial nerve is close to this contact. The autosphenotic also has an extensive junction anterodorsally with the back of the prominent, 'V'-shaped descending lamina of the frontal. The anterior of the hyomandibular facet is partially accommodated on the posterior of the bone.

The pterosphenoid anterodorsally has a significant, raised contact with the descending
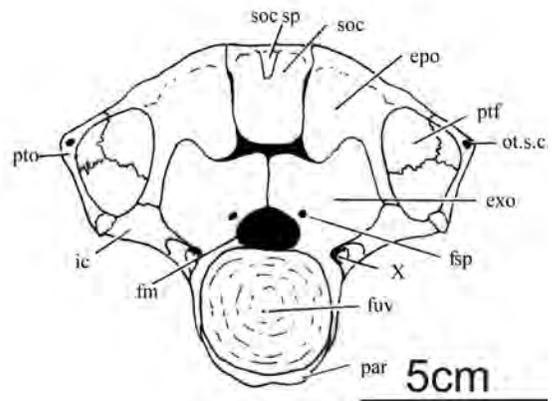

FIG. 4. *Flindersichthys denmeadi* Longman. Composite reconstruction of posterior of neurocranium.
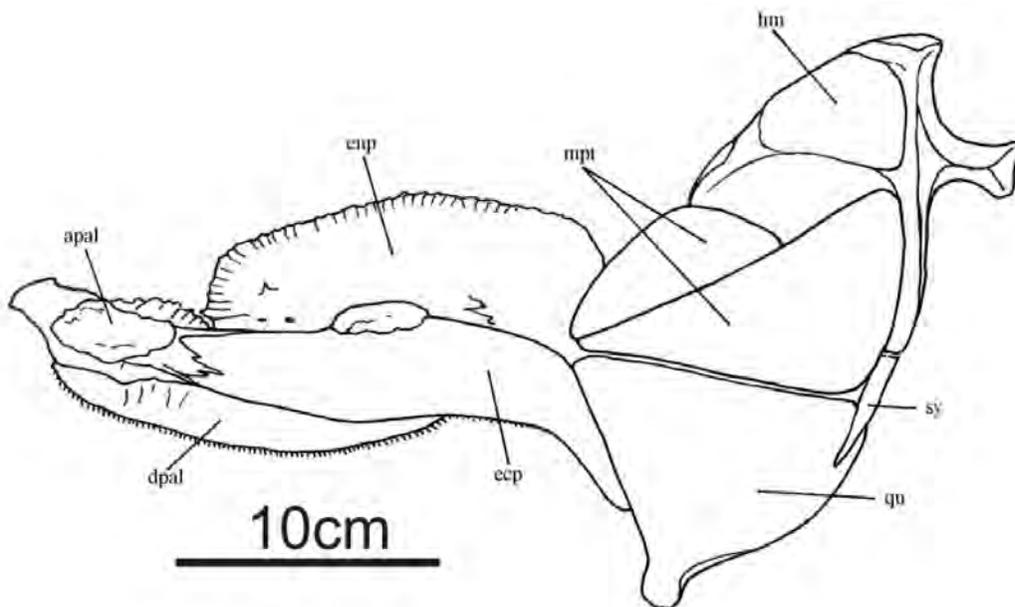

FIG. 5. *Flindersichthys denmeadi* Longman. Composite reconstruction of left hyopalatine bones in lateral view.
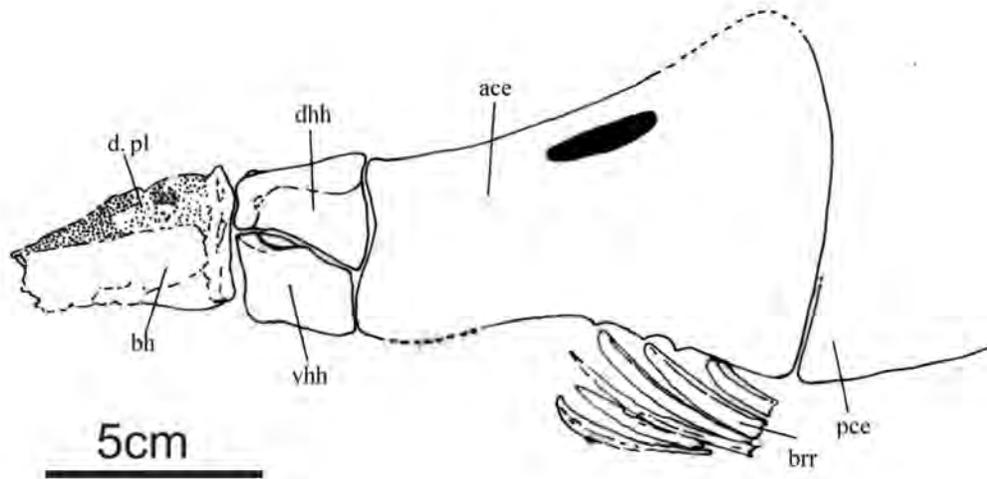
FIG. 6. *Flindersichthys denmeadi* Longman. Medial view of partial right hyoid bar and remains of anterior branchiostegal rays in QMF5798.

lamina of the frontal and a short contact with the orbitosphenoid, behind the raised wall of the large foramen at the back of that element. The bone also appears to provide a dorsal margin for the large opening for the optic tract.

The orbitosphenoid is a very large element, ventrally extending well anterior to the pterosphenoid. Posterodorsally, the bone unites with the anterior of the large, 'V'-shaped, descending lamina of the frontal along a raised rim. The dorsal part of the orbitosphenoid is laterally bulbous. An extensive, ossified, interorbital septum is present and its contact with the orbitosphenoid is sometimes deeply and coarsely interdigitated but the junction is often difficult to see. The contact is 'Y'-shaped in section and the anteroventrally angled septum meets the upper surface of the parasphenoid over an elongated contact. Posteriorly, the orbit-

osphenoid bears a large, foramen in front of the short junction with the pterosphenoid, surrounded by high walls around its base. The anterior margin of the orbitosphenoid is occasionally overlain by irregular flanges of bone from the lateral ethmoid.

The basisphenoid has not been identified in any specimen.

The lateral ethmoid is large and is curved anteroventrally to contact the posterior of the lateral dermethmoid process, below the anterior of the supraorbital. It also underlies the supraorbital below the back of the olfactory capsule, where it contacts the mesethmoid medially. It provides smooth anterior and dorsal upper surfaces for the front of the orbit and appears to meet its counterpart from the other side at the midline. It is sutured to the frontal posteriorly and is sometimes incompletely

ossified where it meets and sometimes overlaps the anterior of the orbitosphenoid. The dorsal surface in some specimens appears to be exposed minimally between the back of the olfactory capsule, the possible lateral margin of the nasal and the supraorbital. Anteroventrally, it is terminated medial to this area by a large cartilaginous meniscus but does not otherwise meet the parasphenoid.

The parasphenoid is elongate and near planar, extending posteriorly from its contact with the vomer but is not well exposed in most specimens. It extends back to a position near the posterior rim of the basioccipital. Towards the junction with the vomer, the bone deepens dorsally assuming an inverted 'Y'-shape and is sandwiched laterally between the posterior arms of that bone. It is relatively narrow below the orbit, broadening posteriorly and forming the anterior floor of the posterior myodome. The central area is ventrally produced into a sharp, strongly developed median ridge, below the orbital area. This is reduced to a more rounded ridge anterior to the ascending wing, immediately anterior to an elevated medial foramen, presumably for the buccohypophysial canal. The bone then subdivides into two irregular and bulbous areas before reducing rapidly to reach the attached vertebra of the basioccipital. The notch between the posteriorly arms is penetrated by a large foramen leading into the myodome. The anterior of the base of each of the posterior arms is penetrated by a well defined foramen for the internal carotid artery. The posterior of the broad, ascending wing is slightly longer than the anterior and is produced dorsally. A small area of villiform teeth exists on the ventral surface of the parasphenoid below the back of the orbit in some individuals.

The vomer is incompletely exposed in all specimens. It is broadly attached to the base of the mesethmoid. It appears to have a broadened, heart-shaped dentigenous head covered with villiform teeth that are somewhat smaller than those on the dermopalatine. The middle of the toothed surface appears to have been longitudinally subdivided by an area of even smaller teeth. It extends and tapers posteriorly below the anterior of the parasphenoid and has elevated wings that sandwich the sides of the anterior of the parasphenoid.

Very large anterior sclerotic plates are present but posterior plates have been preserved only rarely.

Hyopalatine bones. The series is deeper than it is long in adult specimens, with the quadrate-mandibular articulation lying well behind the back of the orbit.

The hyomandibular is angled slightly posterior to the vertical. The head of the bone has anteriorly inclined, anterior and posterior articulating surfaces that fit into the relevant parts of the hyomandibular facet. Externally, the surface is marked by a strong ridge descending from below the posterior part of the head of the bone. Posterior to this ridge is a deep groove separating it from a short, thin posterodorsal margin above the opercular process. The opercular process is elongate and is strengthened by a sharply crested central ridge that merges with that from the posterior head of the bone. A sharp ridge curves anterodorsally from the main body of the bone, broadening to the anterior head of the bone. The anterior of the hyomandibular is expanded transversely and longitudinally into a cup-shaped surface. The area between the anterior ridge and the dorsal margin was thin, as was that ventral to the anterior ridge. The ventral limit of the main shaft of the bone appears to broadly abut the symplectic.

The symplectic is rarely seen but is elongate, curved and inclined anteriorly at approximately 45° to the vertical. It fits into a deep groove in the back of the quadrate and is partially overlain by the preoperculum over much of its length.

The quadrate is a very large, large fan-shaped bone. Posterodorsally, the back of the bone behind the deep notch for the symplectic, continues the scooped surface from the hyomandibular to accommodate the anterior base of the preoperculum. The external ridge formed by this, extends to just above the expanded condylar surface. Posterior to the condyle is a notch that probably limited the extent of the gape. The dorsal margin of the quadrate has a cartilage connection with the shallow groove along the ventral edge of the metapterygoid. Anterodorsally, the quadrate is laterally shelved to accommodate the uppermost supramaxilla.

The metapterygoid is a significant element. The thin posterior of the bone is broadly curved to fit into the cup-shaped anteroventral surface of the hyomandibular and preoperculum. It is flexed along a line approximately 30° to the horizontal that separates the bulk of the bone from a thin, anterodorsal wing that overlaps the back of the endopterygoid and part of the anteroventral margin of the hyomandibular. A partially separated, well-defined ridge is occasionally present along the flexure anteriorly.

The endopterygoid extends posteriorly to be overlapped laterally by part of the metapterygoid. The bone is thin and has a broadly convex dorsal margin. It is also shallowly curved medially along a longitudinal line. The bone is relatively deep, meeting the ectopterygoid along an elongated junction and apparently overlies part of the dermopalatine. Teeth appear to have been lacking on the endopterygoid.

The ectopterygoid is reasonably well-exposed in the holotype. It is shallow anteriorly, with a dorsolaterally developed process, presumably to support infraorbital bones. The posterior moiety of the bone is curved ventrally to meet the quadrate along the upper two-thirds of its anterior margin. The ventral margin of the ectopterygoid overlies the upper margin of the dermopalatine. The bone appears to be edentulous.

The autopalatine is ossified but appears to be edentate. It interdigitates deeply with the ectopterygoid. It is irregular dorsally and carries a large articulating surface for cartilaginous contact with the lateral ethmoid. Anteriorly, it has a strong, elongate process for additional articulations with the mesethmoid and maxilla.

The dermopalatine is plate-like and very elongate and carries multiserial, recurved teeth that were at least as well developed or even larger than the largest of the teeth on the jaws and are developed in continuity with those of the vomer. It extends anteriorly below the autopalatine to meet the back of the vomer.

Dermal upper jaw. The upper jaw extends from the tip of the snout, somewhat posterior to the anterior of the symphysis of the lower jaws, back to below the posterior of the orbit. The premaxilla is small, comprising slightly less than 14% of the total length of the upper jaw. The upper jaw is gently convex laterally over its posterior moiety, with the maxilla becoming more convex anteriorly towards the snout. Convexity increases even more around the anterior of the premaxilla. The oral border is gently sinuous in lateral view.

The premaxilla is relatively deep anteriorly, with its maximum depth equal to about 80% of its length. The bone tapers posteriorly, meets its counterpart medially and overlies the anterolateral base of the maxilla. The oral border is gently transversely curved into a plate-like structure that extends outwards beyond the line of the bulk of the external surface. The oral plate bears numerous, very small, multiserial, villiform teeth (ca. 400 per square centimeter). Nearly all have been lost n preserved specimens and are represented only by their shallow, round sockets.

The maxilla is elongate and relatively robust. Measurements for its length vary from 17.5 cm. to 25.2 cm. while maximum depth ranges from 3.1 cm to 4.0 cm. Anteriorly, the maxilla

is ventrolaterally grooved to accommodate the overlying end of the premaxilla. It also extends and curves dorsomedially and is raised into a simple rounded head that would have abutted the anterolateral surface of the mesethmoid. Posterior to this articulating surface and internally, there is an emargination of the inner surface of the maxilla that together with a strong, elongate but low dorsal process for the cartilagenous attachment of the front of the palatine. The maxilla is deepest below the orbit (ca. 20% of its length) becoming slightly shallower posteriorly. However, its minimal depth occurs immediately posterior to the palatine attachment. The dorsal margin in lateral view is shallowly curved below the orbital area and is grooved dorsolaterally to accommodate the supramaxillae over the posterior moiety. The grooving does not reach the thin posterior margin, which is ornamented with a number of fine, near-longitudinal ridges. As with the premaxilla, the oral border is plate-like and is expanded laterally along its entire length as a slightly transversely convex platform that provides a base for numerous, small, multi-serial, villiform teeth, largely represented by their sockets. These are circular and shallow and are present in similar numbers to those on the premaxilla. Teeth are rarely preserved but, where present, are small to very small, conical or slightly recurved and are enameled. Posteriorly, the tooth plate extends slightly beyond the lateral surface of the bone.

Two supramaxillae are present, partially overlying each other. The anterior supramaxilla is extended as a narrow spine to below the middle of the orbit. Its anterior limit is slightly overlain by a weakly developed and thin dorsal flange from the maxilla and extends only slightly more anteriorly than the overlying anterior spine of the posterior supramaxilla. The lateral face of the anterior supramaxilla bears an irregular, longitudinal, shallow groove that disappears ventrally. Posterodorsally, the
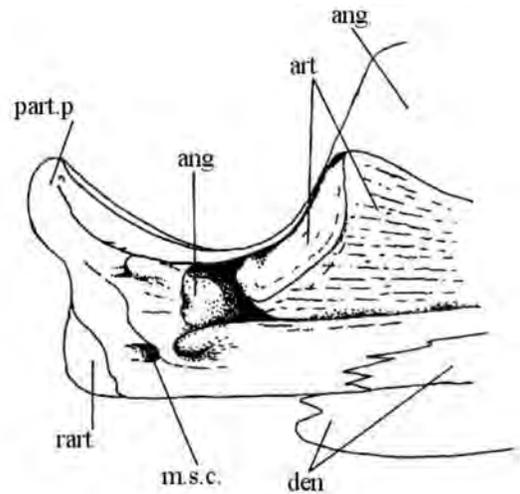

FIG. 7. *Flindersichthys denmeadi* Longman. Composite reconstruction of medial view of posterior of left mandible, mostly from QMF52273, approximately natural size.

bone is extended into a point set at about 60° to the horizontal that is ornamented dorsally for a short distance by an area of minor serrations. The posterior supramaxilla is a hook-shaped element whose anterior and anteroventral margins are slightly overlain by the anterior supramaxilla. The bone extends anteriorly in a narrow spine and is posterodorsally flanged and irregularly serrated at the margin to overlie the quadrate. The posteroventral expansion loosely overlies the upper margin of the maxilla and is also irregularly serrated at its margin. The dorsal part of the bone is thin and steps up abruptly to the much thicker ventral part. The longitudinal base of the step is slightly grooved and bears shallow pockets mesially.

Mandible. Regardless of the fact that the mandible protrudes in front of the premaxilla, giving the mouth an upwardly directed, prognathous gape, the total length of the lower jaw is only slightly longer than that of the upper jaw. The symphysis is relatively shallow and slopes

posteriorly, giving the skull a rounded anterior outline in lateral view.

The dentary forms more than two-thirds of the mandible. The thin ventral margin is considerably inflected. The anterior of the dentary is markedly curved inwardly towards the symphysis. In lateral view, the oral margin is slightly concave and the dentary increases gradually in depth below this margin to a maximum depth anterior to a relatively weakly developed coronoid process. Teeth are borne on the surface of a transversely flattened to slightly convex oral plate. The teeth are rarely preserved but are represented by circular sockets of numerous, small, multiserial, villiform teeth. Where present, these are tiny, enamel-capped and often slightly recurved. The oral plate expands posteriorly and is generally extended beyond the lateral surface of the mandible. The plate is sometimes free of the extreme posterodorsal surface of the dentary, indicating presence of cartilage in young individuals. The longitudinal base of the lateral surface of the mandible is broadly rounded above the well defined groove that separates this surface from the expanded and inflected ventral flange. The ventral flange extends backwards over the entire length of the dentary and is deepest about one-third the distance back from the symphysis. At least nine large foramina for the mandibular sensory canal are present within the longitudinal groove in the dentary.

The posterior of the dentary laterally overlies a moderately large angular. Near the posteroventral corner of the mandible, this has a short, angled, sutured junction with the retroarticular. A well-defined groove is present immediately above the ventral margin of the angular, overlying the posterior of the mandibular canal. The angular is ornamented with relatively coarse ridges that are slightly inclined from the horizontal. Dorsally, it provides the lateral rim of the articulatory cup and extends around and higher than the posterior of the cup, being

produced into a strong, extended, postarticular process. Internally, the angular and articular bones are distinct, with each contributing to the articulatory facet. The posterior, angular part of the facet is separated from the articular part by a transverse, presumably cartilage-filled fissure. The mandibular sensory canal opens medially above the retroarticular.

The retroarticular caps the posteroventral corner of the mandible. It extends anterolaterally to unite with the angular and posteriorly forms a truncated, near vertical back to the lower one-third of the postarticular process. Internally, it remains distinct and does not contribute to the articulatory facet. A small nugget of bone is present internally within the posterior surface of the mandible on some specimens and this is interpreted as an endosteal articular element. However, there does not appear to be any connection between this and the symplectic.

Circumorbital series. The circumorbital ring is poorly preserved or absent in all specimens. Dorsal components are rarely preserved and individual elements are often difficult to distinguish from underlying bones. Most, especially those in the cheek, were very thin and were generally distorted and fragmented during preservation where they were preserved.

The antorbital is present meeting the anterior base of the supraorbital. It barely reaches the anterior margin of the orbit below the lateral and posterior margins of the olfactory capsule. It is sigmoidal in shape and expands ventrally, while broadly meeting the anterior of the first infraorbital.

The supraorbital meets the antorbital towards the middle of the lateral margin of olfactory capsule and extends backwards, tapering above the anterodorsal margin of the orbit. It is a relatively small bone that also lies along the outer margin of the anteroventral process of the lateral ethmoid and the posterior and posterolateral margins of the olfactory capsule.
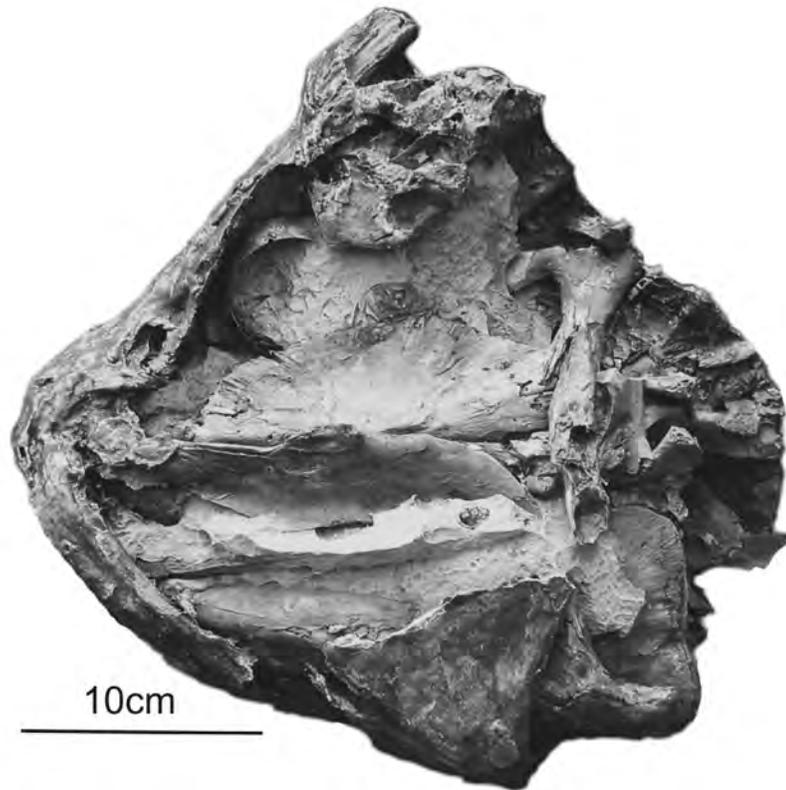
FIG. 8. *Flindersichthys denmeadi* Longman. QMF52273, view of left side of anterior of skull showing dermethmoid and olfactory capsule, anterior hyopalatine bones and remains of displaced gill arches, 'Dunraven' Station, nr. Hughenden, cobble bed nr. Pelican Bore, NCQ.

The anteroventral margin is ornamented with short digitations. Posteriorly, it does not reach the anterior of the dermosphenotic but terminates bluntly against the frontal, leaving the circumorbital ring incomplete.

The first infraorbital appears relatively well developed as an elongated sub-triangular element contributing the anterior and anteroventral margins of the orbit. It tapers posteriorly along its base and is ornamented by a number fine ridges that give the surface the appearance of a series of small, lozenge-shaped components.

The second infraorbital is not well represented but appears sigmoidal in shape. It is a small bone, tapered anteriorly and posteriorly, contributing the middle of the ventral orbital margin above the anterior spines of the supramaxillae. The third infraorbital appears to have been the largest element, elongate and deep. It has a thickened anterodorsal margin that carries the infraorbital sensory canal. The fourth infraorbital is also large and provides the posterior part of the orbital margin. The fifth infraorbital is elongate and large. In lateral view it expands

anterodorsally, in front of and below the autosphenotic ridge and provides the posterodorsal margin of the orbit. Foramina for the infraorbital sensory canal vary greatly in size. Those in the first infraorbital appear very small, while that in the third infraorbital is quite large with the opening supported by marginal ridges. Ornamentation of infraorbitals 3-5 is only present over part of their surfaces and comprises numerous, short ridges, subparallel to the upper and lower margins, attenuated anteriorly and thickened posteriorly. A thin covering of ganoine is present.

The dermosphenotic is a truncated wedge-shaped element and is inserted anterior to and around the front of the autosphenotic ridge and above the back of the orbit. It is penetrated by several large pores from the infraorbital sensory canal and has a rugose dorsal surface. Ventrally, it has numerous, very short, pointed projections. The anterior of the dermosphenotic is rough but did not meet the posterior of the supraorbital.

Hyoid arch, gill arches and gular plate. The ceratohyal is composed of both anterior and posterior parts, united by cartilage. The posterior ceratohyal has not been completely exposed in any of the prepared specimens and evidence for the presence of an interhyal is also lacking. The anterior ceratohyal is a very large bone, much deeper posteriorly than anteriorly. Posterior depth of the anterior ceratohyal varies from 6.5 cm to 9.6 cm. It is thickened at its anterior margin but is relatively thin posteriorly. It is strongly fenestrated close to its dorsal margin about half- way along its length.

The upper and lower hypohyals are separated from one another and from the front of the anterior ceratohyal by short gaps that would have been filled with cartilage in life. The upper hypohyal is much larger than the lower and its anterior curves medially. Its anterior margin appears thicker than its posterior margin.

Several small knobs are present anterolaterally on its dorsal surface, presumably to lie against the basihyal. A foramen exists on the inner side of the upper hypohyal for the passage of the afferent hyoidean artery, although this foramen would normally be expected on the dorsal surface of the bone. The lateral surface of the upper hypohyal bears a significant foramen close to its posterior margin. A broken end of an oval-sectioned bone lies between the upper parts of the two upper hypohyals. This is probably an ossified part of the urohyal.

A plate covered with very fine rounded tooth sockets, similar to those on the mandibular and maxillary tooth plates, is present anterior to the upper hypohyals. This is interpreted as a basihyal toothplate and was possibly associated with underlying bone, interpreted as part of the basihyal. This has a posteroventral articu-lation to meet the processes of the hypohyals. The element appears to be about as long as the hypohyals.

Gill arches are generally incomplete and usually displaced. Those in QMF52273 are the best yet observed and are illustrated in Figure 8. It is likely that those exposed mostly represent anterior elements. They include parts of what are believed to be hypobranchials (possibly 1 and 2). Part of an anterior end of a ceratobranchial has a greatly deepened ventral flange immediately behind its articulatory end, separated from the medial body of the element by a sharply angular ridge that strengthens posteriorly up the face of the bone, broadening the dorsomedial surface. The most obvious component comprises a very large, robust epi-branchial, probably epibranchial 1. Distally, this presents a large, oval socket, set at a right angle to the proximal head of the bone. It is 12 cm. long and 4.1cm. wide at its proximal end. The uncinate process is robust, short and only slightly separated by a shallow groove. A strong flange defines a deep medial groove, broadening the width of the body of the bone

towards its centre. Remains of a further wide epibranchial (possibly epibranchial 2) with its uncinate process lost and lacking its distal moiety is preserved immediately posterior to the possible epibranchial 1. This has an angular anterolateral margin and is deeply 'spoon'-shaped along the medial shaft of the bone, at which point it is 2.2 cm. wide. A partial, stout, short infrapharangobranchial (possibly the first) is present above the possible epibranchial 1 and the back of the neurocranium. Numerous disassociated tooth plates bearing sockets for minute, multiserial, villiform teeth are widely distributed among the gill arch elements. No attempt has been made to reconstruct the gill arch because of the uncertainty relating to identi-fication of the component elements.

There are at least 14 branchiostegal rays present on each side. The most anterior of these are subdivided towards their tips while the posterior rays are increasingly spathiform. At least the first five rays of the series are attached to the ventral margin of the anterior ceratohyal, which is scalloped to receive them.

The gular plate is elongate, extending poster-iorly to below the articulatory cup. It is relatively narrow and bears broad, concentric, posteriorly convex ridges. Its posterior margin tapers and is marked by a central emargination.

Opercular series. The preoperculum is a large bone, with a relatively elongate, curved lower margin to below the middle of the quadrate and a more gently curved posterior margin from above the anteroventral limit of the operculum. It has a raised anterior rim. This provides a smoothly concave anterior face that is more deeply developed from about the middle of the metapterygoid to the mid-quadrate. The raised rim fits behind the raised posterior of the quadrate. The dorsal moiety of the anterior rim of the preoperculum fits and supplements the main ridge of the hyomandibular, ventral to the level of the opercular process. The preo-

percular ridge is ornamented by short, irregular ridges and grooves that parallel the anterior face of the bone in the upper two-thirds of the structure. The dorsal margin of the bone is extended into an elongated dorsal process lateral to the opercular process. The anterior moiety of the bone is thickened, especially ventrally and is often separated abruptly from the thin posterior of the element. At least nine foramina are present along the posterior base of this thickened anterior rim, associated with the preopercular sensory canal. The posterior of the rim is gently curved back onto the dorsolateral surface of the bone, becoming more angular ventrally. A series of minor, irregular, ridges radiate across the surface from the back of the rim, opposite the level of the dorsal limit of the quadrate.

The operculum is a large element, apparently rounded ventrally but with a prominent post-eroventrally inclined demarcation above the ventral edge, set at about 40° to the horizontal. The bone articulates with the opercular process of the hyomandibular and this is achieved through a short but broad, anterolaterally and slightly dorsally directed process and facet. Below this process, the anterior margin is stepped medially to allow the back of the preoperculum to slightly overlie it. A slightly raised ridge closely parallels this step and is occasionally better developed. This appears to carry a sensory canal that opens through foramina. The surface of the operculum is ornamented by a radiating series of shallow grooves emanating from behind the articulating process and the surface is sometimes dimpled.

The suboperculum is also a large, elongate, deep element, extending slightly beyond the front of the operculum. It has a curved lower margin that is ornamented by fine ridges para-lleling much broader and stronger, flattened ridges that radiate from a centre about one-third the distance from the anterior of the element. The upper one-half of the bone is occasionally

somewhat rugose and is overlain to a reasonable degree by the ventral edge of the operculum.

The interoperculum appears to have been a small element.

Pectoral girdle and fin. The supratemporal is considered here, although it is not strictly a part of the pectoral girdle. It is an extremely large, thin element, extending from the back of the braincase to near the dorsal end of the supra-cleithrum, covering much of the post-temporal. It curves ventrolaterally to a rounded lower margin and has a bilobate posterior margin with the smaller upper lobe separated from the lower by a cleft. The supratemporal commissure is at least partially open, with several deep, longitudinal grooves running posteriorly from near the front of the upper moiety. Fine ridges paralleling the lower margins are supplemented by similar ridges radiating across the lower surface.

The post-temporal is a smaller, flat plate of bone that is slightly convex laterally. Its dorsal margin is slightly convex and posteriorly curls into a broad groove on the supracleithrum. The middle of its anteroventral margin is extended into a blunt, obtuse, triangular point separating two shallow indentations. Much of the bone underlies the supratemporal. The middle projection of the anteroventral margin has a large foramen ventrally associated with the lateral line. This opens from a roofed canal that itself opens into a groove along the margin, towards the supracleithrum. The ventral inter-calary limb is acutely angled ventrally and is slightly curved ventrally but is slender, linking the bone to the back corner of the post-temporal fossa. A process to the epiotic process has not been observed. Additional foramina penetrate the lateral surface in the ventral moiety of the bone.

The supracleithrum is a very large bone that is dorsoventrally deep and slightly convex laterally, more so in the area of an extended posterodorsal process that underlies the post-temporal. In this area the bone is thin but the anterior of the bone is much thicker. The external surface anteroposteriorly is moderately convex and is extended along its front margin into a broad, convex plate that underlies the operculum and is separated by a significantly concave upper margin from the posterodorsal process. The lateral line canal is externally roofed, running obliquely across the upper part of the bone to a posteriorly directed foramen and groove at the back of the medial surface. The supracleithrum is ornamented by weak, dorsoventral ridges and a deep medial groove from near the middle of the upper part of the lateral surface.

The cleithrum is a large element that curves anteroventrally and that has a wavy external surface. A large, near vertical, roofed canal extends within a well-defined plication from a large foramen at the ventral margin. The dorsal margin of the cleithrum extends beneath the ventral part of the supracleithrum.

A moderately large, thin, postcleithrum is present behind the junction of the cleithrum and supracleithrum. This is ornamented with fine radiating ridges. Other post-cleithral elements have not been observed.

The coracoid is elongate and has a slightly concave ventral margin. It forms a sharp keel ventrally where it meets its counterpart from the other side. Between the coracoid and the cleithrum there is a large interosseous foramen. Posteriorly, the coracoid contacts the scapula laterally. Its contact with the mesocoracoid has not been observed.

The scapula spreads over the inner side of the cleithrum and encloses the scapular foramen. Support for the first of the fin rays is directly to the endochondral girdle but radial elements have not been preserved.

At least 15 pectoral fin rays are present but are only known proximally. A pectoral splint is present.

Vertebral column. No specimen in the available collections possesses a complete vertebral column. It is thus impossible to assess the number of vertebrae present. Vertebral centra are large, near cylindrical, with anterior centra circular in section and much shorter than they are deep. All are amphicoelous and pierced by the notochord. Laterally, all centra are marked by very fine longitudinal ridges, many of which subdivide or anastomose. Neural arches are autogenous and each centrum bears two deep pits dorsally to accommodate them. Anterior neural arches are expanded and bear strong, slender, straight neural spines that are separate from their counterparts and that are marked by a central groove. The centrum present as part of the neurocranium lacks dorsal pits and the first neural arch is not as expanded as those following. Parapophyses are present on all anterior vertebrae except that attached as part of the neurocranium. These are more ventral on the most anterior centra and are positioned progressively more dorsally along the abdominal part of the column.

Other skeletal elements. These are not present in the available sample.

DISCUSSION

Taverne (1999), in describing the genus, *Arratiaelops* from the Early Cretaceous Wealden of Europe, has analysed characters that could be considered to determine the superordinal position of that taxon. Six were regarded as supportive of assigning the genus to the Elopomorpha, these being :

(1) oral dentition borne on dental plates;

(2) retroarticular fused to angular (a principal apomorphy of Elopomorpha, see Nelson, 1973);

(3) premaxillae articulate with the mesethmoid;

(4) parasphenoid has lost its basipterygoid process;

(5) hyomandibular has a long, narrow shaft; and

(6) pectoral fin has a pectoral splint.

Of these, *Flindersichthys* clearly possesses characters 1, 4, 5 and 6 and is believed to possess character 3. To these, Forey et al. (1996) additionally regarded the presence of rostral ossicles a putative character of elopomorphs but this character was not emphasised by Taverne (1999). No rostral ossicle has yet been observed in *Flindersichthys* .

Regarding fusion of the retroarticular and angular, Nelson (1973) suggested that the posterior of the primitive teleost mandible is comprised of three separate bones, the angular, the articular and the retroarticular. The Elopomorpha were regarded as derived because of fusion of the angular and retroarticular, with both elements contributing to the articularatory facet. *Flindersichthys* usually has the retroarticular separate from the angular, with the former not contributing to the jaw articulation. Only the British Museum (Natural History) specimen numbered P. 59694, illustrated by Taverne (1999) and undoubtedly referable to *F. denmeadi,* appears to have the retroarticular fused to the angular without an obvious suture, but the area of possible separation of the bones could have been obscured because of outward rotation of the oral margin of the mandible. Taverne (1999), however, states in his description that the retroarticular is fused to the angular. If this is so, then the character may be variable, reducing reliability of any suggestion that *Flindersichthys* is not an elopomorph. It is concluded that *Flindersichthys* should be included within the Superorder Elopomorpha and that early radiation within the Elopomorpha included taxa with a non-fused retroarticular.

Forey et al. (1996) concluded that the Elopomorpha contained three orders, the Elopiformes, the Albuliformes and the Notacanthiformes, with the Order Elopiformes embracing two families, the Elopidae and the Megalopidae. The Albuliformes were believed to include albulids, pterothrissids and possible stem-

group Cretaceous albulids (*Osmeroides* and *Brannerion*). Again, Taverne (1999) has provided apomorphic character states for *Arratiaelops* that serve to support referral of that genus to the Elopiformes. *Flindersichthys* has generalised morphology suggesting it also is referable to the Order Elopiformes. Applying Taverne's listed character states for the elopiformes, *Flindersichthys* has a very prognathous mandible, with a deep dentary; its post-temporal fossa is large and deep; it has a large, rounded, olfactory capsule, surrounded anteriorly by a lateral dermethmoid process and posteriorly by the lateral ethmoid (at least in part); however, the mesethmoid appears to be incompletely ossified in some individuals; parasphenoid dentition is reduced; the supratemporal is very large; and the parietal is penetrated by the supraorbital sensory canal. Referral of *Flindersichthys* to the Order Elopiformes is herein proposed, but with less certainty than at the superordinal level. Although *Flindersichthys* appears to super-ficially resemble the megalopid elopids, it is difficult to reconcile a number of its character states with diagnoses at the familial level, as outlined by Forey (1973). For this reason, the genus is considered *incertae sedis* below the ordinal level.

Longman (1932) observed that the holotype of *Flindersichthys denmeadi*, QMF2210, had been subjected to 'considerable distortion' with the roof of the skull crushed down obliquely, displacing several of the elements. The marked, longitudinal depression in the posterior of the neurocranial roof of the holotype, regarded by him as one of the morphological characters of diagnostic importance, is re-interpreted as being emphasised by the same distortion. The sample now available shows that nearly all specimens referred to *F. denmeadi* have been distorted to some extent, reflecting the position of the body at the time of burial and preservation and the relative low strength of many of the neurocranial elements. In some, e.g. QMF13714 and QMF13719,

lateral compression has resulted in the collapse of the neurocranial roof along the mid-line, giving the impression that the species in life was much narrower relative to its depth than it must have been. Other specimens (e.g. QMF12707, QMF13715 and QMF13888) were crushed dorsoventrally, artificially spreading the neurocranial elements, reducing the convexity of the skull roof and resulting in the impression of a more fusiform body shape than the animal had, in reality, during life. No specimen appears completely undistorted and the reconstruction of the skull in Figure 1 is based upon aspects of those individuals in which distortion is believed to have had minimal effect (e.g. the lateral view of the holotype, together with those of QMF13720 and QMF52274). QMF13720 is illustrated as prepared in Figure 2.

The additional material available has per-mitted a reassessment of the morphological characters considered by Longman (1932) to be of diagnostic significance in defining the taxon. A detailed composite reconstruction of the neurocranium in *Flindersichthys denmeadi*, based upon the holotype and referred material, is presented in Figures 3 and 4. Longman (1932) had suggested that the parietals were not separated posteriorly on the neurocranial roof. However, these elements are partially separated posteriorly by a short, anterior extension of the supraoccipital, similar to the situation observed by Forey (1973) in living *Elops hawaiensis* and *Tarpon atlanticus*. However, the parietals in *F. denmeadi* are usually relatively smaller bones. The 'oblique furrows' on the dorsal surface of the pterotic of the holotype, noted by Longman (1932), are present on all specimens studied but are variable in both strength and number from specimen to specimen and extend onto the frontal as well. The lateral spine of the autosphenotic, with its 'oblique trough' in its median surface (the anterior base of the dilatator fossa), also noted by Longman (1932), is present as a significant feature in all specimens where it

is preserved but again, it is somewhat variable. Longman (1932) regarded the autosphenotic spine in *F. denmeadi* as a remarkable feature in the supraorbital region and considered it 'perhaps as distinctive as that in … *Xiphactinus*'. Morphologically, the autosphenotic spines in these two genera are very different, with that in *Flindersichthys* being longitudinally and obliquely elongated in lateral extent and more appropriately described as an autosphenotic ridge, while that in *Xiphactinus* is distinctly peg-like (as depicted in Bardak, 1965).

Width of the neurocranial roof is quite variable, reflecting the extent and direction of the crushing that occurred during preservation, as well as the maturity of the individual at the time of death, together with intraspecific variation. Certainly, Longman's (1932) estimated width of at least 75 mm across the occipital area for the holotype, appears in error. The measure was at least 105 mm, in keeping with the autosphenotic width of 101 mm. Longman (1932) correctly noted that the autosphenotic width approximated that at the occipital margin.

The bone regarded by Longman (1932) as the suborbital plate is a part of the very expanded metapterygoid. A similar portion of a bone identified by Longman as a post-orbital plate is also part of the expanded metapterygoid, while the anterior of the bone considered by him to represent a preorbital part of the 'massive plate of bone' exposed in the cheek area is here shown to represent part of the endopterygoid. A composite reconstruction of the hyopalatine bones in *F. denmeadi* is provided in Figure 5.

The operculum in *F. denmeadi* is not sutured to the suboperculum as suggested by Longman (1932) but, as shown in Figures 1 and 2, their relationship includes ventral overlap (below an angled flexure on the operculum), with the overlap covering about 50% of the surface of the suboperculum.

Longman (1932) correctly suggested the presence of a gular plate. However, he mistook the flanged lower margins of the dentaries as part of a pair of gular plates. The single plate is narrow and elongate but is largely masked in the holotype. The holotype also exhibits parts of the anterior and posterior ceratohyals (the latter identified by Longman as an epihyal). Figure 6 is a composite reconstruction. Longman further suggested that there was a minimum of eight branchiostegal rays on each side, whereas the number is here shown to be at least 14. There is evidence on vertebral centra of the presence of a small, central perforation for a persistent notochord, a character that was considered absent by Longman (1932).

Circumorbital bones are very rarely preserved and, where present, are fragmented and distorted and difficult to separate from underlying elements. Apart from those positioned anteriorly and dorsally, they were generally very thin bones that were not strongly attached, although all were often lost before they were able to be preserved *in situ*. Those for QMF52274 are the best preserved but the reconstruction shown in Figure 1 is composite. The poor state of preservation of the base of the neurocranium, especially of the anterior of the prootic, is possibly attributable to thin bones as much as to crushing during fossilisation.

The massive expansion of the orbitosphenoid dorsoventrally and anteriorly by the ossification of the interorbital septum produces a development that parallels that of the ossified orbitosphenoid septum in some albuliformes (especially osmeroidids and albulids). This represents a significant morphological difference from described megalopids. However, *F. denmeadi* is not believed to be closely related to albuloids, differing in many characters including possession of covered sensory canals and large, sub-parallel post-temporal fossae; lack of a sub-epiotic fossa; presence of a larger intercalary and prootic-intercalar bridge;

and with the quadrate/mandibular articulation positioned well behind the orbit.

As noted above, the posterior of the lower jaw in *Flindersichthys* (Fig. 7) provides an interesting organisation of component elements. Nelson (1973) has reported on different patterns of bone fusion in this area of the lower jaws in a number of Late Mesozoic and Early Tertiary teleosts as a guide to clarifying relationships within the main groups. A prominent postarticular process of the angular bone is shown to be especially well developed in the Cretaceous forms. The articulatory facet in *F. denmeadi* is divided between two of the bones of the posterior of the mandible (unlike that in the pachyrhizodontids which Nelson records as being single and large, reflecting the fusion of the angular and articular, leaving the retroarticular separate). Nelson (1973) indicates that this arrangement in pachyrhizodontids is reflected in a medial opening of the mandibular sensory canal on the angular, more like that in the Ichthyodectiformes. An enclosed mandibular canal with the posterior opening positioned medially is a condition that Maisey & Blum (1991) conclude supports the view of Patterson & Rosen (1977) that this primitively characterises teleosts. In modern elopiform genera like *Elops* and *Megalops,* Nelson (1973) notes that the posterior part of the articulatory facet is partly separated from the articular portion by a transverse, cartilage-filled fissure and partly by the separation between the angular component and the articular bone. This is similar to the situation in *F. denmeadi* but the modern elopiforms mentioned lack the unfused retroarticular observed but possibly variable in *Flindersichthys.* It is possible that the presence of a usually separate retroarticular, medial opening of the mandibular sensory canal on the angular, separation of the angular and articular parts of the articulatory facet and the high postarticular process, as well as exclusion of the retroarticular from the articulatory facet,

define presumably more primitive character states retained in some lineages within the early elopiform radiation, including that containing *Flindersichthys.*

Again as noted above, Taverne (1999) in redescribing the European Lower Cretaceous elopiform *Oligopleurus vectensis* Smith Woodward, 1890 and assigning it to the new genus, *Arratiaelops,* compared it with an incomplete skull of *F. denmeadi,* numbered P. 59694 from the collections of the British Museum (Natural History). The specimen as illustrated (Taverne, 1999, fig. 11) is somewhat distorted, with a number of elements redistributed. With access to a larger sample in the current study, it is probable that some of Taverne's morphological interpretations may not be correct. The question of a fused retroarticular and angular has been addressed above. The relatively low postarticular process, as illustrated, may also reflect outwards rotation of the oral surface of the mandible. The identity of the two fragments identified as infraorbitals 1 and 2 are difficult to determine from the drawing but differ greatly from infraorbitals 1 and 2 in the Queensland Museum specimens. The dermal upper jaw has been illustrated below the main part of the skull, while the suggested basibranchial is comparatively too elongate and is most likely part of the endopterygoid. The suggested fibrous membrane of the eye is probably from the ossified interorbital septum. The dermethmoid does not appear to present a medial ridge and a pit at the raised anterior margin to the interfrontal fontanelle. Sufficient morphological distinctions exist, especially in the circumorbital series, the hyopalatine series and the internal bones of the orbital area, having regard to Taverne's (1999) description and illustrations for *Arratiaelops*, to conclude that *Flindersichthys* is distinct.

The dentition and other morphological features in *F. denmeadi* are not dissimilar to those in a number of other Cretaceous teleosts, both elopoid and albuloid. For example, Maisey

& Blum (1991) have shown almost identical dentition in the large albuloid, *Paraelops* Silva Santos, 1971, from the Lower Cretaceous Santana Formation, Lagoa de Dentro, Chapado do Araripe, Pernambuco, Brazil, South America, described as numerous, small and conical teeth, attached to inflated bony pads extending laterally onto labial surfaces of maxilla, premaxilla and dentary. The lateral expansion onto the dentary appears to have been even greater than in *F. denmeadi*. The similarity between the dentition in such genera and the nature of their support is considered to represent synapomorphy.

The presence of small, isolated teleost vertebrae within the mouth in QMF13720 and the nature of the dentition, supports the conclusion that *F. denmeadi* was a predator of as yet unidentified smaller, shallow water marine fishes. Almost all specimens here referred have been collected from sediments deposited close to the suggested inflow /outflow point for the marine transgressions and subsequent regressions to and from the epeiric sea of the Great Artesian Basin and the Carpentaria Basin. This suggests that *F. denmeadi* was probably not able to exist comfortably at any great distance from the open oceans and, as such was probably not greatly different or was even conspecific with contemporaneous, extracontinental elopomorphs.

LITERATURE CITED

Bardack, D. 1965. Anatomy and evolution of chirocentrid fishes. *Paleont. Contr. Uni. Kansas,* Vertebrata. **10**: 1-88.

Bartholomai, A. 1969. The Lower Cretaceous elopoid fish *Pachyrhizodus marathonensis* (Etheridge Jnr.). Pp. 249-263 *In* Campbell, K.S.W. (ed.) *Stratigraphy and Palaeontology. Essays in Honour of Dorothy Hill.* (Australian National University Press, Canberra.)

2004. The large aspidorhynchid fish, *Richmondichthys sweeti* (Etheridge Jnr and Smith Woodward, 1891) from Albian marine deposits of Queensland. *Memoirs of the Queensland Museum* **49**(2): 521-36.

Burger, D. 1986. Palynology, cyclic sedimentation and palaeoenvironments in the Late Mesozoic of the Eromanga Basin. Pp 53-70. In Gravestock, D. I., Moore, P.S. & Pitt, G.M., (eds). *Contributions to the Geology and Hydrocarbon Potential of the Eromanga Basin. Geoogical Society of Australia Special Publication,* **12**.

Etheridge, R. 1872. Description of Palaeozoic and Mesozoic fossils of Queensland. *Quarterly Journal of the Geological Society,* **28**: 317-360.

Etheridge, R. Jnr. 1905. Description of the mutilated cranium of a large fish from the Lower Cretaceous of Queensland. *Records of the Australian Museum* **6**: 5-8.

Forey, P.L. 1973. A revision of the elopiform fishes, fossil and recent. *Bulletin British Museum (Natural History),* Geology, Supplement **10:** 1-222.

Forey, P.L., Littlewood, D.T.J., Ritchie, P. & Mayer, A. 1996. Interrelationships of elopomorph fishes. Pp 175-191 In Striassny, M.J., Parenti, L. & Johnson, G.D. (eds) *Interrelationships of Fishes.* (Academic Press, San Diego)

Greenwood, P.H., Rosen, D.E., Weitzman, S.H. & Myers, G.S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin American Museum Natural History* **131**: 339-456.

Henderson, R.A. 2004. A mid-Cretaceous association of shell beds and organic-rich shale: bivalve exploitation of a nutrient-rich, anoxic sea-floor environment. *Palaios* 19: 156-69.

Kear, B.P. 2007. First record of a pachycormid fish (Actinopterygii: Pachycormiformes) from the Lower Cretaceous of Australia. *Journal. Vertebrate Paleontology* **27**(4): 1034-8.

Lees, T. 1990. A probable neoteleost, *Dugaldia emmelta* gen. and sp. nov. from the Lower Cretaceous of Queensland, Australia. *Memoirs of the Queensland Museum* **28**(1): 79-88.

Lees, T. & Bartholomai, A. 1987. Study of a Lower Cretaceous actinopterygian (Class Pisces) *Cooyoo australis* from Queensland, Australia. *Memoirs of the Queensland Museum* **25**(1): 177-92.

Longman, H.A. 1932. A new Cretaceous fish. *Memoirs of the Queensland Museum* **10**(2): 89-97.

Maisey, J.G. & Blum, S. 1991. *Pareolops* Silva Santos, 1971. Pp. 238-247 *In* Maisey, J.G. (ed.) *Santana Fossils : An Illustrated Atlas.* Contributions to IUGS Project No. 242, the Cretaceous of South America (T.F.H. Publications, Inc., Neptune City)

McMinn, A. & Burger, D. 1986. Palynology and palaeoenvironment of the Toolebuc Formation.

Pp 139-154. *In* Gravestock, D.I., Moore, P.S. & Pitt, G.M., (eds). *Contributions to the Geology and Hydrocarbon Potential of the Eromanga Basin. Geological Society of Australia Special Publication,* **12**.

Moore, P.S., Pitt, G.M. & Dettmann, M.E. 1986. The Early Cretaceous Coorikiana Sandstone and Toolebuc Formation: their relationship in the southwestern Eromanga Basin. Pp 97-114. *In* Gravestock, D.I., Moore, P.S. & Pitt, G.M., (eds). *Contributions to the Geology and Hydrocarbon Potential of the Eromanga Basin. Geogical Society of Australia Special Publication,* **12**.

Nelson, G. 1973. Notes on the structure and relation-ships of certain Cretaceous and Eocene teleostean fishes. *American Museum Novitates,* **2524**: 1-31.

Parfrey, S. 1990. Catch of the week. *Queensland Government Mining Journal,* June, 1990: 276.

Patterson, C. & Rosen, D.E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin, American Museum of Natural History* **158**(2): 81-172.

Silva Santos, R. da. 1971. Nouveau genre et epéce d' Elopidae du bassin sédimentairede la Chapada do Araripa. *Anais da Academia Brasileira de Ciências* **43**(2): 439-442.

Wade, M. 1993. New Kelaenida and Vampyromorpha: Cretaceous squid from Queensland. *Memoirs Association of Australasian Palaeontologists* **15**: 353-374.