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New teleosts (Elopomorpha: Albuliformes) from the Lower Cretaceous (Late Albian) of the Eromanga Basin, Queensland, Australia

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ABSTRACT

Descriptions of *Marathonichthys coyleorum* gen. et sp. nov. and *Stewartichthys leichhardti* gen. et sp. nov. add to the recognised diversity of the Lower Cretaceous (Late Albian) fish fauna of the marine Toolebuc Formation of the Eromanga Basin, Queensland, Australia. Both taxa are referable to the elopomorph Order Albuliformes. The new taxa are morphologically distinct from both extant and fossil albulids by having their subepiotic and subtemporal fossae poorly developed and in exhibiting separation or apparently partial separation of the parietals by dorsal development of the supraoccipital. The parietal in *Stewartichthys* is triradiate. Coarse ornamentation of the dorsal neurocranial roof and its much shallower and broader otic region separates *M. coyleorum* from *S. leichhardti*. *Euroka dunravenensis* Bartholomai, 2010, also from the Toolebuc Formation, is much larger than either of the new taxa and has its parasphenoid broadened, much shortened posteriorly and anteriorly complex. It is concluded that early evolutionary radiation of the Albuliformes in the Late Albian epeiric inland sea of the Eromanga Basin was reasonably extensive and diverse. □ *Elopomorpha*, *Albuliformes*, *Lower Cretaceous*, *Late Albian*, *Eromanga Basin*, *Toolebuc Formation*, *Marathonichthys coyleorum*, *Stewartichthys leichhardti*.

Mayrinck *et al.* (2010) outlined the history of the currently accepted classification of the elopomorph Order Albuliformes and phylogenetically significant characters. They noted that the order has low diversity and has uncertain internal and external relationships and suggested that the systematics of taxa within the group are therefore of particular interest. Recognition of two albuliform clades by Greenwood *et al.* (1966), the Albuloidae and the Halosauroidae, was modified by Forey *et al.* (1996), who concluded that the Suborder Albuloidae itself involved two clades with each including both extant and fossil taxa within the Families Albulidae and Pterothrissidae. In addition to fossils referred directly to these, a

number of taxa were considered plesions of the Albuliformes *sensu* Forey *et al.* (1996), viz. the Lower Cretaceous South American *Brannerion* (see, Blum 1991) and *Paraelops* (see, Maisey & Blum 1991) and the Upper Cretaceous *Osmeroides* from England (Forey 1973). Recent descriptions of additional plesions have added *Bullichthys* Mayrinck *et al.*, 2010, from the Romualdo Member of the Santana Formation of the Lower Cretaceous (Albian) of Brazil and *Beugeichthys* Filleul, 2000, from the Lower Cretaceous (Hauterivarian) of the Massif des Bauges, France.

During detailed examination of the fossil fishes in the collections of the Queensland Museum, it became apparent that additional

albuliform taxa were present in the marine sediments of the Toolebuc Formation of Lower Cretaceous (Late Albian) age, deposited in the north and central west of the Eromanga Basin of Queensland. Unfortunately, few robust morphological character states are represented in the partial neurocrania which are the basis for the descriptions of the new genera and species described herein. Each does exhibit a limited but interesting suite of characters that supports their referral to the Albuliformes *sensu* Forey *et al.* (1996) but that relies in large measure on consideration of largely gross morphological similarities with the above mentioned albuliform *incertae sedis* taxa and with the very specialised, contemporaneous, Toolebuc ?albuloid, *Euroka*, attributed to a new family, the Eurokidae, by Bartholomai (2010a). Description of the new taxa has not been undertaken to consider modification of the phylogeny proposed by Forey *et al.* (1996) but is intended to illustrate the greater diversity of the albuliform fishes during their early radiation, especially in the Southern Hemisphere.

General knowledge of the Australian Late Albian fish fauna has expanded as a result of recent research. Kear (2007) described the first occurrence of a pachycormid, *Australopachycormus hurleyi*, from the Toolebuc Formation near Boulia, SWQ, while Bartholomai (2008) added an additional chimaeroid species, *Ptyktoptychion wadeae* from the same formation from near Richmond, NCQ, from near Boulia, CWQ and from the Allaru Mudstone, near Dartmouth, CQ. Bartholomai (2010a) described the ?albuloid *Euroka dunravenensis* from the Toolebuc Formation near Richmond and he also revised the earlier described aspidorhynchid *Richmondichthys sweeti* and the elopiform *Flindersichthys denmeadi* from the Toolebuc, Allaru and Normanton Formations (Bartholomai 2004, 2010b respectively), with the Normanton Formation having been deposited in the adjacent Carpentaria Basin (Jell *et al.* 2013). Further description of the pachyrhizodontid, *Pachyrhizodus marathonensis* and an additional, more gracile species, *P. grawi*, have also been undertaken (Bartholomai 2012).

Deposition of marine sediments in the Eromanga Basin has been summarised in Cook *et al.* (2013). By the Late Albian, an epeiric sea covered what is now the centre of Queensland and extended to parts of New South Wales and South Australia. Wade (1993), in describing the Cretaceous squid from the Great Artesian Superbasin, provided a summary of the current understanding of fossilisation within the marine sediments deposited in the area and the conditions of deposition prevailing during both Aptian and Albian times. Most of the fossil fish fauna and associated marine vertebrates have come from the Toolebuc Formation, a thin (25-45 m thick), very widespread unit dated as Late Albian and from the conformably overlying, thicker (360-400 m) Allaru Mudstone (Cook *et al.* 2013). Terrestrial and other contemporaneous vertebrate faunal elements that lived along the coastline or that were washed out to sea and were interred and subsequently preserved off-shore have also been recovered from the marine sediments of the Eromanga Basin, including the Mackunda Formation (Late Albian - early Cenomanian) that conformably overlies the Allaru Mudstone (Cook *et al.* 2013).

Surface exposures of the Toolebuc Formation are limited and outcrop sporadically south of the Euroka Arch, the basement structure separating the Eromanga and Carpentaria Basins (Jell *et al.* 2013) and in an arc along the north-western and western margins of the Eromanga Basin (Henderson, 2004). Slow erosion due to the existing climatic conditions, low dips and minimal surface elevation contributes to difficulties associated with locating additional and more complete specimens. Many of the earlier collections were in calcilutite concretions concentrated on the surface. In recent years, increased public and regional interests in locating fossil vertebrates and greater field research efforts are beginning to provide expanded knowledge of the teleost and other fish faunas. Establishment of local museums in regional centres has encouraged greater collecting as well as deposition of specimens previously held in private collections.

ABBREVIATIONS USED IN FIGURES

atfc	anterior opening of pars jugularis
bocbasioccipital
bsp	basisphenoid
df	dilatator fossa
epo	epiotic
exoexoccipital
fahm	facet for hyomandibular articulation
fep	foramen for efferent pseudobranchial artery
ficaforamen for internal carotid artery
fm	foramen magnum
foa	foramen for orbital artery
fptf	foramen to post-temporal fossa
fr	frontal
fsp	foramen for occipital nerve
fuv.fused vertebral centrum
hm.hyomandibular
ic	intercalar
le	lateral ethmoid
myp	posterior myodome
np	notochordal pit
op	operculum
orsorbitosphenoid
otsc	otic sensory canal
pa	parietal
par.parasphenoid
pop	preoperculum
proprootic
psp	pterosphenoid
ptf	post-temporal fossa
ptfc	posterior opening of pars jugularis
pto.	pterotic
ptt.post-temporal
sclsupracleithrum
socsupraoccipital
sosc	supraorbital sensory canal
sp	sphenotic
stt	supratemporal
vc	vertebral centrum
vl	ventral limb of post-temporal
vo	vomer

I	foramen for olfactory tract
IIforamen for optic tract
III	foramen for oculomotor nerve
VII hm	foramen for hyomandibular trunk of facial nerve
VII ot	foramen for otic branch of facial nerve
IX	foramen for glossopharyngeal nerve
X	foramen for vagus nerve

SYSTEMATIC PALAEOONTOLOGY

Actinopterygii Cope, 1887

Teleostei Müller, 1845

Elopomorpha Müller, 1845

Order Albuliformes *sensu* Forey *et al.*, 1996

***Marathonichthys* gen. nov.**

Type Species. *Marathonichthys coyleorum* sp. nov., from the marine Toolebuc Formation, Lower Cretaceous (Late Albian), Eromanga Basin, Great Artesian Superbasin, Queensland.

Etymology. Named for “Marathon” Station, east of Richmond, NCQ, from which the type species was collected.

Generic Diagnosis. As for the type species, by monotypy.

***Marathonichthys coyleorum* sp. nov.**
(Figs 1–4, 5E)

Etymology. Named for the Coyle family – Leigh, Thomas, Shannon and Declan, for their enthusiastic interest and encouragement for my work.

Material Examined. Holotype. QMF 53953, partial neurocranium exhibiting some dorsoventral crushing that emphasises the shallowness of the neurocranium and results in some fracturing and minor dislocation of ventral elements. Slight rolling and ventral fracturing, as well as minor loss of marginal and anterior bone, also occurred. Collected from the Flinders River on “Marathon” Station, east of Richmond, NCQ.

Age and Formation. From the marine Toolebuc Formation of Lower Cretaceous (Late Albian) age.

Preservation and Preparation. The holotype of *M. coyleorum* sp. nov. is preserved in a

fragmented, flaky slab of poorly bedded coquina that contained disassociated and broken remains of a variety of different teleosts. Most of the preserved specimens in the recovered parts of the slab are cranial in origin and it is suggested that deposition was in a shallow, marine environment where there was sufficient water movement to sort out much of the less compact, smaller and lighter skeletal material. Regardless, at least two of the taxa represented (including that here described as *M. coyleorum*) are new to the marine fish fauna from the Toolebuc Formation and the Late Albian Allaru Mudstone. The second taxon is insufficiently represented to be formally described at this time. Three left valves of the pelecypod, *Aucellina hughendenensis* (Etheridge, 1872) are firmly adhered to the dorsal cranial roof of the holotype of *M. coyleorum*. Unfortunately, this specimen could not be fully acetic acid prepared at this time, acid preparation facilities being protractedly unavailable. For that reason, mechanical preparation has been undertaken but was restricted to one-half of the ventral neurocranial surface, leaving the other half of the holotype for more delicate acid preparation in the future (Fig. 2).

Specific Diagnosis. Within Albuliformes, *Marathonichthys coyleorum*, is diagnosed by the following characters: a large species with a shallow, broad, flattened posterior and narrow anterior skull roof (shared with albulids and some *Osmeroides*); coarse posterodorsal surface ornamentation is more pronounced than in other albuliforms; the supraorbital canal opens anteriorly close to the front of the orbit (shared with *O. latifrons*); the parietals are lobate, about as wide as long (shared with *Albula*) and separated medially by a dorsal development of the supraoccipital (shared with *Euroka*); the pterotics are posteriorly narrow, forming lateral margin of post-temporal fossa (shared with *Stewartichthys*); the supraoccipital dorsally is short and rectangular; the post-temporal fossa opening is reduced and the fossa is angled anteromedially (shared with *Stewartichthys* and *Euroka*); the subepiotic and subtemporal fossae are poorly developed (shared with *Stewartichthys*); the dilator fossa

is minimally developed and the otic bulla is poorly developed; the parasphenoid is narrow and edentulous and anteriorly has an open median trough between thin, dorsolateral wings from around the posterior of the vomer (shared with albulids) to below the orbits (shared with *Baugeichthys*); the vomer has a medial suture; the orbitosphenoid is expanded by an ossified septum; the intercalar is large, contributing to an intercalar-prootic bridge, which is emphasised by crushing.

Description. A relatively large fish, with preserved portion of neurocranium very flat dorsally, very broad posteriorly and very shallow, 16.8 cm long, 10.5 cm wide across autosphenotic spines and 10.0 cm wide at occiput; depth is 4.4 cm at occiput (but is somewhat reduced by dorsoventral crushing and slight rotation of ventral elements alluded to above; dorsoventral crushing more pronounced at anterior of skull); maximum length of orbit 6.3 cm; otic bullae are minimally inflated; subtemporal and subepiotic fossae poorly developed (dorsoventral compression mentioned above most probably reduced depth of subtemporal fossae and, possibly, extent of inflation of otic bullae); post-temporal fossa opening small, with fossa directed anteromedially; neurocranial roof heavily ossified. Dermethmoid, nasals and anterior of vomer missing.

Frontals very large and moderately deeply medially depressed posteriorly, a feature possibly emphasised by dorsoventral crushing. Anterior to orbits, margin of each frontal narrows markedly. Dorsal frontal surface only very weakly ornamented by insignificant, broad longitudinal ridges and rare but occasionally deeper, narrow grooves; median frontal suture slightly raised, with this dividing into low ridges towards each centre of ossification above back of orbits; medial suture becomes more sinuous posteriorly, especially between centres of ossification. Contact posteriorly with parietal raised, broadly, and deeply zig-zagged. Posterolateral contact with pterotic more regular. Supraorbital canal runs within strong ridge opening anteriorly into narrow, lateral groove above and just in front of orbit. The posterior extent of canal is generally masked



FIG. 1. *Marathonichthys coyleorum* gen. et sp. nov., Holotype, F 53953, dorsal view of partial neurocranium.



FIG. 2. *Marathonichthys coyleorum* gen. et sp. nov., Holotype, F 53953, ventral view of partial neurocranium.

by surface ornamentation but rare pores are present associated with ridges, anteromedial and medial to centre of ossification and posterolaterally near contact with pterotic. Posterior surface strongly ornamented with significant ridges and tubercles that largely radiate from centres of ossification; other ornamentation of numerous, relatively fine ridges radiating anterolaterally from centre of ossification; coarser but less numerous ridges, radiate anteromedially and medially from this centre, with medial ridges becoming much stronger and higher towards median suture. Laterally, a dished area with broad swellings expands towards margin, immediately anterior to sphenotic spine, separated posteriorly by broad, swollen ridges from strong, angular ridges radiating posteriorly over all of back of frontal, often confluent with ridges on parietal.

Parietals relatively small, lobate, widely separated by dorsal development of supraoccipital, about as long as broad, each with an irregular margin that deeply and coarsely meets frontal, supraoccipital, epiotic and pterotic. Ornamentation is strong and coarse and sometimes continues that from frontals. The bone forms dorsomedial margin of small opening to post-temporal fossa.

Pterotic posterodorsally narrow, excluded from small opening to post-temporal fossa by parietal and epiotic; laterally, it caps posterodorsal corner of braincase. Heavy, irregular, dorsal ornamentation of ridges present,

uniting to form shallow, posterolateral pocket and others curving around above posterior margin. Dorsolateral surface provides roof for dilatator fossa. Otic division of cephalic sensory canal system opens anteriorly through large opening behind sphenotic spine and posteriorly through large pore at posterior margin. Lateral face of pterotic forms margin of almost horizontal, very wide, brain case by contributing to hyomandibular facet, posterior part of dilatator fossa and part of insignificant subtemporal fossa. Dilatator fossa anteriorly deeply roofed, relatively shallow and short but probably reduced by dorsoventral distortion. Pterotic also forms minor anterior part of roof and ventrolateral wall and floor of anteromedially directed post-temporal fossa; opening of post-temporal fossa very small and posterolaterally angled.

Supraoccipital moderately wide and shallow, especially mesially, penetrated by large foramina close to remains of a posteromedial crest whose base extended ventrally to just above foramen magnum. Junction between dorsal and posterior surfaces produced posteriorly into rugose transverse crest, confluent with the top of posteromedial crest. Supraoccipital extends onto dorsal neurocranial surface, rectangular, widely separating parietals.

Epiotic meets raised rim of supraoccipital mesially and contributes to dorsolateral margin and most of medial margin of opening of post-temporal fossa. It carries strong but moderately

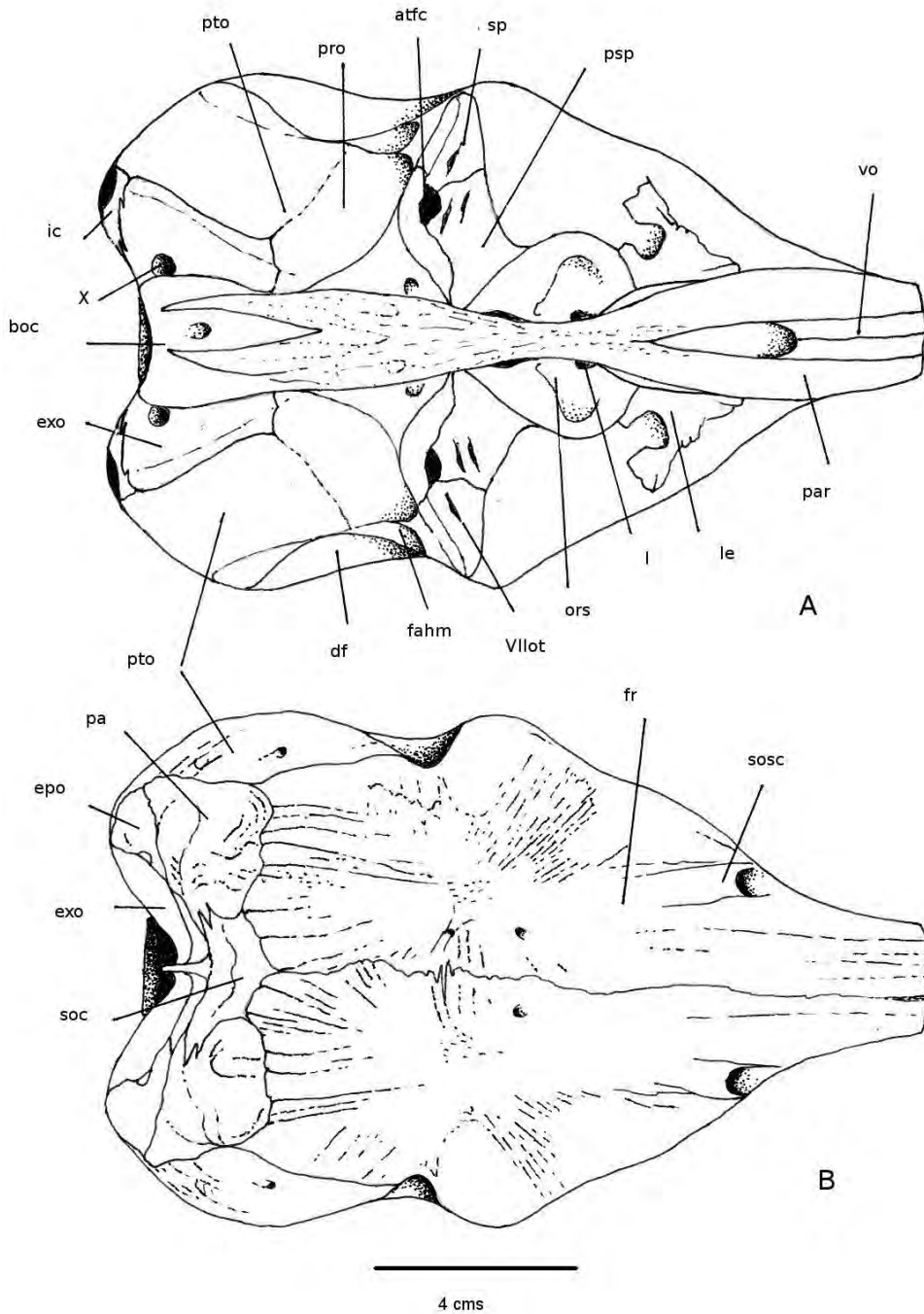


FIG. 3. *Marathonichthys coyleorum* gen. et sp. nov., reconstruction of neurocranium based on the Holotype. **A**, ventral view; **B**, dorsal view.

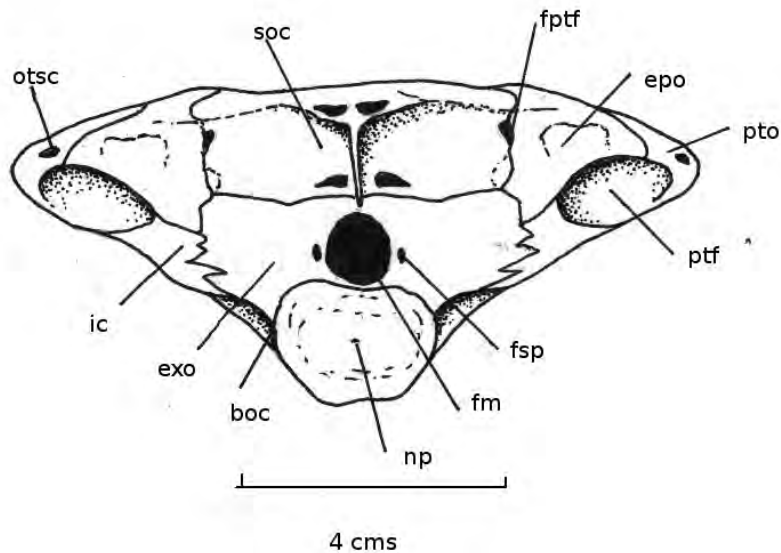


FIG. 4. *Marathonichthys coyleorum* gen. et sp. nov., reconstruction of posterior of neurocranium based on the Holotype, F 53953.

rounded epiotic process dorsally for contact with post-temporal. Subepiotic fossa almost poorly developed. Although emphasised by dorsoventral crushing, posterior surface of the neurocranium divided by a transverse ridge across epiotic/exoccipital suture, separating fossa into sloping, anteriorly directed, dorsal and ventral surfaces.

Exoccipital posterior surface relatively deep but excluded from inner margin of post-temporal fossa by epiotic and vertical arm of intercalar. Element extends onto lateral surface of brain case, penetrated, close to posterior of skull in a slightly elevated, large foramen for nerve X. Bulk of contribution to lateral surface of brain case near horizontal. Lateral to this, surface largely masked by closely adhering element of gill arches but extends towards the hyomandibular facet. Subtemporal fossa obscured but apparently poorly developed. Junction with lateral part of basioccipital along a sharp, longitudinal ridge, probably emphasised by dorsoventral crushing.

Intercalar relatively large, with narrow dorsal arm, forming ventromedial margin of post-temporal fossa. Posterior coarsely

ridged to accommodate tendons from ventral arm of post-temporal and appears to be penetrated by foramen angled posterodorsally from post-temporal fossa. Prominent anteromedial ridge meets similar ridge from prootic to form prootic-intercalar bridge (emphasised by crushing) lateral to the foramen for the vagus nerve.

Basioccipital forms occipital condyle. Element overlain ventrally by posterior prongs of parasphenoid below posteriorly directed opening into posterior myodome, forming its roof. Lateral junction with exoccipital along sharp, longitudinal ridge (emphasised by crushing), close to but below foramen for vagus nerve and separated from base of bone by strong, broad groove. Additional foramen present on one lateral edge of occipital condyle.

Prootic partially covered by matrix and by displaced and closely pressed element from gill arches, possibly an epibranchial. Prootic contributes anterior moiety of sharp, well defined prootic-intercalar bridge. Element penetrated by posteriorly directed foramen of jugular canal positioned close to suture with exoccipital but

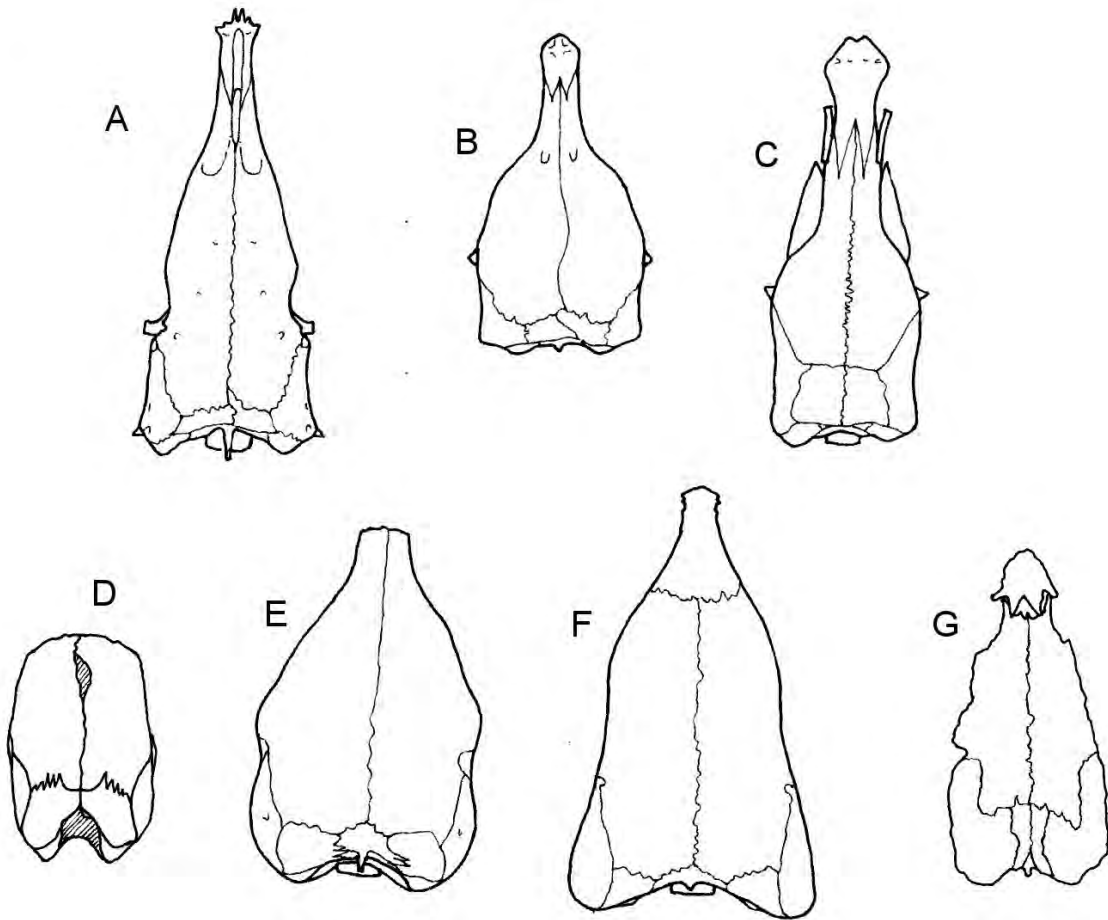


FIG. 5. Comparison of neurocranial dorsal surfaces (not to scale) of selected elopiform fishes: **A**, *Albula vulpes*, adapted from Forey (1973, fig. 75); **B**, *Osmeroides latifrons*, adapted from Forey (1973, fig. 55); **C**, *O. lewesiensis*, adapted from Forey (1973, fig. 46); **D**, *Stewartichthys leichhardti* gen. et sp. nov., Holotype (hatching across bone loss areas); **E**, *Marathonichthys coyleorum* gen. et sp. nov., Holotype (with slight correction for bone loss and distortion); **F**, *Euroka dunravenensis*, composite reconstruction based on the holotype and F 12759; **G**, *Paraelops caerensis*, (from Maisey 1991, p. 262, figure A).

between base of weakly expanded otic bulla and ridge to intercalar. Anteromedial border of the hyomandibular facet with ridge, while deep excavation at base of ascending process of parasphenoid largely masked. Anterior prootic face penetrated by large anterior opening of pars jugularis, close to margin of sphenotic.

Basisphenoid not exposed.

Sphenotic triangular, with apex pointed laterally and inclined posterodorsally as

reduced autosphenotic spine but spine possibly slightly reduced by bone loss. Ventral edge is relatively deep. Posterolateral surface slightly fluted and separated from anterolateral edge of hyomandibular facet by thin ridge less well developed than that along anteromesial margin of facet. Anterior face of sphenotic inclined, relatively expanded, penetrated by otic component of nerve VII, while posterodorsal face forms anterior of dilatator fossa.

Pterosphenoid extended anterodorsally, inclined anteriorly. Contact with basisphenoid obscured by dorsoventral crushing. Small, antero-dorsal foramen possibly carried trochlear nerve, while large notch at medial edge possibly for anterior cerebral vein.

Orbitosphenoid and associated ossified septum greatly expanded anteriorly, meeting pterosphenoid posteriorly but just excluded from contact with sphenotic. Junction between septum and orbitosphenoid not recognisable. Anterolateral expansion “ear-like” in shape and centrally depressed. Combined elements reached and probably contacted parasphenoid. Dorsolaterally, orbitosphenoid unites with ventral surface of frontal, half-way to lateral orbital margin. Large foramen for olfactory nerves lies towards anteroventral base.

Lateral ethmoid incomplete, relatively large, defining anterior extent of orbit. Bone relatively short, meeting thin dorsolateral wing of parasphenoid ventrally and attached dorsally to frontal at crests of two longitudinal swellings, leaving large foramen between all elements involved. Posterior border curved to form orbital border. Lateral ethmoid appears to meet counterpart medially. A prominent, poorly developed, rounded articulation for contact with palatine present.

Parasphenoid moderately broad but, although dorsoventrally skewed during preservation, appears to have also been raised ventrally into sharp, central, longitudinal ridge below orbital area. No evidence present of any parasphenoid teeth. Notch present at anteroventral base of reduced ascending parasphenoid wing, apparently for passage of orbital artery. Parasphenoid fractured transversely, separated slightly just anterior to prootic. Dorsolateral wings extend anteriorly from below orbits to meet lateral ethmoids and are spread and flattened, allowing body of element to move closer to lateral ethmoid and frontal; anteriorly, these dorsolateral wings also border medial, ventrally open trench, extending from body of parasphenoid to body of back of vomer.

Posterior base of vomer sandwiched between divided dorsolateral wings of parasphenoid. Longitudinal, medial groove present, suggesting possible division of vomer during development. No vomerine teeth preserved, nor any evidence for pedicels.

Order ?Albuliformes sensu Forey et al., 1996

***Stewartichthys* gen. nov.**

Type species. *Stewartichthys leichhardti* sp. nov., from the marine Toolebuc Formation, Lower Cretaceous (Late Albian) age, Eromanga Basin. Great Artesian Superbasin, Queensland.

Etymology. Named for Stewart Creek on “Dunraven” Station, northeast of Richmond, NCQ, from which the type specimen was collected.

Generic Diagnosis. As for the type species, by monotypy.

***Stewartichthys leichhardti* sp. nov.**

(Figs 6- 13, 5D)

Materials. Holotype. QMF 13861, posterior of partial cranium and extreme anterior of body, with some depression of neurocranial surface above braincase by crushing and lacking most of the supraoccipital and most of parasphenoid, from an unnamed tributary of Stewart Creek, on “Dunraven” Station, northeast of Richmond, NCQ. The specimen has been prepared by use of unbuffered, about 10%, acetic acid.

Age and Formation. From the marine Toolebuc Formation of Lower Cretaceous (Late Albian) age.

Etymology. Named for the 19th century explorer, Ludwig Leichhardt.

Specific Diagnosis. Moderately large species. Neurocranial roof medially flattened, depressed above braincase, relatively narrow (shared with *Osmeroides levis*), ornamented with low, irregular and interrupted ridges, often anastomosing (shared with *O. lewesensis*). Parietals large, triradiate, long, apparently partially separated posteriorly by small dorsal wedge of supraoccipital, contributing to roof of post-temporal fossa dorsolaterally. Supraorbital sensory canal extends into parietal. Dilator fossa short but anteriorly broad and deep, with its floor separated by significant cleft between sphenotic and pterotic. Sphenotic spine non-existent. Pterotic very narrow posteriorly, not

contributing to dorsal rim of post-temporal fossa (shared with *Marathonichthys*) with otic sensory canal uncovered. Post-temporal fossa large, angled anteromedially. Epitotic broad with buttress strongly developed above a poorly developed subepitotic fossa. Basisoccipital with first vertebral centrum incorporated. Parasphenoid somewhat angled posterodorsally, extending to neurocranial limit (shared with *Bullichthys*). Intercalar well developed, with triradiate wings, one of which contributes to the strong intercalar-prootic ridge and another that excludes the epitotic from the medial margin of the post-temporal fossa; intercalar-prootic ridge continues across prootic, curving above prominent foramina for posterior opening of pars jugularis and orbital artery to base of parasphenoid wing just above foramen for internal carotid artery (shared with *O. latifrons*). Subtemporal fossa very shallow. Prootic lateral margin to large posterior myodome strongly flared. Basisphenoid dorsally narrowed, angled anteroventrally (shared with *Bullichthys*) and with posteroventral base supported by slender vertical parasphenoid splint. Pterospheonid and upper part of posterior of orbitospheonid strongly sutured to deep ventromedial process of frontal. Orbitospheonid widely separated dorsally from frontal and penetrated anteriorly by large foramen for olfactory tract. Hyomandibular head broadly V-shaped and with shaft near vertical. Anterior vertebral centra with lateral surface deeply and irregularly pitted.

Description. A relatively large ?albuliform, probably approaching 0.4- 0.5 m in length. Neurocranium relatively narrow but broader across autosphenotics than across posterior of otic region. Neurocranial roof flattened medially, curves gently ventrolaterally. In dorsal view, lateral margin gently convex from near front of orbit, with autosphenotic spines almost non-existent. Surface above braincase depressed, but accentuated through damage during fossilisation. Posterior of neurocranium deeply V-shaped. All preserved external bone surfaces ornamented by densely organised, low, irregular and interrupted ridges, also present along the anterodorsal margins of preoperculum and operculum, becoming more broadly

developed posterodorsally on latter. Above supraorbital sensory canals, surface slightly raised, with canals extending posteriorly into parietals. In lateral view, skull roof slightly arched above orbits and slightly depressed immediately posterior to centres of ossification of frontals.

Frontal large, solid, extending posteriorly to cover most of anterior of cranial vault, meeting counterpart medially along deeply interdigitated suture. Element firmly united with autosphenotic and pterotic laterally and parietal posteriorly. Lateral margin above orbit has swollen appearance and, from remaining portion of orbital margin, it appears that orbit not excessively large. Within orbit, ventral frontal surface bears prominent, deep, V-shaped process to interdigitate deeply with anterodorsal margin of pterospheonid and posterodorsal margin of orbitospheonid. Dorsal surface ornamented with low, irregular, interrupted but often anastomosing ridges. Part of a short, solid process of the lateral ethmoid firmly attached to the ventrolateral surface of frontal, curving anteroventrally to begin to define orbit.

Parietal, triradiate, long, apparently excluded from meeting all of its counterpart medially by insertion of dorsal wedge of the supraoccipital (very poorly present). Narrow anterior arm of parietal deeply sutured to frontal and pterotic; a lobate arm posterolaterally contributes the margin to the roof of the post-temporal fossa, while medial arm is short, meeting most of its counterpart along the medial suture. Because of its size, bone reduces size of pterotic laterally and contributes to posterolateral roof of opening of post-temporal fossa. Contact with epitotic posteriorly relatively long. Posterior of infraorbital sensory canal curves medially to within back of parietal.

Pterotic with relatively large dorsal expression but posteriorly narrow, extending from back of autosphenotic to contribute about one-third of dorsal roof of post-temporal fossa. Suture with parietal angles laterally within post-temporal fossa, excluded pterotic from dorsal margin of opening. Anterolaterally, pterotic roofs dilator

fossa and posterolaterally curves ventrally to posteroventral corner of post-temporal fossa. Lateral margin grooved, associated with unroofed otic sensory canal. Dilator fossa deep anteriorly and broadens medially above junction of sphenotic and pterotic; base of dilator fossa slopes dorsomedially and junction between sphenotic and pterotic widely cleft, leading to large foramen that appears to open into post-temporal fossa. Dilator fossa disappears posteriorly, well anterior to back of braincase. Lateral face of pterotic deeply shelved to provide posterior roof of dorsally curved two-thirds of hyomandibular facet. It also provides lateral margin of post-temporal fossa and expands medially within post-temporal fossa, curving to form much of its internal base. It continues to curve dorsomedially to meet epiotic along a dorsally curved suture but excluded from medial part of basal margin of post-temporal fossa by short, lateral wing of intercalar. Post-temporal fossa angled anteromedially and anteriorly appears to unite with counterpart.

Epiotic moderately large, narrowly meeting supraoccipital medially but with much greater contact with parietal; bone extends as short, broad dorsal development; posteriorly it meets exoccipital and vertical splint of intercalar and provides most of internal, medial wall of post-temporal fossa. Element precluded from most of inner margin of post-temporal fossa opening by intercalar and from its dorsolateral margin by parietal. Posterodorsal surface broadly shelved medially as epiotic buttress to support anterior of supratemporal and slopes anterodorsally above its contact with exoccipital. Posterior surface of skull slopes gently anteroventrally below epiotic buttress, with subepiotic fossa poorly developed.

Supraoccipital mostly unpreserved, small. From its scar, it appears to have extended onto dorsal neurocranial surface as small wedge but would only partially separate the parietals posteriorly (if at all) and forms medial part of remaining posterior V-shape of neurocranium. It slopes strongly anterodorsally from its ventral junction with exoccipital.

Exoccipital also poorly represented, especially in relation to dorsomedial corner of its posterior face. It is excluded from medial margin of post-temporal fossa by vertical splint of intercalar and meets epiotic along an angled ventromedial suture. It surrounds and meets counterpart along floor of large foramen magnum. Posterior surface slopes slightly anteroventrally below abruptly angled junction with supraoccipital and epiotic. Small foramen for occipital nerve present lateral to foramen magnum. Lateral face separated from posterior face by strong pedicle that broadens and flares ventromedially to be strongly sutured to basioccipital. Lateral junction with basioccipital broadly curved ventrally; anterior junction with prootic sinuous and that dorsally with intercalar short. A large foramen for nerve X present close to intercalar junction and that for nerve IX positioned immediately below.

Intercalar moderately large, triradiate element that caps ventromedial margin of post-temporal fossa. A narrow, vertical splint provides much of medial margin of post-temporal fossa; a short but broader wing interdigitates laterally with pterotic forming ventromedial margin of post-temporal fossa; larger medially directed portion supports exoccipital and anteriorly raises into a strong ridge that unites with a similar ridge from prootic to form prootic-intercalar ridge. Posteriorly, base of bone expands and strengthens into a strong, process that supported anteroventral arm of post-temporal.

Basioccipital has a fused vertebral centrum providing slightly ovate articulation with vertebral column, penetrated by a small foramen for the notochord; dorsally, it bears a pair of deep depressions for a detached neural arch. Junction with exoccipital and prootic along its lateral face is steeply angled anteriorly, where it remains slightly open. The surface steps medially subparallel to anterior margin. In ventral view, its lateral junction with parasphenoid, behind parasphenoid wing, somewhat sinuous and a medial splint of parasphenoid extends posteriorly to a foramen in advance of posterior margin into posterior myodome.



FIG. 6. *Stewartichthys leichhardti* gen. et sp. nov. Holotype, F 13861, left lateral view of partial neurocranium.

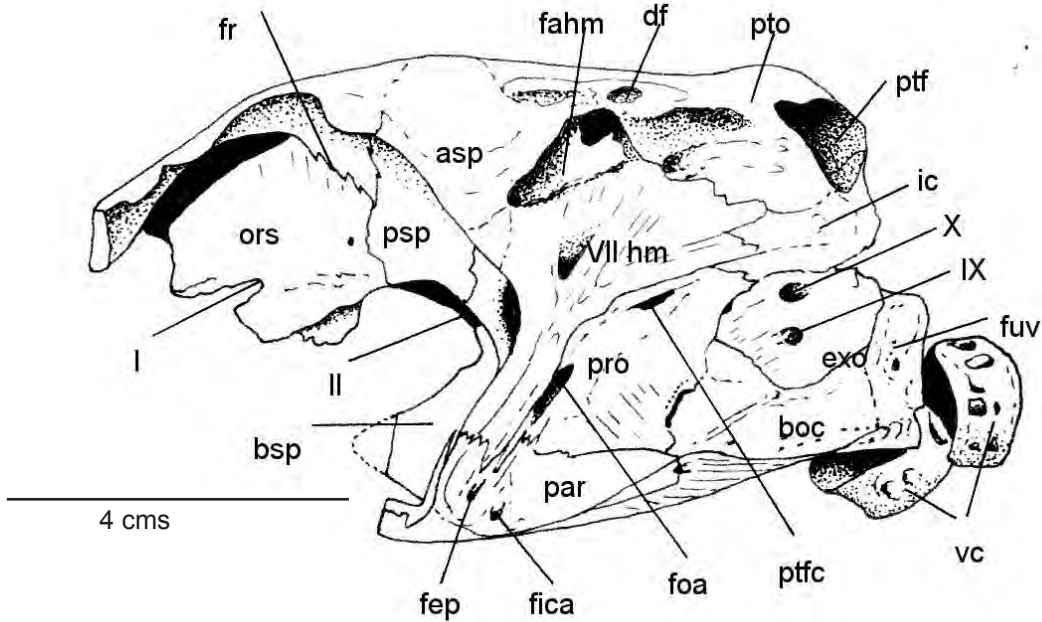


FIG. 7. *Stewartichthys leichhardti* gen. et sp. nov. Drawing of partial neurocranium of Holotype, F 13861, in left lateral view.

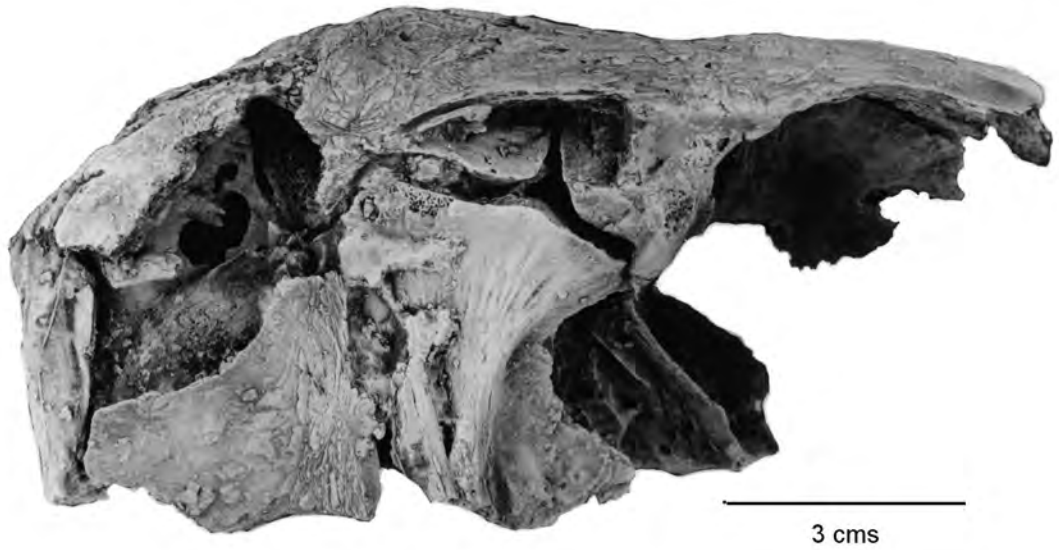


FIG. 8. *Stewartichthys leichhardti* gen. et sp. nov. Holotype, F 13861, right lateral view of partial neurocranium.

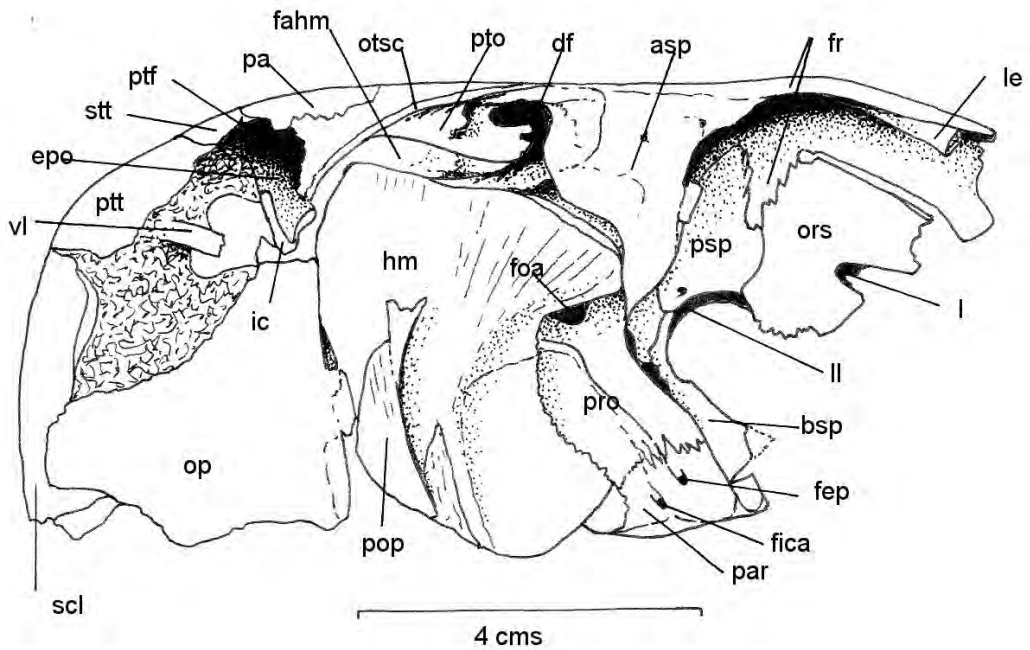


FIG. 9. *Stewartichthys leichhardti* gen. et sp. nov. Drawing of partial neurocranium of Holotype, F 13861, in right lateral view.



FIG. 10. *Stewartichthys leichhardti* gen. et sp. nov. Holotype, F 13861, ventral view of partial neurocranium.



FIG. 11. *Stewartichthys leichhardti* gen. et sp. nov. Holotype, F13861, dorsal view of partial neurocranium.



FIG. 12. *Stewartichthys leichhardti* gen. et sp. nov. Holotype, F 13861, orbital view of partial neurocranium.

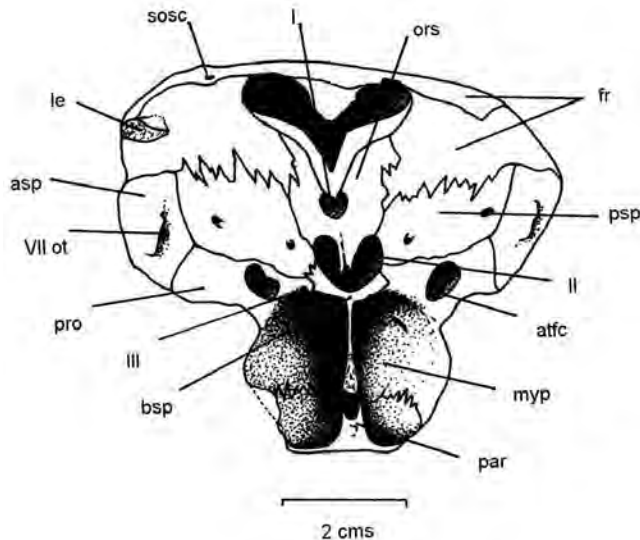


FIG. 13. *Stewartichthys leichhardti* gen. et sp. nov. Drawing of Holotype, F 13861, view of neurocranium, in orbital view.

Prootic large, forming much of anterior face of side of braincase. It contributes minimally to very poorly developed subtemporal fossa but provides floor of anterior of hyomandibular facet, meeting base of autosphenotic medially within facet. Its lateral junction with pterotic angles posteroventrally and continues cleft from base of dilator fossa across hyomandibular facet. A strong prootic-intercalar ridge extends anteriorly and reduces slightly before curving abruptly anteroventrally to near base of parasphenoid wing. Two large foramina occur immediately below this ridge, the most anterior for the orbital artery, while the other appears for elongated pars jugularis. A large foramen, possibly for the hyomandibular trunk of the facial nerve exists anterodorsal to prootic-intercalar ridge. Anterior face of prootic forms part of posterior of orbit. Lateral rim of entrance to posterior myodome widely flared. Prootic excluded from optic foramen by upper wing of basisphenoid. Face of bone penetrated by two foramina; largest and more laterally positioned for anterior opening of pars jugularis and smaller one, close to the suture with the basisphenoid, is believed for oculomotor nerve. Former has a broad groove passing vertically onto surface of pterosphenoid and probably accommodated the superficial ophthalmic branches of trigeminal and facial nerves. Foramina present in the medial wall of the pars jugularis, believed for passage of trigeminal and facial nerves. Prootic ridge penetrated by a number of foramina. Otic bulla development is weak.

Sphenotic caps posterodorsal corner of orbit, and lacks any sphenotic spine development. Dorsal surface expression limited. Anterior face bears a rounded knob and has a small foramen for otic ramus of nerve VII. Sphenotic joins pterosphenoid anteriorly and

ventrally meets prootic. Surface broadly and convexly rounded posteroventrally as anterior articulating surface for hyomandibular, with its dorsal edge forming back of open cleft in base of dilator fossa. Posterodorsally, it forms anterior of dilator fossa.

Pterosphenoid large, loosely abutting sphenotic, prootic and orbitosphenoid and strongly sutured to deep, strong, ventral V-shaped process of frontal. Anterodorsal margin slightly fluted, penetrated by two foramina. Posterior foramen positioned below superficial orbital groove probably for anterior cerebral vein while dorsal foramen probably for trochlearis.

Basisphenoid in anterior view has basal, medial stem supporting two, broadly U-shaped dorsal wings. Stem deep and narrow but expanded anteroventrally above parasphenoid. Wings sutured along prootic at posterolateral margin of opening for orbital tract and extend minimally along the internal corner of pterosphenoid. Base of stem separated from top of parasphenoid but probably connected it with cartilage. Stem with shallow groove paralleling back towards base, accommodating fine splints of bone from parasphenoid.

Orbitosphenoid moderately large, separated dorsally from frontal by large gap. Posterodorsally, a strong interdigitated suture links it to large, ventral, V-shaped process of frontal; posteriorly a looser junction exists with pterosphenoid. Posteroventral margin irregular, suggesting presence of a partial, cartilaginous, interorbital septum. A large foramen for olfactory tracts present in middle of anterior margin.

Parasphenoid largely missing but sloped gently posterodorsally. Parasphenoid ascending wings present, broadly but only weakly developed, ascending at a high angle and forming posteroventral part of flared opening to posterior myodome. Lateral base of ascending wing pierced by a foramen for internal carotid artery and, anterodorsal to this by a small foramen for efferent pseudobranchial artery. Posterior of bone strengthened dorsally by deep, longitudinal, lateral margins and a longitudinal, medial strut but surface has largely been

lost. Apparently, bone extended to posterior of basioccipital. No parasphenoid teeth are present in the minimal remains preserved.

Supratemporal incomplete but apparently relatively large. It does not appear to have met its counterpart on the other side.

Post-temporal very incomplete but linked to intercalary by a thin, strut-like ventral limb.

Hyomandibular only partially preserved and represents only element of hyopalatine bones preserved. Bone broad with a large head broadly V-shaped but with single, continuous, articulating surface. Lateral surface with a strong, broad ridge curving from anterior part of head towards shaft. Posterior margin strongly curved anteroventrally and bearing a stout but very short opercular process. Median ridge running down length of shaft very strong, while anterodorsal flange thin with a rounded ventral margin. Extent of overlap by the metapterygoid unknown.

Opercular series very incompletely known, with anterodorsal margin of operculum nearly vertical. Only dorsal tip of preoperculum present.

Three vertebral centra preserved. First ovate, being broader than deep but centra become rounder in section by third bone. Length of centra is shorter than deep. With exception of first centrum, others bear autogenous parapophyses for pleural ribs. Deep, large, depressions exist dorsally for neural spines but depressions for haemal spines lacking. Laterally, centra marked by deep, irregular but generally large fenestrations.

DISCUSSION

Both *Marathonichthys* and *Stewartichthys*, are considered referable to the Elopomorpha on the basis of their overall morphology. Mayrinck *et al.* (2010), in describing the albuliform, *Bullichthys santanensis* from the Romualdo Member of the Santana Formation, in northeastern Brazil (generally considered to be of Albian age) concluded that most of the characters that define the Elopomorpha are not represented in

fossil species, as they are based on soft tissue, or on elements that are not often preserved. Forey *et al.* (1996) identified three characters supporting elopomorph monophyly. These are an enclosed ethmoid commissure within the premaxilla, the rostral ossicles and the presence of a pectoral splint. These characters are either not preserved or not present in either *M. coyleorum* or *S. leichhardti*. The presence of a pectoral splint was evident in *B. santanensis*.

In considering the ordinal position of *Marathonichthys* and *Stewartichthys*, fewer potentially relevant characters are preserved in *M. coyleorum* than are present in *S. leichhardti*. Morphologically, the two taxa differ markedly from one another. Forey *et al.* (1996) suggest that a number of Lower Cretaceous plesions may be stem group albuloids. Subsequently described plesions could also be similarly considered. Figures 1-2 illustrate the neurocranial remains preserved in the holotype of *M. coyleorum*, while Figures 3-4 illustrate partial reconstructions, taking account of the dorsoventral crushing of the specimen. The orbitosphenoid and associated ossified septum is more extensively developed in *M. coyleorum* than that in *S. leichhardti* and the dorsal surface of the neurocranium is very different, being much broader and shallower posteriorly, narrowing abruptly anteriorly beyond the orbits (Figures 1, 3 and 5E). The neurocranial roof in *S. leichhardti* is relatively broad but does not appear to narrow as markedly (Figure 5D). The parietals are separated or partially separated in both new taxa by a short dorsal expression of the supraoccipital (Figures 1, 3, 5D, E) but that in *Stewartichthys* does so minimally or may even be excluded, as evidenced by the space left by loss of the bone. Both species also possess poorly developed subepiotic and subtemporal fossae, have a weakly developed bulla containing the saccolith and a moderately developed intercalar that contributes to a prominent intercalar-prootic bridge (as in *M. coyleorum*) or ridge (seen in *S. leichhardti*), as seen in Figures 3 and 6-7. Both have post-temporal fossae that are angled anteromedially but that in *S. leichhardti* has a much larger posterior opening. The sphenotic spine in *M. coyleorum* is better developed, while

S. leichhardti has a much better developed, deeper dilator fossa (Figures 8-9). Both genera are nonetheless considered more reasonably referable to the Order Albuliformes *sensu* Forey *et al.*, 1996 than to the Elopiformes on gross morphological grounds, taking account of Forey's (1973) albuloid diagnosis. However, on this basis, comparison with the extant albuloid, *Albula* Linnaeus, the skull of which was described by Ridewood (1904) and redescribed by Forey (1973), together with the eurokid *Euroka* Bartholomai, 2010 and the plesion *Osmeroides* indicates that *Marathonichthys* has some features (e.g. skull shape and anterior parasphenoid development) that overlap with the Elopiformes (Figure 5 for dorsal skull shape comparisons).

Morphological comparisons yielding a mixture of similarities and differences can be made between the new Queensland taxa and the neurocrania of fossil albuliform plesions, *Brannerion* (see Blum 1991) and *Paraelops* (see Maisey & Blum 1991), *Bullichthys* (Mayrinck *et al.* 2010), *Baugeichthys* (see Filleul 2000), *Osmeroides* (Forey 1973) and *Euroka* (see Bartholomai 2010a). *Marathonichthys* and *Stewartichthys* differ sufficiently from these to justify their description as new species (see diagnoses above).

Figures 3 and 4 present reconstructions that attempt to correct the distortions evident in the holotype of *M. coyleorum* in dorsal, ventral and posterior views and to add the slight marginal neurocranial bone that was lost. The species does present features that make it difficult to relate it firmly to either of the recognised families within the Albuloidae. The elongated snout and more triangular overall shape in dorsal view, together with the nearly completely uncovered supraorbital sensory canals and expansive, unseparated development of the parietals in the extant and fossil members of the Family Pterothrissidae (see Forey, 1973 for revisions and figures of pterothrissids) makes it difficult to seriously consider its reference to that family. Dorsal neurocranial roof shape is more like that in the Family Albulidae, as are the posteriorly more covered supraorbital sensory canals and much smaller, separated parietals (Figure

5A). The poor development of subepiotic and subtemporal fossae and otic bulla, the almost horizontal nature of the lateral surface of the cranial vault, the expanded orbitosphenoid/orbitosphenoid septum, the relatively strong prootic-intercalar bridge, the edentate and relatively narrow, mid-anterior area of the parasphenoid, the dorsal development of the supraoccipital (at least in *M. coyleorum*) and the very coarse posterodorsal ornamentation of the cranium represent a mix of characters that nonetheless suggest that reference to the Albulidae would be difficult to justify. Similarly, although the development of the posterior of the neurocranium is similar to that in the eurokid, *Euroka* (in the transverse subdivision of the subepiotic fossa and separation of small, lozenge-shaped parietals by a dorsal expression of the supraoccipital), the subtriangular dorsal outline, dorsal ornamentation and the nature of the parasphenoid (Bartholomai 2010a) readily separates them on the basis of characters represented in both. The deeper, narrower and ornamented neurocranium in *S. leichhardti* is similarly different from that in *Euroka*. *Stewartichthys*, illustrated in Figures 6-13, 5D differs from the Albulidae in having its neurocranial roof narrower posteriorly than across the sphenotics, in lacking sphenotic spines, in possessing very reduced subtemporal and subepiotic fossae and in having a strong prootic-intercalar ridge that extends across the prootic to the base of the parasphenoid wing. It has the dilator fossa shortened, and deepened, with a deeply cleft base and with the base of the prootic widely flared lateral to the opening of the posterior myodome.

Baugeichthys caeruleus from the Lower Cretaceous (Hauterivian) of France, is the earliest known fossil albuliform (Filleul 2000), slightly predating the Queensland taxa. Few of the characters considered diagnostic are present in the new Queensland taxa. It differs markedly from *Marathonichthys* by having its snout appearing relatively shorter (but the snout in *Stewartichthys* was most likely shortened). Further, the parasphenoid in *B. caeruleus* has expanded lateral wings under the orbit, the parietals are much larger and meet along a

full length midline suture, differing from possible partial medial separation of parietals in *S. leichhardti* and their full separation by the superoccipital in *M. coyleorum*. The dorsal neurocranial bones appear unornamented (see Filleul, 2000, figure 6). Also unlike *S. leichhardti*, supraorbital sensory canals do not extend onto the parietals and the roof of the cranial vault is broadened. The Santana albuliform, *Bullichthys santanensis*, described by Mayrinck *et al.*, (2010) differs from *M. coyleorum* and *S. leichhardti* in having a strongly developed subtemporal fossa and otic bulla and a small intercalar. It lacks an orbitosphenoid septum (as in *Stewartichthys*). The parasphenoid is pierced by a foramen, probably for the efferent pseudobranchial artery in both *Bullichthys* and *Stewartichthys* and a Y-shaped basisphenoid and shallow subepiotic fossa are present in both. However, an intercalar-prootic bridge present in *Bullichthys* is only present in *Marathonichthys*, being extended in *Stewartichthys* as an intercalar-prootic ridge that curves across the prootic to the base of the parasphenoid wing and parasphenoid dentition is absent. Mayrinck *et al.* (2010, fig. 1) lists *Paraelops*, *Brannerion* and *Bullichthys* from the Santana Formation of Lower Cretaceous (Albian) age in Brazil as *Albuloides incertae sedis*. *Paraelops* has been redescribed by Maisey and Blum (1991), while *Brannerion* has also been redescribed by Blum (1991). The former taxon differs from *M. coyleorum* in having a much deeper braincase. It differs from both new taxa in having the parietals about three times longer than wide (Figure 5G), with the pterotic large and L-shaped; extremely deep subtemporal and subepiotic fossae are present; an intercalar-prootic bridge is lacking (present in *M. coyleorum*). *Brannerion* differs from *M. coyleorum* in having a blunt snout, a much narrower, unornamented, convex dorsal surface to the neurocranium, a much deeper brain case and a broad, toothed, parasphenoid tooth plate. The neurocranium in *S. leichhardti* is relatively narrower across the otic region than in *Brannerion* and has a posterodorsally narrow development of the pterotic. *Stewartichthys* has large, triradiate parietals and has much larger intercalars than those noted by Maisey

and Blum (1991) for *Brannerion*, although these authors noted that the intercalar is not as reduced in *Brannerion* as in other “albuloids” and that the intercalar bridge to the prootic persists (similar to the intercalar development in *Marathonichthys*).

Forey (1973) indicates that coarse rugae are present on the roofing bones of the skull of *Dinelops ornatus* Woodward, 1907, from the Upper Cenomanian of southeastern England, and that the frontals narrow rapidly in front of the orbits, apparently basically similar to *Osmeroides latifrons* and *M. coyleorum* but differing from *S. leichhardti*. Unfortunately, this taxon was not illustrated. A shallow depression medially above the cranial vault, similar to that in the holotype of *S. leichhardti* (accentuated in this by crushing) is described as present in *D. ornatus*. Forey (1973) indicates that the rugae of the roof of the cranial vault continue anteriorly onto the dermethmoid in *D. ornatus* and that a medial branch of the supraorbital sensory canal, unlike that in *Marathonichthys*, opens apparently further back on the frontal at the posterior of the orbit.

The posterior of the neurocranium of the Toolebuc albuliform, *Euroka dunravenensis*, possesses some characters that are similar to those in *M. coyleorum*. Both have very broad, flat, neurocranial roofs, with the parietals separated by a dorsal expansion of the supraoccipital and both are shallow in the otic region. Both have a shallow subepiotic fossa subdivided into upper and lower moieties by a transverse ridge. *Euroka*, however, has an almost unornamented cranial dorsal surface and is more angular posteroventrally (Figure 5F). Its dilator fossa is much deeper anteriorly, the anterior of the hyomandibular facet is less emphatically defined, the intercalar is larger with a less well-defined intercalar-prootic ridge, the parasphenoid terminates posteriorly in stout, blunt prongs, well before the posterior of the basioccipital and there is a thickened and very stout orbitosphenoid interseptum (Bartholomai 2010a). The frontals are broadened well anterior to the orbits before narrowing to unite with the broadened posterior of the dermosphenotic (Figure 5F). Fortunately, sufficient differences also exist

in the areas preserved in *Stewartichthys* to separate it from *Euroka* without needing to include comparisons with that taxon’s highly specialised morphology of the hypopalatine area, the anterior of the neurocranium and mandible. The triradiate parietals and their possible near separation, the narrower and ornamented neurocranial roof, deeper otic region of the skull and lack of an ossified orbitosphenoid septum are morphological features in *S. leichhardti* that are lacking in *Euroka*.

The species of the genus *Osmeroides*, also considered by Mayrinck *et al.* (2010) as Albuliformes *incertae sedis sensu* Forey *et al.* (1996), are all from sediments younger than the Toolebuc Formation. Forey (1973) concluded that *Osmeroides* belonged within a separate family, the Osmeroididae but later, the genus was referred as a plesion of the Albuliformes, along with *Brannerion* by Forey *et al.* (1996). *Osmeroides* is recorded by Forey (1973) from southern England in sediments extending from the Lower Cretaceous (Albian) to the Upper Cretaceous (Coniacian). *Marathonichthys coyleorum* has stout and heavy dermal bones of the cranium and a flat cranial roof similar to that in *Osmeroides*, with the dilator roofed by the pterotic but with a narrower, edentulous parasphenoid. The lateral ethmoid appears to have been connected to the parasphenoid, as in *Osmeroides* but this may be related to dorsoventral crushing. The brain case appears to have been much shallower. The short, separated, lobate parietals differ markedly from those in *Osmeroides* (Figures 5B-C), although, as described by Forey (1973), the dermal bones in *O. lewesiensis* have prominent, coarse, radiating ornamentation. Orbitosphenoid ossification in *O. lewesiensis* is extensive (but includes the interorbital septum as in *Marathonichthys*). The distribution of elements on the dorsal cranial surface is similar to those in *M. coyleorum* but the Queensland species has a very small subtemporal fossa, much heavier ornamentation of the posterior dorsal neurocranial surface and lacks both an expanded otic bulla and has a considerably narrower, edentate parasphenoid. An incipient prootic-exoccipital bridge (rather than a ridge) exists in *O. latifrons*. *Stewartichthys leichhardti* has

many morphological similarities to the species of *Osmeroides* revised by Forey (1973) but differs from the generic diagnosis for *Osmeroides* in having a more complex and larger intercalar and in lacking villiform teeth on the preserved part of the parasphenoid. At the specific level, *S. leichhardti* was probably of similar size to *O. lewesiensis* but larger than the other *Osmeroides* species. Its parietals are triradiate, not rectilinear and had possible short medial contact with the supraoccipital that apparently partially separates them. Dorsal surface ornamentation is present, as in *O. lewesiensis*, and the parasphenoid is similarly extended to the rear of the neurocranium. However, an ossified interorbital septum is absent and the sphenotic spines are not developed. Compared with *O. levis*, also revised by Forey, 1973, the dorsal shape of the neurocranium is similar but the Queensland taxon is much larger and the surface ornamentation is much more strongly developed. The interorbital septum in *O. levis* is partially ossified, the posterior of the parasphenoid ends under the mid-otic area and the parietals are rectangular and are not separated by any of the supraoccipital. The parietals in *O. latifrons* are more lobate than in the other English taxa but are not separated by the supraoccipital and are not triradiate as in *S. leichhardti*. Dorsal ornamentation of neurocranial bone is much less developed than in *S. leichhardti* but lack of an ossified interorbital septum is similar, as is the posterior extent of the parasphenoid. Width of the parasphenoid and expansion of the otic bulla in *S. leichhardti* is considerably less than in *O. latifrons*. The lateral surface of the braincase in *S. leichhardti* is similar to those in the larger English species with the extension of the prootic-intercalar ridge angled across the prootic to the base of the lateral wing of the parasphenoid, although the subtemporal fossa is much less developed.

The Lower Cretaceous (Late Albian) marine epicontinental sediments of the Eromanga Basin generally have increasing importance in adding to the recorded knowledge of the early teleosts in the southern hemisphere. The stem-lineage ichthyodectiform teleosts from the Toolebuc Formation, including *Cooyoo*

australis, revised by Lees and Bartholomai (1987), was included in work by Calvin *et al.* (2013). It was suggested that the radiation of *Cooyoo* and the Mexican *Unamichthys* was as a lineage of sister genera, a relationship that is difficult to interpret palaeogeographically. Because of Australia's isolation, Calvin *et al.* (2013) suggested that the relationship reflected dispersal events around the Southern Atlantic and/or the Tethys. However, they suggest that the sister group relationship evidence was acknowledged as weak and may have influenced the distributional interpretation. Similar problems appear to apply to relationships and distributions within the known pelagic Albian albuliforms.

The current study broadens understanding of fossil elopomorphs by expanding recognition of an increased bony fish diversification from a part of the oceanic world not generally included in the major interpretative work undertaken to this time. *Marathonichthys* presents a range of characters that are more comparable with those in the living albuloids, while *Stewartichthys* has more general similarities with Santana taxa such as *Bullichthys* and *Brannerion* and even with the English *Osmeroides*. It is hoped that future finds will provide detail of the skeletons of the Eromanga Basin species to help clarify their phylogenetic relationships. Features in *Marathonichthys* suggest tantalising possible qualitative similarities, broadly including *Albula*, while major differences in *Stewartichthys* indicate morphological divergence from the general evolutionary interpretation of the albuliformes. *Marathonichthys* and *Stewartichthys* lived in the Eromanga Basin at a time when, at least during deposition of the Toolebuc Formation under the layered epeiric marine sea that exhibited dysoxic to anoxic conditions (Cook *et al.* 2013). This suggests that open water, pelagic fish species would dominate in the fauna.

Some isolation was possibly a factor in the evolution of the species present, although Kear (2003) suggests that Australian Cretaceous shelf deposits appear to produce some similar pelagic taxa. Marine conditions prevailed for approximately 26 MY in the Eromanga Basin. Cook *et al.* (2013) indicate that marine

sediments were deposited through most of the Early Cretaceous with terminal paralic, fluvial and lacustrine conditions in the effective regression of the Early Cretaceous extending into the early Late Cretaceous (Cenomanian). It is believed that limitations to augmentation of the gene pool across the Euroka Arch and existence of new palaeoecological conditions would have promoted at least some differing evolutionary trends inside the Basin from those existing beyond the Australian continent, where there was ready access to wide oceanic gene pools. For this reason, description of the new genera and species adds breadth to knowledge of the early but probably localised diversification of the group and is in keeping with the development of much more specialised morphological characters seen in the albuliform, *Euroka dunravenensis*, also from the Toolebuc Formation of the Eromanga Basin (Bartholomai 2010a).

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