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The pachyrhizodontid teleosts from the marine Lower Cretaceous (latest mid to late-albian) sediments of the Eromanga Basin, Queensland, Australia

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ABSTRACT

Two species of the fossil pachyrhizodontid teleost, *Pachyrhizodus*, are present in the marine Lower Cretaceous (mid to late Albian) Toolebuc and Allaru Formations of the Eromanga Basin in Queensland, Australia. New morphological data on *P. marathonensis* (Etheridge Jnr., 1905) is provided as part of a revision of the species. The smaller and much less common *P. grawi* sp. nov. is described and is shown to co-exist with *P. marathonensis* but has a more restricted distribution. *Pachyrhizodus grawi* is more gracile than the larger species, with a shorter premaxilla and with its jaw articulation positioned more anteriorly, below and just behind the back of the orbit. ❐ *Pachyrhizodontidae, Pachyrhizodus, P. marathonensis, P. grawi sp. nov., Toolebuc Formation, Allaru Formation, Lower Cretaceous, Albian, Eromanga Basin, Queensland, Australia.*

As part of a general review of Queensland's Lower Cretaceous fossil marine fishes, recently collected specimens added to the Queensland Museum collections expand representation of material referrable to the Family Pachyrhizodontidae.

This material was largely collected from poorly exposed surface exposures of both the Toolebuc and Allaru Formations, that occur as an arc around the northern and western edge of the Eromanga Basin (part of the Great Artesian Basin) and that were deposited within the epeiric sea of that time.

For over a century, fossil teleosts that were originally described by Etheridge Jnr. (1905) as *Ichthyodectes marathonensis* appeared to represent the only pachyrhizodontid present in the Australian Cretaceous sediments. Bardack (1962) suggested that this species should have been referred to *Pachyrhizodus* but considered the age of the deposits from which it was derived to be Upper Cretaceous. Bartholomai (1969) agreed with Bardack's (1962) suggestion regarding the taxonomic position of the species, provided a more complete description of its skeletal morphology, and corrected the age of the deposits from which it was derived to Lower Cretaceous (Albian). Forey (1977) has subsequently added further comments on the morphology of *P. marathonensis,* based on a specimen, P 55858, in the collections of the British Museum (Natural History).

The thin, widespread and organic-rich Toolebuc Formation (and the contemporaneous but considerably thicker Allaru Formation) is now dated as latest mid to late Albian, the *Pseudoceratium ludbrookiae* dinoflagellate zone/upper *Coptospora paradoxa- Phimopollenites pannosus* spore- pollen zone (Moore *et al*. 1986; McMinn & Burger 1986). Henderson (2004, Fig.1) has provided a map of the Great Artesian Basin and its subdivisions that also illustrates the surface expression of the Toolebuc Formation. He has suggested the age should be refined further to late Albian on the basis of ammonite and nannofossil biostratigraphy. However, the author prefers to retain the more conservative age determination for the purposes of the current study. Material referred in the study to a new, more gracile species has come from localities close to Richmond, CNQ, close to the oceanic inflow area over the basement Euroka Ridge between the Eromanga and Carpentaria Basins. Distribution of the larger species, *P. marathonensis* is wider, extending from near the Euroka Ridge area to the western margin of the Eromanga Basin, near Boulia, CWQ, east of the Northern Territory border.

Nearly all pachyrhizodontid material studied is neurocranial and only rarely are more than anterior parts of the body present. This reflects the fact that the bulk of specimens have come from the poorly layerered coquinite that represents the majority of the rare surface exposures of the Toolebuc Formation. Little material has been collected from the Allaru Formation. Many preserved specimens form the nucleus of calcilutite concretions that are developed within the coquinites and that are released and exposed on the surface by weathering and erosion of the containing sediment. Excavation of exposed coquinites by the Kronosaurus Korner, Richmond, NCQ, has recently provided almost complete specimens of several of the early teleosts, including an almost complete skeleton and body outline identified by the author as *S. achyrizodus* sp. and a large specimen of the ichthyodectid, *Cooyoo australis* (Smith Woodward, 1894). Similar excavations have been undertaken below surface finds by the Stonehouse Museum, Boulia, CWQ but, to date, success there has mostly been in regard to articulated remains of marine reptiles and cranial remains of fishes. Recently exposed fish remains are often of higher quality compared to those that have remained on the surface for longer periods. Much of the material in the Queensland Museum has been prepared using acetic acid but that held externally on loan is often either unprepared or has been cleared manually of supporting matrix.

ABBREVIATIONS

Material examinied listed with prefix 'F' refers to fossils in the palaeontological collection at the Queensland Museum at Hendra Brisbane.

Ang.	angular
Ao.	antorbital
Atfc.	anterior opening jugular canal
Asp	autosphenotic
Bhtp	basihyal tooth plate
Boc	basioccipital
Bsp	basisphenoid
Cb	ceratobranchial (1-4)
Cea	anterior ceratohyal
Cl	cleithrum
De	dermethmoid
Den.	dentary
df	dilitator fossa
Dsp	dermosphenotic
Eb	epibranchial (1-3)
Ect.	ectopterygoid
Enpt	endopterygoid
Epo	epiotic
Exo	exoccipital
fm	foramen magnum
fmcv	foramen for middle cerebral vein
focc	foramen for occipital nerve
fVIIot	foramen for otic branch of VII
Fr	frontal
H.	hypural
Hm	hyomandibular
Ic	intercalar
Io.	infraorbital (1-5)
Le	lateral ethmoid
Me.	mesethmoid
Mpt.	metapterygoid

Mx	maxilla
Op.	operculum
Ors	orbitosphenoid
Pa	parietal
Pal.	palatine
Par	parasphenoid
Ph	parhypural
Pmx	premaxilla
Pop	preoperculum
Pro	prootic
Psp	pterosphenoid
Pto	pterotic
Pu	preural centrum (1-2)
Qu.	quadrate
Rart.	retroarticular
Smx.	supramaxilla
So	supraorbital
Soc	supraoccipital
Sop	suboperculum
Sosc	supraorbital sensory canal
Spl.	clerotic plate
Un.	uroneural (1-2)
I.	foramen for olfactory tract
II	optic nerve opening
III	foramen for occulomotor
V	foramen for trigeminal

Cohort Elopomorpha *incertae sedis*

Suborder Pachyrhizodontoidei Forey, 1977

Family Pachyrhizodontidae Cope, 1872

Genus *Pachyrhizodus* Dixon, 1850

Type species. *Pachyrhizodus basalis* Dixon,1850

Generic Diagnosis. An emended generic diagnosis is provided in Forey (1977).

The Queensland material essentially conforms with that diagnosis but possesses the following features: Dermethmoid broad, laterally with muted posteroventral processes, lacking definitive bone-enclosed ethmoid commissure. Exoccipitals meet above and below foramen magnum. Endochondral elements of posterior of otic region meet loosely without interdigitating sutures. Dilitator fossa present, sometimes emphasised anteriorly by a large fenestra between autosphenotic and pterotic below excavated frontal margin behind autosphenotic 'crest'; pterotic roof of dilitator diminishes posteriorly to virtually disappear. Fenestration of anterior ceratohyal variably present. Preoperculum varies from minimally expanded ventrally to significantly expanded posteroventrally, with preopercular sensory canal moderately branched across preopercular base.

Discussion. Forey (1977) undertook a complete redescription of the osteology of a number of Cretaceous teleosts referred to the genera *Notelops* Smith Woodward, 1901, *Rhacolepis* Agassiz, 1841 and *Pachyrhizodus* Dixon, 1850 (including its junior synonym, *Thrissopater* Günther 1872) and provided comments on *Elopopsis* Heckel, 1856. He provided emended generic diagnoses and erected a new suborder, the Pachyrhizodontoidei for *Notelops, Rhacolepis, Pachyrhizodus* and *Elopopsis.* This was proposed on the assumption that *Pachyrhizodus, Rhacolepis* and *Notelops* form a monophyletic group suggested by the common possession of patterns of derived character states in the circumorbitals and the caudal skeleton. He separated *Notelops* within a new family, the Notelopidae, regarding it as a plesiomorphic sister group of the Pachyrhizodontidae Cope, 1872, to which he referred the other genera. A full discussion of the earlier history of the pachyrhizodontoids was included in Forey (1977).

Taverne (1987) concluded that *Pachyrhizodus* is the plesiomorphic sister group of *Rhacolepis,* indicating that some species of the former genus still possess a primitive mesethmoid, with well ossified supraethmoid and hypoethmoid, while *Rhacolepis* has an evolved small and cartilaginous mesethmoid. The taxonomic positions of *Rhacolepis* and *Pachyrhizodus* were also reviewed by Maisey (1991a), who suggested that these genera are clearly elopocephalans (*sensu* Patterson & Rosen 1977) with some evidence supporting an elopomorph relationship. However, Maisey observed that much of the morphological basis for this had been shown by Forey (1977) to represent primitive character states. In reviewing the taxonomy and morphology of the early South American albuloid, *Paraelops,* Maisey (1991b) showed that the principal characters used by Forey (1977) to establish pachyrhizodontoid monophyly also occurred in this genus. He suggested that this introduced doubt that the pachyrhizodontoids are monophyletic. As a consequence, he treated notelopids as being referrable to the Cohort Elopomorpha *incertae sedis.*

While detailed descriptions of the osteology of *N. brama, R. buccalis* and *P. megalops* were provided by Forey (1977), no exhaustive revision of all of the described species was undertaken. Only minimal discussion of the Australian and North American species of *Pachyrhizodus* was undertaken. Nonetheless, his descriptions of those species studied in detail and his comments on other described pachyrhizodontoid taxa, provide an invaluable basis for further work, in the current instance on the morphology and evolutionary radiation of pachyrhizodontids in the Australian region.

The genus *Pachyrhizodus* is represented by numerous fossil species from marine Cretaceous deposits of England, France, Italy, North America, New Zealand and Australia. Forey (1977) concluded that six species of *Pachyrhizodus* range in age from the Albian to the possible Santonian in England. Subsequent work by Wenz and Fricot (1985) records one of these species from the Albian of France, while Sorbini (1976) records two of the English species and an additional taxon from the Turonian/Cenomanian deposits of northern Italy. Applegate (1970) recognised three different species of *Pachyrhizodus* in North American Turonian to Campanian sediments. A single species, identified as conspecific with one of the North American species, *P. caninus* Cope, has been recorded from the Late Cretaceous of New Zealand by Wiffen (1983). Until the current study, only *P. marathonensis* (Etheridge Jnr. 1905) was described from Australia (Bardack 1962; Bartholomai 1969).

A prepared specimen in the collections of the British Museum (Natural History), numbered BM(NH) P 55858, from the marine Cretaceous (Albian) of Queensland, was illustrated and referred by Forey (1977, Fig. 33) to *P. marathonensis.* He listed the features he regarded as 'typical' for *Pachyrhizodus* but added that the specimen possessed a large basibranchial tooth plate and a spine-like anterior tip of the preoperculum, features seen in *Rhacolepis.* He also observed the fenestrated anterior ceratohyal in the specimen, noting it was 'the only species (of *Pachyrhizodus*) in which a fenestrated anterior ceratohyal is recorded'. He illustrated a clearly defined antorbital in the specimen but ascribed it to part of the supraorbital.

Forey (1977) concluded that although the pachyrhizodontoids as a group possess a compliment of derived character states comparable with protocanthopterygian euteleosts, they should be left as Teleostei *incertae sedis,* in keeping with Nelson's (1973) earlier conclusion to this effect, based upon a comparative study of lower jaws. Maisey (1991a) noted that *Pachyrhizodus* and *Rhacolepis* share several specialised features and that a number of other characters unite these genera with *Notelops.* He added that the principal characters applied by Forey (1977) to establish pachyrhizodontoid monophyly are also found in the early albuloid, *Paraelops,* concluding that it is no longer clear that pachyrhizodontoids are monophyletic, leading to their treatment as *incertae sedis* elopomorphs. Maisey (1991a) also concluded that separation of *Pachyrhizodus* and *Rhacolepis* is not as straightforward as that between *Rhacolepis* and *Notelops.* Indeed, where preserved, most of the character states considered diagnostic for *Rhacolepis* by Maisey (1991a) are shared by one or both of the Australian species of *Pachyrhizodus* recognised below.

Pachyrhizodus marathonensis
(Etheridge Jnr., 1905)
(Figs 1- 7)

1905 *Ichthyodectes marathonensis* Etheridge Jnr., 5
1962 *Pachyrhizodus marathonensis* (Etheridge Jnr.); Bardack, 387
1969 *Pachyrhizodus marathonensis* (Etheridge Jnr.); Bartholomai, 250
1977 *Pachyrhizodus marathonensis* (Etheridge Jnr.); Forey, 178

Material examined. L 504 (Australian Museum, Sydney), cast of holotype, partial skull with 10 attached vertebrae, original apparently lost, Flinders River, nr. 'Marathon' Station, nr. Richmond, NCQ. F 355, skull, Flinders River, nr. Hughenden, NCQ., figd. Bartholomai (1969, pl. 15). F 3349, skull and anterior of body, 14 miles N of 'Springvale' Station, SE of Boulia, CWQ., figd. in part Bartholomai (1969, figs. 47-8). F 5687, skull and anterior of body, 'Boree Park' Station, nr. Richmond, at MR 622415 Richmond 1: 250 000 sheet, NCQ., figd. Bartholomai (1969, pl. 14). F 5688, incomplete posterior of skull and anterior of body, 'Boree Park' Station, nr. Richmond, at MR 627413 Richmond 1: 250 000 sheet, NCQ. F 5690, incomplete anterior of skull, 'Boree Park' Station, nr. Richmond, NCQ. F 5691, very distorted partial neurocranium, 'Sylvania' Station, nr. Hughenden, NCQ. F 5692, fragments of skull and skeleton, 'Dinga Ding' Station, nr. McKinlay, at MR 404304 McKinlay 1:250 000 sheet, CWQ., figd. in part Bartholomai (1969, fig. 49). F 5705, partial vertebral column and isolated fin, 'Boree Park' Station, at MR 627413 Richmond 1:250 000 sheet, NCQ. F 10111, partial skull, locality unknown. F 13713, partial anterior of body, 'Dunraven' Station, unnamed tributary of Stewart Creek, N of Hughenden, NCQ. F 13725, partial skull, locality as for F 13713. F 14422, skull and anterior of body, 'Canary' Station, nr. Boulia, CWQ. F 14423, skull and anterior of body, 'Canary' Station, nr. Boulia, CWQ. Uni.Qd. F 10210, skull, 'Boree Park' Station, NCQ. F 15212, partial neurocranium, 'Marathon' Station, N of homestead along anabranch of Flinders River, at MR 123396 Richmond 1:250 000 map (E of Richmond), NCQ. F 18919, base of neurocranium, 'Boree Park' Station, NW of Richmond, NCQ. F 48771, incomplete base of neurocranium, QML 754, 'Marathon' Station about 1.5- 3 kms. from homestead, upstream along Flinders River (E of Richmond), NCQ. F 49152, partial skull and anterior of body, 'Warra' Station, nr. Boulia, CWQ. F 49170, very weathered partial skull, Elizabeth Springs, S of extremity of Toolebuc adjacent to spring (W of spring) nr. Boulia, CWQ. F 49172, skull, anterior of body and abdominal scales, 'Lorna Downs' Station, nr. Boulia, CWQ. F 49173, Partial skull, 'Slashers Creek' Station, approx. 1 km. W of homestead, just N of Gidgee Gully, nr. Boulia, CWQ. F 49175, partial skull, 'Slashers Creek' Station, nr. Boulia, CWQ. F 49201, partial skull, 'Elizabeth Springs' Station, nr. Boulia, CWQ. F 54815, partial skull, Richmond, NCQ.

Formations and age. All specimens have been derived from the marine Toolebuc and Allaru Formations of the Great Artesian Basin in Queensland, Australia but most have come from Toolebuc sediments. They are all of Lower Cretaceous (latest middle to late Albian) age.

Emended diagnosis. Relatively large, fusiform species of *Pachyrhizodus,* exceeding ca. 80 cm. total length with body depth of ca.17.5 cm. Skull roof width at autosphenotics slightly narrower than across otic region; orbit length about 26% of neurocranial length; large, separate antorbital present; supraorbital large, ornamented, sutured to dermosphenotic; posterior infraorbitals separate, elongated; supraoccipital often with foramina leading to post-temporal fossa on each side of solid, posteriorly directed process; vomer with at least one, large, recurved, internal tooth; complex external expression of mesethmoid present at posterolateral margin of olfactory capsule; dilitator fossa roofed but with roof reduced posteriorly; large foramen penetrates dilitator fossa anteriorly between autosphenotic and pterotic; hyomandibular with very slightly anteriorly curved shaft and with prominent, thin, anteriorly directed crest supporting posterodorsal margin of metapterygoid; inner wing of metapterygoid strongly flexed, reduced and rounded; ectopterygoid carries numerous, fine, recurved teeth; endopterygoid large, narrowing anteriorly; palatine slightly expanded anteriorly; lateral ethmoid large, ossified, meeting posterior of vomer and anterior of parasphenoid; autosphenotic spine more crest-like, added to ventrally by prootic; anterior and lateral surfaces of prootic separated by sharply angled, anterolateral flange; premaxilla with strong dorsal wing; marginal premaxillary and maxillary teeth similar with largest up to 5.1 mm long; six incurved marginal premaxillary teeth and up to three mesially angled internal teeth present, with central one largest (ca. 8 mm long); maxilla with ca. 22 marginal teeth; dentary with fewer but larger, incurved marginal teeth in a single row (ca. <11 present, up to 9.0 mm long), with anterior teeth slightly backwardly inclined; dentary with deep, slightly inflected, ventral flange; retroarticular separate, expanded medially and with angular and articular also unfused posteriorly; dorsally, articulatory facet with a thin sliver of articular overlying angular, excluding contribution by angular at least to upper part of facet; anterior ceratohyal with large dorsal fenestra; preoperculum not greatly expanded posteroventrally, acutely pointed anteroventrally; supratemporals large, not meeting along mid-line, each with radiating grooves leading from area of anterior supratemporal commissure; post-temporal with elongate, stout, epiotic limb and extended, thin, intercalar limb; pectoral fin large with up to 18 fin rays and with the outer fin ray very robust.

Descriptive remarks. Although a detailed description of the cranial osteology of this relatively large species was provided in Bartholomai (1969) and additional morphological comments were published in Forey (1977), an expanded description is provided because of the additional details/information now available. The skull showing external and internal bony elements is shown in Figs. 1 and 2 respectively and was also illustrated by Bartholomai (1969, Pls. 14 and 15).

Neurocranium. The incomplete cranial roof in F 13725 (Fig. 3) is only slightly distorted. Similar to that figured by Forey (1977) for *P. megalops* (Smith Woodward) from the Cenomanian Lower Chalk of Sussex, England, it has lateral emargination, exaggerated in some specimens, originating from just anterior to the autosphenotic 'spines'. *Pachyrhizodus megalops* has frontals that are relatively more elongated anterior to the emargination. Greatest depth of the braincase is about 43% of total neurocranial length and occurs above the upward flexure of the parasphenoid. Length of the orbit, at 26% of neurocranial length, is less than recorded for English species in Forey (1977), viz. 50% in *P. megalops*; 30% in *P. magnus* and *P. subulidens* but is about the same as in *P. salmonius.* The skull roof has a shallow median frontal depression, often accentuated where lateral compression occurred during fossilisation, a character not present in *Rhacolepis,* as redefined by Maisey (1991a). The skull roof is somewhat convex across the otic region and is also slightly arched dorsally above the posterior of the orbits. The gape is elongate and set at an angle of about 35º to the horizontal.

The dermethmoid is solid, medially dished and anteriorly bluntly pointed and is overlain posteriorly by the frontals (Fig. 4A, B). Laterally it is notched above the olfactory capsule and is extended into muted posteroventrally projecting arms on each side, around the anteroventral base of the margin of the olfactory capsule, similar to those depicted by Forey (1977) for *Notelops* and *Rhacolepis.* This feature is lacking in *P. megalops* and consequently was applied by Maisey (1991a) in his emended generic diagnosis for *Rhacolepis.* The bone broadens posteriorly and, like *P. megalops,* is marked by fine lateral ridges and grooves radiating from the mid-dorsal surface over raised 'humps' and that appear to represent the crests of anterodorsally angled, fused plates that extend onto the ventrolateral arms; a number of fine pores are present within the grooves and it is possible that this structure includes an enclosed ethmoid commissure. However, a bone encased commissure is generally lacking in *Rhacolepis* and *Pachyrhizodus* as noted by both Forey (1977) and Maisey (1991a). Posterolaterally, the dorsal surface has small, overlapping, posteriorly directed, ossified sheets. Anterolateral facets are present for ligamentary attachment of the dorsal processes of the premaxillae and, as in *P. megalops,* there is a deep, spongy ossification interpreted as part of the mesethmoid.

The posterior of the olfactory capsule cups a complex, more compact lateral part of the possible mesethmoid (Figs. 4A, B). Anteromedially this lines the capsule and posterolaterally extends beyond the margin of the dermethmoid, separated by a short process that masks a laterally directed small pore. A larger, associated part floors the posterolateral part of the capsule. Dorsally, this carries a deep, thin flange with a small, lateral pore that meets the base of the short process mentioned above. Basally, it bears two, elongated ridges with the dorsal one curving ventrally to the front of the antorbital (see below) and with the ventral one extending to meet the supraorbital. Each has a small pore towards the external edge, at its extremity.

No nasal has been found in any of the referred specimens of *P. marathonensis* and Forey (1977) states that no nasal has been located in any *Pachyrhizodus* available to him. However, Taverne (1987) records an element identified as a nasal in *P. subulidens* from Italy.

The frontal represents the major component of the neurocranial roof (Fig. 3 and Bartholomai 1969, Fig. 48). It is deeply emarginated just posterior to the autosphenotic spine and the skull roof is shallowly depressed medially. Laterally, the emarginated area joins with a minimal contribution from the pterotic to provide a roof for the anterior of the dilitator fossa. The interfrontal suture is dentate. Ornamentation of the frontal, apart from the longitudinal ridge associated with the supraorbital sensory canal, is variably developed from one individual to another. The supraorbital sensory canal opens just posterior to the dermethmoid junction (see Figs. 4A, B) and well-defined, short, posterior and medial processes terminating in elevated pores are present close to the centre of ossification in F 14422. Ornamentation in most individuals is, however, usually weak anteriorly, radiating from the centre of ossification anterolaterally and laterally, with intervening bone with very fine tubercles in the anterior moiety. Ridges curving gently posterolaterally from the centre of ossification in F 14422 are sometimes stronger, while those across the medial suture are even coarser. A well developed pore is sometimes present near the lateral margin of the parietal suggesting that the supraorbital sensory canal extends into this element. No lateral branch opening above the autosphenotic spine has been observed.

Continuation of the posterolateral ridges from the frontal occurs onto the dorsal surface of the pterotic. This element provides the bulk of the posterolateral cranial roof. The pterotic roofs the bulk of the dilitator fossa but is progressively reduced posteriorly. The posterior of the dilitator fossa itself narrows and diminishes to almost disappear posteriorly. Laterally, the bone carries the posterior one-half of the hyomandibular facet and contributes to the lateral and anterodorsal sides of the post-temporal fossa. No pterotic spine is present. However, the detail of the extent of the pterotic on the lateral cranial surface is usually masked by the hyomandibular or upper circumorbitals.

The parietal is small, wider than long and, as shown by Bartholomai (1969, Fig. 48), is widely separated from its counterpart by a dorsal wedge of the supraoccipital. It is ornamented by muted ridges and, as mentioned above, appears to carry an extension of the supraorbital sensory canal.

The supraoccipital is relatively small and separates the parietals dorsally. It carries a short, posteriorly directed but variable supraoccipital process that usually appears thinner dorsally than in *P. megalops* and is generally less developed and shorter than in *Rhacolepis* or *Notelops,* as figured by Forey (1977). Foramina leading to the post-temporal fossa are variably present on each side of the upper part of the process but are said to occur in other pachyrhizodontid genera (Forey 1977). The posterior junctions of the supraoccipital with the epiotic and exoccipital are loose and often open and apparently cartillagenous (see Bartholomai 1969, fig. 47).

The epiotic is a slightly larger element than the supraoccipital. Posteriorly, it is sometimes quite dished. Its lateral margin contributes most of the medial rim of the post-temporal fossa but this can be somewhat reduced by dorsal expansion of a narrow arm of the intercalar. The epiotic process is present dorsomedially but is not strongly developed. Contact between the epiotic and exoccipital is often loose.

The exoccipital meets its counterpart both above and below the foramen magnum, differing from those in *P. megalops* and *Rhacolepis* but similar to that recorded by Forey (1977) in *Notelops,* with the dorsal abutment with the basioccipital loose and sloping anteroventrally at an angle of about 40^{o} to the vertical. The posterior surface of the bone is angled anteromedially, with the outer margin more posterior than the inner edge. The junction below the foramen magnum with the basioccipital is solidly pedestal-like and is basally flared and fluted posterolaterally in F 14222. A very small foramen is present beside and very close to the foramen magnum for the passage of the occipital nerve. The posterior and lateral surfaces of the exoccipital meet along an acute ventrolateral flange close to the base of the bone and laterally this is penetrated near its base by a large foramen for the vagus nerve. However, that for the glossopharangeal nerve is masked by other elements, as is the ventrolateral base of much of the braincase.

The basioccipital appears to have formed the occipital condyle through incorporation of a fused, partial, vertebral centrum. Dorsally it bears a well-defined pit on each side of the midline, posteroventral to the foramen magnum, for insertion of a divided neural arch. Laterally, the bone appears reduced and is loosely overlapped by the posterior arms of the parasphenoid. The hyomandibular masks the posterolateral view of much of the braincase in all individuals found to date.

The intercalar is small but frequently has a vertical arm that extends further up the medial rim of the post-temporal fossa in most individuals than was shown for F 3349 by Bartholomai (1969, Fig. 47).

The autosphenotic is large, posterolaterally forming much of the anterior of the dilatator fossa and the anterior one-half of the hyomandibular facet. It bears a well-defined, sharp, autosphenotic crest rather than a ‘spine’. This crest curves ventrolaterally from below the frontal emargination. Anteriorly, the bone forms much of the posterodorsal margin of the orbit. A foramen for the otic branch of the facial nerve penetrates the anterior face of the autosphenotic. The autosphenotic flares ventrolaterally to roof the sharply inclined anterior moiety of the hyomandibular facet. Posterior to the autosphenotic crest, a broad groove leads dorsally into the large fenestra within the dilitator fossa between the autosphenotic and the pterotic, with the bone forming its anterior wall and floor. Only the anterior tip of the pterotic is involved in the fenestra, contributing its posterior wall. As observed by Forey (1977) in *Notelops* and some specimens of *Tarpon* Jordan and Evermann, the large fenestra appears to provide a link between the dilitator fossa and the post-temporal fossa. The fenestra is not stated to be present in *Rhacolepis* or *P. megalops* and was apparently not present in the British Museum (Natural History) specimen, BM(NH) P 55858, that he illustrated and referred to *P. marathonensis.*

The lateral face of the prootic is largely covered by the hyomandibular. It is separated from its anterior face by a prominent, sharp, narrow, anterolaterally directed flange. The anterior face is partially visible in F 14422. It is relatively narrow, deep and cupped and is angled posteroventrally, but this may have been emphasised by lateral crushing around a posteriorly sloping, dorsoventral axis. It is penetrated by separate openings for the anterior jugular canal and a smaller foramen for the trigeminal nerve, both close to the strongly concave, acute lateral margin of the prootic. The foramen for the profundus ciliaris is close to that for the trigeminal nerve and slightly dorsomesiad to it. The large foramen for the oculomotor nerve is situated slightly dorsomesiad to the trigeminal foramen and ventral to it, adjacent to an obliquely angled suture between the prootic and one of the upper arms of the basisphenoid.

The pterosphenoid is relatively small and appears to make only a short contribution to the margin of the optic foramen. Even allowing for distortion, it appears to be angled more anteriorly than shown for *P. megalops* by Forey (1977). The inner margin is notched for passage of the trochlea nerve but this is very close to the junction with the prootic. A relatively large foramen is present well posterodorsal to this notch, presumably for the middle cerebral vein. The suture with the orbitosphenoid is deeply interdigitated but the interdigitated suture with the autosphenotic is not raised to form a groove in that element.

The orbitosphenoid is also small but in F 14422, as is usual, it appears to have extended ventrally to form the dorsal margin of the optic foramen. Dorsally it unites with ventral flanges of the frontal. Any penetration of the bone for the passage of the olfactory nerve has been masked.

The basisphenoid in F 14422 has detached from its contact with the prootic. It is similar in depth or even relatively deeper than that in *P. megalops* described by Forey (1977) but has a broader pedicel that remains attached to the parasphenoid and that has the basal margin of the optic foramen smoothly 'U'-shaped, rather than more sharply 'V'-shaped.

The parasphenoid is elongate, with the posterior extending slightly beyond the articulating surface of the basioccipital. The posterior part is flexed upwards from just behind the level of the weakly developed ascending wings and covers much of the lateral surface of the basioccipital and lateral base of the exoccipital (and, presumably, that of the prootic). In F 14422, the anterior of the bone curves slightly convexly in lateral view and is triangular in mid-section, with its base slightly dished transversely close to the ascending wings and also close to the vomer. There is a short, shallow, longitudinal groove along the lateral margin anterior to the ascending wings, while just below the dorsal margin in F 14423 there is a longitudinal groove to accommodate the dorsal margin of a thin, anteriorly deepening, lateral splint of the vomer from beneath the orbit. The parasphenoid deepens anteriorly to also overlie a ventral splint of bone from the vomer. No parasphenoid teeth have been observed.

The vomer in F 14423 appears only partially ossified and is anteriorly largely associated with perichondral bone. It bears at least one conical but recurved tooth, similar in size to the smaller teeth of the dentary, immediately anterior to the parasphenoid. That in F 5690 has two vomerine teeth present posteromedially. Maisey (1991a) includes a vomer with two recurved teeth as one character state diagnostic for *Rhacolepis.*

The lateral ethmoid is also composed of perichondral bone. It is a very robust element minimally contacting the frontal dorsally and appears to meet the mesethmoid anteriorly. The posterior border is broad and smoothly concave, forming the anterior margin of the orbit. Ventrally, it meets the anterodorsal surface of the parasphenoid and the vomer. Its margin, especially dorsolaterally, is acute and presents numerous, large tubercles and a short lateral process. As in *P. megalops,* it lacks a foramen in the orbital wall. A dorsal gap is present below a groove in the longitudinal, ventral ridge strengthening the frontal from the olfactory capsule. This was presumably for the passage of the olfactory nerve and the nasal artery.

Strong, broad, sclerotic plates are present.

Hyopalatine series. The hyopalatine series is not fully exposed in any specimen (Fig. 2; and Bartholomai 1969, pl.15).

The hyomandibular is a large, hatchet-shaped bone set almost vertically. It has an expanded, dorsal articulating surface, divided into an elongate, posterior part that is gently curved dorsally to lie within the hyomandibular facet and a crescent-shaped anterior articulation to the back of the autosphenotic. Two, angular ridges descend from the posterodorsal corner of the expanded articulation, with the inner ridge produced into a short, relatively deep and robust opercular process. The two ridges are separated by a deep, 'U'-shaped valley that disappears ventrally and that is penetrated by a large hyomandibular foramen at the base of the opercular process. Both ridges contribute to the robustness of the posterior of the hyomandibular shaft. The anterodorsally inclined head of the bone is supported by a robust, posteroventral ridge that becomes confluent with the outer ridge of the shaft. This is broadened and cupped anteriorly, continuing the line of curvature of the back of the orbit from the autosphenotic. This continues beneath the metapterygoid as an extensive, thin flange that comprises the base of the 'head' of the hatchet. A strong, sharply crenulated ridge that meets the edge of the metapterygoid is angled and diminishes posteroventrally, parallel to the posterior shaft. A cup-shaped depression is present immediately below the dorsal articulating head of the hyomandibular.

The symplectic has not been exposed.

The metapterygoid is a large bone that is slightly dished dorsoventrally in its larger lateral part. This part is ventrally broad, narrowing anterodorsally and closely adpressed to the upper part of the anterior flange of the hyomandibular, immediately anterior to the sharp, crenulated ridge on the bone. The anterior margin of this portion of the metapterygoid descends broadly sinuously from an upper crenulated edge into a diminishing ridge that separates the lateral, vertical part of the bone from a dorsomedially orientated, much smaller, inner 'wing' of the bone. This has a broadly curved anterior margin.

The quadrate is a smaller, subtriangular bone, thickened posteriorly and vertically grooved and thinned to a flange near the anteroventral margin of the preoperculum. It is also deeply notched posterodorsally for the symplectic. The articulatory head is rounded and ventrolaterally sharp and is notched above posteriorly, presumably to accommodate the sharp anteroventral process of the preoperculum. The articulation is ventromedially broadened and rounded.

The endopterygoid is poorly exposed, except in F 355. It is seen in dorsal view in F 48771 but is strongly distorted. It is elongated, anteriorly flexing and narrowing as it becomes more horizontal. The bone appears to have supported a mass of perichondral bone above in F 14423. The dorsal surface is bulbous and marked by fine ridges radiating laterally. Posteriorly, it meets the ectopterygoid along its lateral margin and is overlain by the edge of the metapterygoid; anteriorly it meets the palatine and medially, it abutts the parasphenoid.

The ectopterygoid, also seen from above in F 48771, is elongated, thin and shallow, with a rounded ventrolateral margin. Internally, it carries numerous, small, recurved, multiserial teeth. A single row of ectopterygoid teeth was identified as diagnostic for *Rhacolepis* by Maisey (1991a). The posteroventral margin is only very slightly downturned to meet the quadrate, while the posterodorsal corner lacks the dorsal process present in *Rhacolepis* (Forey 1977) and minimally overlies the metapterygoid.

The palatine is relatively short and laterally shallow and thin. It flexes anteromedially in front of the endopterygoid into a more expanded flange. It is not known whether the element carried teeth. It has expanded, anterodorsal processes that bear articulatory surfaces that were probably the sites for attachment to anterior cranial elements.

Dermal upper jaw. The upper jaw is elongate, extending well behind the level of the back of the orbit (see Figs. 1, 9). A single supramaxilla is present, in addition to a premaxilla and maxilla.

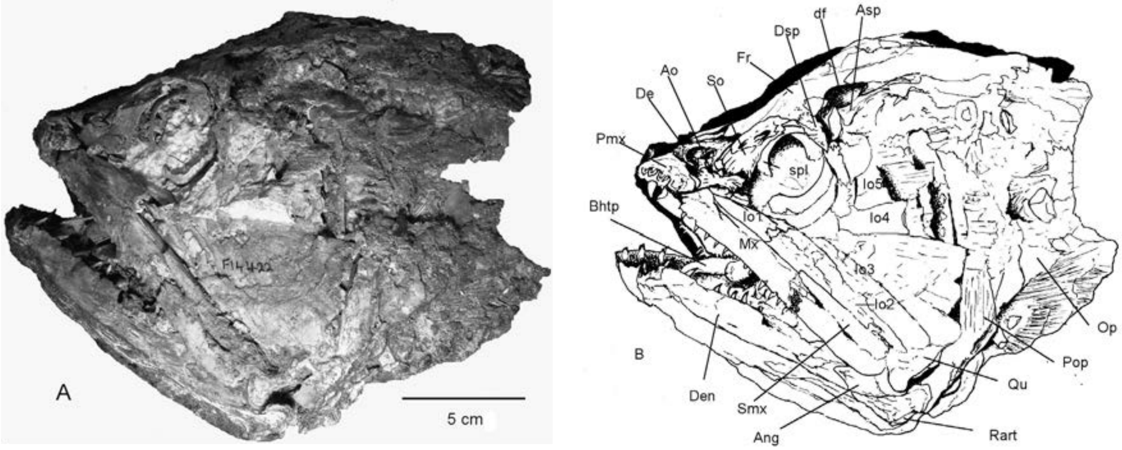

FIG. 1. *Pachyrhizodus marathonensis,* F 14422, **A**, photograph of nearly complete skull, left lateral view (slightly crushed laterally and minimally rotated); **B**, drawing.

The supramaxilla is slender and unornamented and laterally shelves over the posterior of the upper margin of the maxilla from below the mid-orbital area, more like that in *Notelops* and *Rhacolepis* than that depicted for *P. megalops* by Forey (1977).

The premaxilla is small, comprising about 20% of the total upper jaw length. Laterally, it is slightly convex, becoming slightly more rounded anteriorly towards its symphysis with its counterpart from the other side. Posteriorly, it closely overlies an anteromedially directed process of the maxilla (Fig. 4A, B). Its dorsomedial margin is elevated into an elongate, triangular process best seen in F 49152. This has a gently sloping posterior edge leading to a notch that appears to be associated with the front of the antorbital. Anterodorsally, the process is bent medially into a broad flange that posteriorly has an elevated articulation surface for contact with the anteroventral margin of the dermethmoid. The bone carries 5-6 conical, marginal teeth (see Fig. 4A, B), with alveoli for up to four additional teeth. Internally, At least two and possibly three larger, conical teeth are present although the most posterior of these is known only from its socket. The internal teeth are angled posteromedially and, although the second is larger than the marginal teeth, the anterior one is very small. General morphology of these elements is similar to those described for *P. megalops* in Forey (1977). Table 1 compares marginal teeth of the dermal upper jaw in *P. marathonensis* with those recorded by Forey (1977) for the English species of *Pachyrhizodus.*

The maxilla is elongate, moderately stout and very slightly arched laterally; the dental margin is somewhat sigmoidal. The bone is relatively more slender in smaller individuals like F 48771. The dorsal margin is slightly convex dorsoventrally, more so anteriorly than posteriorly. A small facet for articulation with the palatine is present in F 18919, close to the anterior of the anterior process, above the overlap with the premaxilla. A curved, anterodorsal ridge is present laterally, ending in a low, sharp crest immediately behind the articulation with the premaxilla, interpreted by Forey (1977) as a possible point of insertion for a palatomaxillary ligament. Above this is a very low ridge and groove, just below the upper margin of the

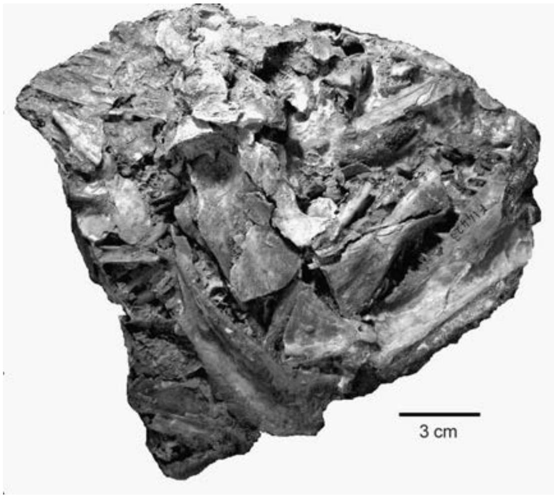

FIG. 2. *Pachyrhizodus marathonensis*, F 14423, photograph of partial skull, internal elements from right lateral view.

bone and into which the base of the first circumorbital lies.

Fewer maxillary teeth are apparently present in *P. marathonensis* than in the English species of *Pachyrhizodus* (Table 1). The maxilla has up to 22 conical, functional, marginal teeth, all ankylosed within shallow sockets on an alveolar shelf, above and within a low, external flange which is shaped to accommodate the external base of each tooth. Bases of teeth are usually more ovate, being compressed anteroposteriorly and set at an obtuse angle to the lateral flange. Small tips of unankylosed, developing teeth are sometimes present between functional teeth within alveoli that often alternate with functional teeth. The marginal teeth are slightly incurved and are generally only slightly smaller than those on the premaxilla. Largest maxillary teeth vary in length from 5.1 mm in F 13725 to 3.6 mm in F 18919. The ventrolateral surface of the bone, especially anteriorly, is ornamented with very fine tubercles in some individuals.

TABLE 1. Comparison of upper marginal teeth in *P. marathonensis* with those recorded for English species of *Pachyrhizodus* by Forey (1977)

Species	Premaxillary Number of teeth	Maxillary Number of teeth
P. marathonensis	5–6	22
P. megalops	9–11	35
P. salmoneus	10	40
P. magnus	14	40
P. subulidens	10	-
P. basalis	9	-
P. dibleyi	-	-

Lower jaw. The lower jaw is robust, slightly longer than the upper jaw and relatively deep. It has only a weakly developed coronoid process. In lateral view, the angular represents only about 25 % of the lower jaw length and is overlapped by the much larger dentary.

The dentary has its lower margin deeply flanged and slightly inflected (see Figs 1, 5). Its very shallow symphysis, best seen in F 5690, is slightly incurved and rugose. The oral border ascends rapidly behind the symphysis before becoming subparallel to the ventral border over much of its length. The lateral surface is solidly convex longitudinally, above a well-defined groove penetrated by a series of fenestra associated with the mandibular sensory canal, along the upper margin of the ventral flange. An alveolar shelf is present medially below a thin, shallow, dorsolateral flange to the oral border. Ornamentation is limited to very small tubercles towards the dental margin. Marginal teeth in a single series are ankylosed within shallow sockets along the alveolar shelf and are partially masked basally in lateral view by the lateral flange. These are much fewer in number than those on the maxilla but are similarly conical in shape; however, they are often angled slightly posteriorly, as well as being medially curved at the tips. Up to 11 functional teeth are present in most individuals. The largest are

FIG. 3. *Pachyrhizodus marathonensis,* F 13725, photograph of neurocranial roof (excluding dermethmoid and posterior), dorsal view, length of specimen 11.5 cm.

generally about twice as large as maxillary teeth, reaching 9.0 mm in length in F 14423. Towards the anterior of the tooth row, larger teeth are sometimes more inclined posteriorly. As in the maxilla, functional teeth are often alternating with alveoli, sometimes with developing teeth.

The angular is anteriorly fused with the articular but the bones are joined but separate posteriorly, meeting along a simple but close suture about one-third the distance from the top of the postarticular process. A thin sliver of the articular overlies the angular at the outer edge of the articulatory facet, excluding a contribution of the angular from the facet. Its upper relationship with the dentary has not been well exposed but no reverse overlap on the lateral surface, recorded by Forey (1977) in *Rhacolepis* and *Notelops,* is present in F 355 of *P. marathonensis* (see Bartholomai 1969, Pl. 15). The posteromedial aspect of the mandible is partially visible in F 14422. In this region, there is some similarity with that in the North American Upper Cretaceous *P. caninus,* illustrated in Nelson (1973, Fig. 2C). The postarticular process is less flared in *P. marathonensis* while the inner development of the retroarticular is much more elevated. However, the retroarticular is posteriorly unfused and does not appear to contribute to the articulatory facet. The posterior opening of the mandibular sensory canal is more medial than in *P. caninus.*

No gular plate is present.

Hyoid bar, branchiostegal rays and gill arches. The ceratohyal exists as two elements, the anterior and posterior ceratohyals (Fig. 2 and Bartholomai 1969, Pl. 15). These are separated by a short gap that would have been filled with cartilage to connect them during life. The anterior ceratohyal is stout and is penetrated by a large fenestra separated from the dorsal margin by a thin splinter of bone and a number of smaller fenestrae immediately anterior and posterior to the large fenestra, within a deep, longitudinal groove. Maisey (1991a) considered a fenestrated anterior ceratohyal as one of the diagnostic characters for *Rhacolepis.* Anterior and posterior margins of the element slope posteroventrally at about 25° to the vertical. The posterior ceratohyal is subtriangular in lateral view, with a slightly upturned, blunt, posterior point for articulation with a very short, rod-like interhyal. Laterally, the posterior ceratohyal lacks a groove but a deep pit is present posteriorly, presumably for insertion of the hyoidean-mandibular ligament.

Two ossified hypohyals are present (Fig. 2), with the dorsal element slightly smaller than the ventral. The upper hypohyal has a very prominent, dorsomedially and bluntly pointed process. The lower bone has a solid, anteromedially directed process bearing a large, ovate, articulating surface. Separation of the two bones is near planar.

A broad, elongate, tooth plate is present anterior to the hypohyals. This is interpreted as the tooth plate on the basihyal. It is bilaterally symmetrical, anteriorly drawn into a short, central point and set on a very thin, bony plate. Its dorsal surface is covered with numerous,

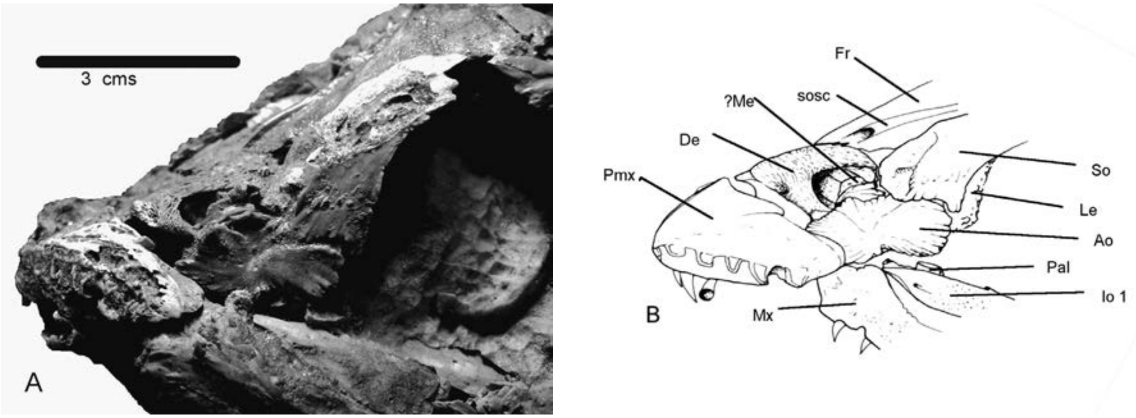

FIG. 4. *Pachyrhizodus marathonensis,* F 14422; **A**, photograph of anterior of skull in lateral view, showing dermethmoid, olfactory capsule, part of mesethmoid, premaxilla (slightly rotated), supraorbital, antorbital, anteriors of maxilla and infraorbital 1; **B**, drawing of above.

small, irregularly positioned, recurved and pointed teeth. A small, ossified, rod-like basihyal element is present beneath the posterior of the tooth plate in F 355, figured in Bartholomai (1969, Pl. 15). No trace of a urohyal exists.

Other elements of the gill arches are exposed in F 14423 as well as in F 355. Anteriors of the hypobranchials exist close to the dorsal margin of the anterior ceratohyal and all bear a strong process close to the anterior margin. Five ceratobranchials have been observed. Cb1 and 2 are long, ‘C’-shaped in section and are equipped with solid, short gill rakers, at least posteriorly. Fine rakers are also present on Cb2. Four epibranchials are present. The anterior ones are more solid than the ceratobranchials and are widely ‘U’-shaped in section. Eb1-3 have anteromedial processes, with that on Eb3 most distinct. Eb4 expands distally but is covered anteriorly by the supracleithrum.

Branchiostegal rays are best seen in F 5687, illustrated by Bartholomai (1969, Pl. 14) and in F 48771 (Fig. 5). Anterior rays are separated and slender, with more posterior rays becoming progressively more spathiform. Attachment of these to the ceratohyal bones is masked in all specimens. At least 20 are present on each side.

Circumorbital series. The circumorbital ring is complete. However, it differs markedly from *P. megalops,* described by Forey (1977), where an antorbital is not present. The series is best seen in F 14422 (Fig. 1) but posterior infraorbitals are well preserved in F 14423 and F 5687 (see Bartholomai 1969, Pl. 14).

The supraorbital is large, at the anterodorsal edge of the orbit. The frontal margin supports the bone medially while the perichondral bone of the lateral ethmoid and the mesethmoid support it anteriorly. It expands anteroventrally to overlap the antorbital and posteriorly, it is sutured to the dermosphenotic. It is ornamented with a large, dorsally directed, sinuous crest from the centre of its ventral border and by a short, lesser crest at a right angle to this. It also has a series of tubercles across its ventrolateral surface, above its overlap with the antorbital and very small tubercles, especially anterodorsally. Minor ridges are associated with plications in the anteroventral margin. Internally, it is penetrated by a number of tracts of the supraorbital sensory system and of the circumorbital sensory canal system from the dermosphenotic through a foramen in the posterior margin. It has a small pore anterodorsally, close to those associated with the posterior processes of the mesethmoid and another behind the smaller crest. A further foramen opens from the anteroventral corner, immediately above another in the posterodorsal corner of the antorbital (Fig. 4A, B).

The antorbital is well displayed in F 14422 (Fig. 4A, B). No separate antorbital is present in those pachyrhizodontoids revised by Forey (1977) although it appears to have been present in BM (NH) P 55858, identified and illustrated by him as *P. marathonensis* but suggested to be part of the supraorbital. The antorbital is a reasonably large, 'bow-tie'-shaped element lying anterior to the base of the orbit and contributing the anteroventral orbital margin. Its dorsolateral surface is shallowly excavated by a broad 'V'-shaped depression that posterodorsally becomes a shelf that supports the ventral margin of the supraorbital. A small pore is present centrally, below the basal point of the 'V' of the depression. Anterior and posterior margins are plicated and are associated with low, curved ridges sweeping centrally. Two small pores are present anterodorsally and anteroventrally along the anterior margin. The anterodorsal edge of the bone is supported by a flange of the mesethmoid.

The first infraorbital is elongate, extending from below the middle of the antorbital to above the anterior moiety of the quadrate. Anteriorly, it is spike-like, closely fitting behind the longitudinal ridge towards the dorsal margin of the maxilla (Fig. 4A, B) and posteriorly, it is shallower than below the orbit and lies along a shallow dorsal groove in the supramaxilla. It provides the ventral margin for the anterior moiety of the orbit. The infraorbital sensory canal is enclosed towards the centre of the bone, with a second enclosed canal close to the dorsal margin. A single, low ridge leading to a single pore is present close to the anteroventral margin (Fig. 4A, B). The bone is ornamented with very small tubercles.

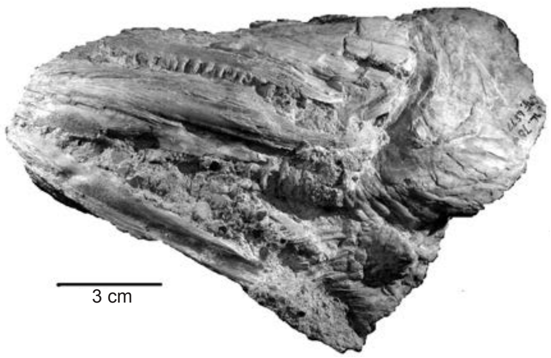

FIG. 5. *Pachyrhizodus marathonensis*, F 48771, photograph of ventral view of partial neurocranium showing partial inflected base of dentary and branchiostegal rays.

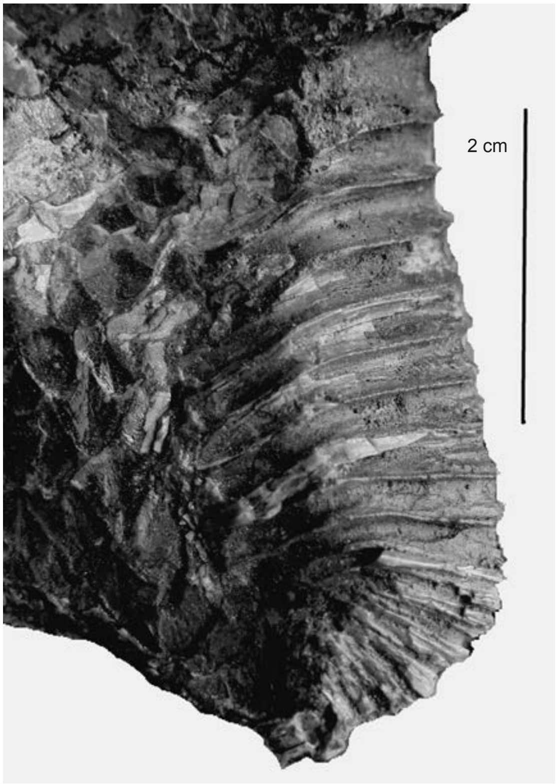

FIG. 6. *Pachyrhizodus marathonensis*, F 49172, photograph of natural mould of base of partial right pectoral fin.

FIG. 7. *Pachyrhizodus marathonensis,* F 49172, natural mould of ventral body scales, each scale ca. 0.5 cm across.

The second infraorbital is well preserved in F 5687 (see Bartholomai 1969, Pl. 14) and F 13725. It is a separate element making only a limited contribution to the posteroventral corner of the orbit where its dorsal margin is somewhat elevated. The bone is generally shallow and much shorter than the first infraorbital but extends slightly more posteriorly. It has several small pores anteriorly and has similar ornamentation to Io1, especially near its posterior edge.

Unlike other pachyrhizodontids redescribed by Forey (1977), the posterior infraorbitals are all separate. Io3-5 are all large, deep, elongate and thin elements. They form the posterior and posterodorsal orbital margins and extend to cover the upper half of the preoperculum and front of the operculum. At the orbital margin, they have an anteroventral process, posteriorly closely followed by an inverted 'V' gap, then by a sweeping overlap by the underlying bone. In Io3, the inverted 'V' underlies a normal 'V' in the previous element, apparently marking the zone occupied by the infraorbital sensory canal (Fig. 1). Small pores are present especially on Io3 above the expected position of the infraorbital canal. However, by Io4 and Io5 the ventral margin of the infraorbital overlies the upper margin of Io3 and Io4 respectively. Openings are difficult to locate in other infraorbitals. The surface of each infraorbital, especially posteriorly, is ornamented by a series of shallow, parallel grooves that often bifurcate posteriorly. The surface is flat between the grooves, terminating in rounded or pointed margins that give the series a posteriorly frilled appearance. The anterolateral surface of Io4 and almost all of Io5 is ornamented with very fine tubercles in F 14423.

The dermosphenotic progressively becomes less elongate dorsally than Io5 but has similar anteroventral structure to that in lower elements. Laterally, it covers the majority of the dilatator fossa and hyomandibular facet and most of the autosphenotic spine. It has a deeply sutured junction with the supraorbital anteriorly and forms the posterodorsal margin of the orbit. The orbital margin is slightly dentate in F 14422. The infraorbital sensory canal runs close to the anterior of the bone but, unlike *P. megalops,* it has an anterior opening to the supraorbital as well as external openings. A posterior branch also opens to the surface. Its surface is ornamented with fine tubercles but the longitudinal grooves are less well-developed anteriorly becoming better defined posteriorly.

Opercular series. This is shown in Bartholomai (1969, Fig. 46 and Pl. 14), and is also based on those in F 5687, F 5688 and F13725. In general, the series is relatively short and deep and the bones are thin.

The preoperculum is moderately short. Its anterior margin is almost vertical except for the anteroventral corner which is curved gently forwards and medially, the latter presumably to enable the postarticular process of the mandible to clear the bone during opening of the mouth. An acutely pointed spine is present anteroventrally (c.f. *Rhacolepis* diagnosis, Maisey 1991a), below the edge that is inserted into the vertical groove in the back of the quadrate. This feature was also reported by Forey (1977) and illustrated in the British Museum specimen of *P. marathonensis.* The ventral margin of the bone is not greatly expanded posteriorly and curves gently to the posterior margin which is subparallel to the anterior margin over much of its depth, except for the upper one-quarter where it narrows progressively. Posterodorsally, the bone is reasonably broad and the back margin turns anteroventrally at about 25º to the horizontal. The preopercular sensory canal runs down the front of the bone, close to the margin and usually leads to numerous, sweeping branches in the lower 25% of the bone. Those in F 5688 are fewer in number and are contained within sweeping, flattened ridges. Internally, the preoperculum in F 13725 is composed of a closely adpressed series of curved, flattened plates that separate into sharp spikes dorsally.

The operculum is anteriorly overlain by the preoperculum. It is short and narrows markedly dorsally. Its ventral margin is obliquely angled posterodorsally and is deeply indented (as also seen in *Rhacolepis*). The surface has weak ornamentation of very fine, irregular grooves that radiate from above the articulation with the hyomandibular. F 5688 has several radiating, flat ridges in its upper area, similar in form to the posterior margins of the infraorbitals and its posterodorsal margin is finely crenulated.

The interoperculum is reasonably well developed, situated below the lower margin of the preoperculum. It is much more elongated than deep.

The suboperculum is obliquely positioned posteroventrally and is a large bone, overlain by the operculum, the preoperculum and, anteriorly by the interoperculum. It overlies the anteriors of the top of the cleithrum and the ventral part of the supracleithrum.

Pectoral girdle and fin. The supratemporal is best seen in F 5687 (Bartholomai 1969, Pl. 14). It is relatively large and semicircular, with an angled anterior margin. It does not meet its counterpart along the mid-line. The outer surface is marked by five deep grooves that radiate posteriorly from an anterodorsal groove. A supratemporal commissure probably ran along this groove with branches into the radiating grooves.

The post-temporal in F 14423 is elongate, narrow anteriorly and broadens posteriorly into an indented, rounded margin. The dorsal epiotic limb is strengthened internally by an elongate ridge, while the ventral limb comprises an elongated, round, anteroventral prop to the intercalar.

The supracleithrum is deep and moderately long and carries a continuation of the lateral line obliquely across its surface. This can be seen best in F 5687 (see Bartholomai 1969, pl. 14). The bone extends ventrally to overlie the top of the cleithrum.

The cleithrum is broadly expanded posteriorly below its junction with the supracleithrum and has its dorsal limb extended along much of the inner margin of the supracleithrum as reported for *P. megalops* by Forey (1977). The posteroventral margin is excavated for insertion of the pectoral fin, exposing parts of the internal bones of the girdle. The concave, inner margin of the cleithrum is very deep, adding strength to the bone. A large interosseus foramen is present anteromedially, above the keel-like coracoid and below the anteriorly pointed end of the cleithrum. Neither the scapula nor the mesocoracoid are exposed in any specimen and postcleithra, although present are difficult to differentiate.

The bases of anterior rays of the pectoral fin are present in a number of specimens. These show the fin to have been set downwards at a low angle to the horizontal and to have been very strong, with the first ray being widest. Up to 13 rays are present in F 5687, while F 3349 presents the bases of 15 rays. F 49172 has the bases of 18 fin rays represented (Fig. 6). Forey (1977) illustrates a partial fin for BM(NH) P 55858 that suggests the pectoral fin was relatively elongated.

Squamation. Cycloid scales are present over the body and extend to between the back of the lower jaws and between the posterior of the supratemporals. They are thin and circular (Fig. 7) and there are many evenly spaced circuli that are ornamented externally with fine tubercles.

Other elements of the skeleton of *P. marathonensis* have not been preserved in any of the museum specimens available.

Pachyrhizodus grawi sp.nov.

(Figs 8 - 11)

Material examined. Holotype, F 48770, almost complete skull from QML 37, Pub Paddock, 'Boree Park' Station, about 16 kms. NW of Richmond, nr. MR 627413 Richmond 1: 250 000 sheet, NCQ.

F 12709, incomplete neurocranium, Mountain Creek, 'Arrara' Station, S of Hughenden, NCQ. F 48769, partial skull, from QML 37, Pub Paddock, 'Boree Park' Station, about 16 kms. NW of Richmond, nr. MR 627413 Richmond 1:250000 sheet, NCQ. F 15585, ventral aspect of lower jaws, 'Dunluce' Station, W of Hughenden, NCQ. F 41517, very incomplete skull, 'Boree Park' Station, about 16 kms. NW of Richmond, NCQ.

Formations and age. Derived from the marine Toolebuc and Allaru Formations of the Great Artesian Basin, Queensland Australia, of Lower Cretaceous (latest mid to late Albian) age.

Etymology. Named for the late Mr B.H. 'Beno' Graw, Manager of 'Boree Park' Station, near Richmond, NCQ, who collected and donated many fossil fish specimens to the Queensland Museum.

Specific diagnosis. A moderately sized, gracile species of *Pachyrhizodus,* estimated to be about 45 cm in total length and with a body depth of about 10 cm. The neurocranium is comparatively narrow, shallow and elongated. Articulation with quadrate is just behind level of back of orbit; gape moderately angled upwards; marginal teeth on maxilla relatively robust with swollen bases, variably represented (up to 18 on maxilla); dentary relatively short, gently shallowing anteriorly; shallow lower margin strongly inflected below squared, swollen, ventrolateral base; coronoid process low; post-articular process reduced, low; separate, prominent, unfused retroarticular present; maxilla shallow, relatively short (ca. 45% of neurocranial length), variably but convexly bowed laterally; anterior ceratohyal blade-like without dorsal fenestra; preoperculum expanded posteroventrally, with strong, sharply pointed anteroventral spine; operculum relatively large and elongated, with obliquely angled but only slightly indented lower margin; suboperculum very large, angled obliquely.

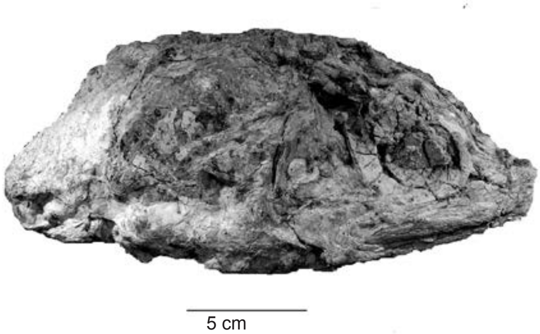

FIG. 8. *Pachyrhizodus grawi* sp. nov., Photograph of Holotype, F 48770, almost complete neurocranium and anterior of body, right lateral view.

Descriptive remarks. The holotype shows characteristics common in many teleost specimens from the Albian marine sediments of the Great Artesian Basin. The side of the neurocranium lying downwards during fossilisation has most of the external bony elements minimally disrupted, while the upper side has lost covering bones by low impact water movements and consequently now presents some of the internal cranial morphology. F 12709 is less crushed than the holotype but has its gape slightly more inclined, possibly as a result of slight dislocation of maxilla. This specimen also has the bases of its dentary teeth exposed, giving the impression of abnormally large teeth on the lower jaw. The shaft of its hyomandibular is also straighter than that in the holotype but the differences noted are not considered sufficient to justify taxonomic separation.

Neurocranium. The holotype is illustrated in Fig. 8. The roof of the skull has been crushed laterally and slightly distorted in all specimens. It appears to have been relatively much narrower than in *P. marathonensis* and posteriorly was more convex transversely. In lateral view, the skull is gracile, being relatively elongated and shallow. The orbit is comparatively larger than in *P. marathonensis,* being 40% of neurocranial length and the articulation between the quadrate and angular is positioned much more anteriorly, below and just behind the back of the orbit. The lateral elements of the holotype are compared with those in *P. marathonensis* in Fig. 9, illustrating the relative differences that contribute to the separation of the two species.

The dermethmoid has not been sufficiently well preserved to allow it to be described and, as is usual in *Pachyrhyzodus,* no nasal is present.

The frontals have limited ornamentation and are elongated but have been laterally crushed in all specimens. A mid-dorsal depression is present. The lateral margin behind the autosphenotic spine does not appear as deeply indented as in *P. marathonensis.*

Small, unornamented parietals are present posteriorly, separated medially by a dorsal wedge of the supraoccipital.

The posterior of the braincase is best seen in F 12709 (Fig. 11A). The supraoccipital makes a significant contribution to the posterodorsal limit of the braincase, similar to that in *P. marathonensis* but has a relatively more elongated posteriorly directed crest. Foramina interpreted as leading into the post-temporal fossa occur close to the dorsal extent of the crest. Dorsolaterally, the margin of the bone swells to support the inner margin of the epiotic process.

The pterotic forms the bulk of the posterolateral corner of the braincase. Its upper surface is subtriangular and is angled ventrolaterally. Its lateral margin contributes to a narrow roof for the dilatator fossa but, like *P. marathonensis,* this diminishes and may be absent posteriorly. The narrow, anterodorsal end of the bone is sutured to the frontal behind the autosphenotic 'spine', while the posterodorsal margin meets the parietal and the epiotic. It contributes to the dorsolateral and lateral margins of the post-temporal fossa. Its lateral surface is slightly dished within the dilatator fossa and ventrally provides a roof for the posterior of the deep hyomandibular facet, which itself is angled anteroventrally and

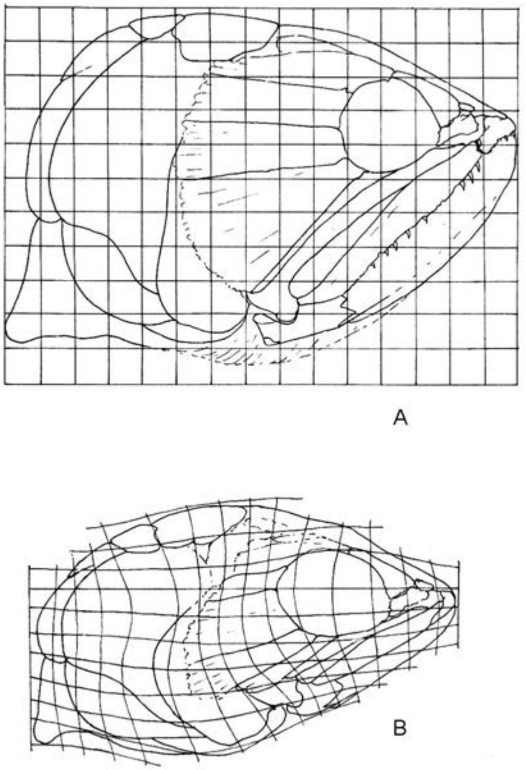

FIG. 9. Comparison of neurocrania of *Pachyrhizodus marathonensis* and *P. grawi* sp. nov., to show more gracile form of the latter (not to same scale).

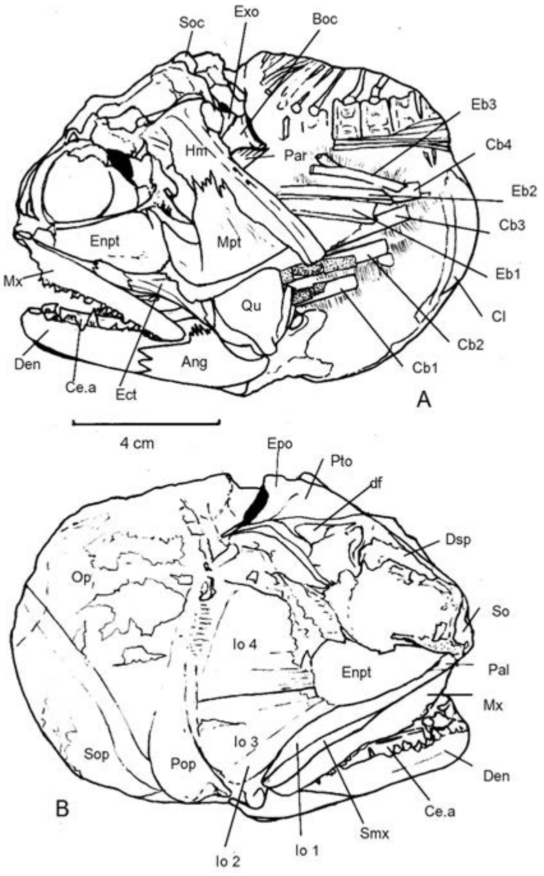

FIG. 10 . *Pachyrhizodus grawi* sp. nov., F 12709, drawings of partial neurocranium; **A**, from left side; **B**, from right side.

then continues with a lesser contribution from the autosphenotic. The dilatator fossa above the near-vertical junction of the pterotic and autosphenotic is deeply excavated; however, the large fenestra, apparently medially directed into the post-temporal fossa in *P. marathonensis*, is lacking.

The epiotic is relatively large and is slightly angled ventrolaterally. The epiotic process is prominent. The bone provides the dorsomedial margin of the narrow but relatively deep post-temporal fossa. The posterior opening of the fossa is angled ventrolaterally and the fossa extends anteriorly to above the autosphenotic 'spine' but does not meet its counterpart.

The exoccipital is relatively larger than that in *P. marathonensis.* As in that species, it meets its counterpart both above and below the foramen magnum, with the lower junction gently angled anterodorsally. Surrounding of the foramen magnum by the exoccipital is similar to that in *Notelops* but unlike those in *Rhacolepis* and *P. megalops,* as noted by Forey (1977). The foramen for the vagus nerve lies posterolaterally, just above the suture with the basioccipital and just anterior to a posteriorly directed foramen above the posterolateral exoccipital flange, also present in *P. megalops* and identified by Forey (1977) as the foramen for the occipital nerve. Another foramen is immediately adjacent to the lateral margin of the foramen magnum, also possibly for an occipital nerve. Much of the lateral face of the exoccipital is masked by the hyomandibular in all available specimens.

The intercalar caps the base of the post-temporal fossa and has a vertical arm that provides much of the medial margin of the fossa, excluding any contribution of the exoccipital, similar to that in *P. megalops* (Forey 1977, Fig. 27).

The basioccipital is relatively small, forming the occipital condyle and posteroventral base of the neurocranium. The dorsal surface posterior to the foramen magnum is marked by two pits, presumably to accommodate the bases of neural arches, in keeping with a vertebral centrum having been incorporated into the basioccipital. The articulating surface is penetrated by a remnant of the notochord. The ventrolateral faces of the bone are angled into a 'V'-surface to accommodate the separated posterior wings of the parasphenoid; a small process carrying a small foramen extends posteriorly from the base of the articulating surface.

The autosphenotic is relatively small and has a reduced lateral 'spine' that is curved ventrally into a sharp, posteriorly inclined crest, like that

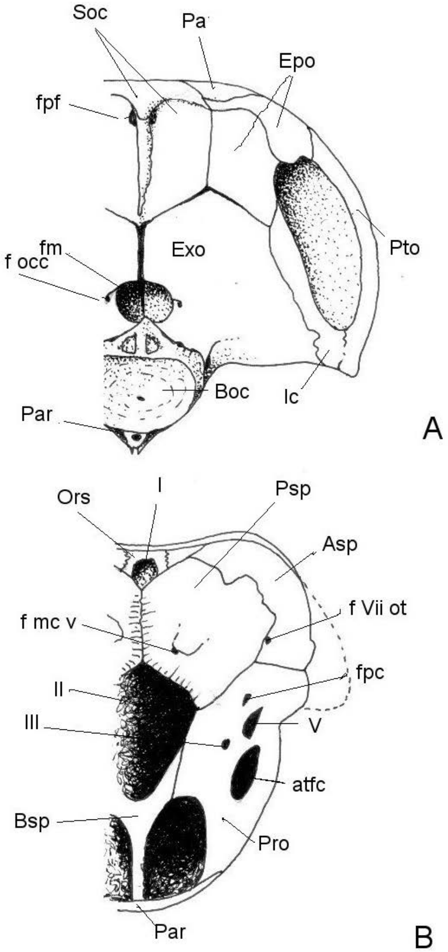

FIG. 11. *Pachyrhizodus grawi* sp. nov., F 12709; **A**, drawing of posterior of braincase; **B**, orbital view of the postorbital part of the braincase.

in *P. marathonensis,* supported below by the narrow dorsal crest of the prootic (Fig. 11B). Laterally, the bone forms the major, anterior part of the dilitator fossa. It also forms the anterior 25% of the hyomandibular facet. Unlike *P. megalops,* the orbital face of the autosphenotic is pierced more medially, on the suture with the pterosphenoid by the foramen for the otic branch of the facial nerve. The lateral suture between the autosphenotic and pterotic is much more like that in *Rhacolepis* than in *P. megalops.* Posterolaterally, the bone meets the pterotic, contributing to the anterior of the dilatator fossa but there is no large fenestra developed into the anterior of the post-temporal fossa.

The prootic is best seen in F 12709, where the anterior face and part of the lateral face are visible. However, the posterior of the lateral face of the prootic is masked by the hyomandibular in all available specimens. Some lateral crushing has occurred and Fig. 11B shows a partially reconstructed anterior face. Little resemblance exists with any of the pachyrhizodontids illustrated by Forey (1977). The most obvious difference relates to the narrowness of the neurocranium in *P. grawi.* However, like *P. megalops,* the foramena for the trigeminal nerve and that for the anterior opening of the jugular canal are separate, while the foramen for the occulomotor nerve lies medial to that for nerve V and the foramen for the profundus ciliaris is above nerve V. The lateral and anterior faces are separated by a well developed, slightly anteriorly orientated crest, that is lobate dorsally just before the junction with the autosphenotic. The foramen for the hyomandibular branch of the facial nerve lies just posterior to the crest opening into the jugular canal, above a small, hooded foramen for the orbital artery. This is again like that for *P. megalops* and *P. magnus,* part of the structure termed a prootic cup by Forey (1977). Suture lines between the prootic, autosphenotic, pterosphenoid and basisphenoid are not zigzag in shape, a feature of *P. megalops.*

The pterosphenoid is an ovate element whose anteroventral margin forms the dorsolateral part of the optic foramen. A small foramen exists on the lateral surface for the middle cerebral vein, anteroventral to a small tubercle. The bone is firmly united with the autosphenotic and dorsally with the back of the orbitosphenoid (Fig. 11B). Medially it meets its counterpart along a vertical suture, excluding the orbitosphenoid from the margin of the optic foramen. It has the dorsolateral surface raised and coarsely, complexly ridged. Its anteromedial margins are finely, radially ridged.

The orbitosphenoid is very small but is poorly preserved and appears to carry a space for the passage of the olfactory nerve.

The basisphenoid is poorly preserved but appears to contribute the 'Y'-shaped base of the optic foramen. A thin, shallow but relatively elongated pedicel links this to the parasphenoid.

The anterior of the parasphenoid is poorly exposed. In that area, it appears sub-parallel to the vertebral column, while the posterior is flexed dorsally, posterior to the more broadly expanded area of the ascending wings, as in the larger species. The posterior is partially keeled, divided and opening into the posterior myodome; it is loosely attached to the base of the prootic and basioccipital. It extends slightly beyond the posterior of the articulating surface of the basioccipital.

Little is known of the vomer.

The lateral ethmoid is small and ossified, curving anteroventrally and broadening towards the vomer and forming the anterior rim of the orbit.

Sclerotic plates are present.

Hyoid bar, branchiostegal rays and gill arches. The hyoid bar is incompletely preserved.

The ceratohyal is divided. The anterior ceratohyal is very slender, blade-like posteriorly and, in F 12709, is elongated, being 4.3 cm long. It lacks a dorsal fenestra. The dorsal margin is anteromedially inflected but this feature reduces and is lacking posteriorly. Anterior and posterior margins are near vertical and contact with the posterior ceratohyal was apparently cartilagenous. A displaced posterior ceratohyal is present. The bone appears similar to that in *P. marathonensis* appearing to have been subtriangular in shape. A short, rod-like interhyal is present apparently associated with a small bony disc that fits a depression on the posteromedial surface of the posterior ceratohyal.

The hypohyal is represented by both upper and lower elements but preservation is too poor for their description.

Branchiostegal rays are preserved as natural moulds in F 15585 and, as in *P. marathonensis*, at least 20 are present on each side, with the rays becoming more spatulate towards the posterior of the series.

The posteriors of the gill arches in F 12709 (Fig. 10A) are moderately well exposed. Most of the endochondral elements are ossified and membrane elements are generally separate from these. No basihyal elements are exposed and the anterior base of what is interpreted as a basibranchial tooth plate is present above the hypohyals within the mouth. Similarly, only the posterior of one of the hypobranchials is visible above the ceratohyal in lateral view. Four ceratobranchials are present and, because the ventral gill arches are relatively undisturbed, it is likely that the most obvious elements are Cb1-4. Ceratobranchials are lunate in section, with Cb1-4 each carrying numerous, fine, short, gill rakers from the concave surface. Ceratobranchial 1 is narrower and deeper in section than Cb2-4. All larger, preserved ceratobranchials carry loose, curved, finely dentate tooth plates. If Cb5 is present it remains coverered by other elements. Three and possibly four epibranchials are present. Eb1-3 are elongate, with a more deeply lunate section than in the ceratobranchials and all carry minutely dentate tooth plates and numerous, short, fine, gill rakers. Eb3 has a prominent, offset, proximal process. Eb4, if correctly identified, is very small and thin and carries small gill rakers but lacks a tooth plate.

Hyopalatine series. The hyopalatine series in F 12709, shown in Fig. 10A, is only slightly incomplete.

The hyomandibular is large and slightly angled posteriorly even allowing for post-mortem movement, whereas that in *P. marathonensis* is near vertical. The shaft is very slightly convex posteriorly, with a strong, dorsoventral, lateral ridge extending ventrally from below the dorsal articulation, about 30% of the way from the posterior corner. The posterior edge is extended into a short, relatively deep but thin opercular process, about one-fifth of the distance down from the dorsal extremity. A strong groove separates these two ridges of the shaft, penetrated by two, large foramina, below the opercular process. The head articulates with the hyomandibular facet. The anterodorsally directed component of the head appears to have been present but is not angled markedly from the major part of the articulation surface. A thin but large anterior flange is present, narrowing ventrally to disappear some distance above the ventral end of the shaft. An anteriorly directed, strong, plicated, lunate ridge descends from below the dorsal head, about one-third of its length from the anterior corner to disappear near the anteroventral corner of the anterior flange. A broad ridge runs from below the anterodorsal extremity of the bone to below the middle of the plicated ridge and continues to the shaft, opposite the opercular process. A shallow, ventrally expanding cup exists between the broad ridge and the centre of the face of the bone, below the dorsal head. Medially, the area between the articulating surface and the base of the opercular process is expanded and rugose.

The metapterygoid is moderately large, with its deeply saw-toothed dorsal margin closely adpressed to the middle of the hyomandibular flange, below and behind its plicated ridge. That in *P. marathonensis* is strongly developed anterior to the plicated ridge. The metapterygoid is slightly cupped medially, allowing its expanded ventral edge to separate from the base of the hyomandibular flange. This edge is slightly convex ventrally and thins anteroventrally. A small, narrow, very pointed part of the metapterygoid is slightly flexed medially, at about 45° to the lateral part of the bone, with a posterior margin that curves posteroventrally to just behind the lower margin of the anterolateral part of the bone. This differs from the larger species where the medial flange is rounded, relatively much larger and less elevated.

The quadrate is smaller than the metapterygoid and is subtriangular with a deep, posterior notch at the back of its sinuous dorsal margin, for insertion of the symplectic. The posterior is shallowly grooved dorsoventrally to accommodate the anterior of the base of the preoperculum. The anterior margin is gently concave, while the lateral surface is shallowly dished, deepening slightly towards the articulatory head. This is rounded posteroventrally, with a relatively deep notch posteriorly above it. The head is also notched along the articulation in posterior view.

The ectopterygoid is small, deepening and gently turned down posteriorly. It is dorsally thin but has a strengthening posteroventral ridge that curves across the outer face to a low, elongate, dorsal process anteriorly. A muted posterodorsal process was probably present as well. A very thin dorsal flange is present above a lateral groove, beside the base of the ventral edge. The ectopterygoid appears to be edentuous, unlike that in *P. marathonensis*.

The endopterygoid is a much larger, subtriangular element, shallowly cupped laterally and carrying fine, recurved teeth anteriorly. The posterior margin is deep and rounded while the dorsal margin is slightly concave, abutting the parasphenoid. Ventrally, the margin is almost straight, fitting within the dorsal groove of the ectopterygoid. Upper and lower margins converge anteriorly to meet the back of the palatine.

The palatine has thin, shallow, inner and outer arms that partially surround the anterior of the ectopterygoid. These converge anteriorly into a dorsomedially directed plate that carries numerous, small, multiserial, recurved teeth, some of which are present on the anterior of the inner arm as well. The anterodorsal curved edge of the expanded plate is raised into two, short but prominent processes, the posterior of which is the more strongly developed. Separation of autopalatine and dermopalatine components has not been possible.

Dermal upper jaw. The upper jaw is composed of three bones, the premaxilla, the maxilla and a single supramaxilla. The gape is elongate and is inclined at an angle of about 45° to the horizontal.

The premaxilla is not preserved in the holotype nor is it present in other referred specimens.

The maxilla is elongate and relatively shallow, extending posteriorly to just behind the level of the back of the orbit. It's curvature is less sigmoid in lateral view than in *P. marathonensis* and, in ventral view, it is moderately convex laterally. The anterior process that would have fitted behind the back of the premaxilla is not well preserved in the holotype but appears to have been elongate, tapered, positioned dorsally and curved anteromedially. Laterally, the maxilla has a thin flange of bone masking the bases of the single series of marginal teeth and providing lateral support for them. The teeth are relatively short (largest being about 1.4 mm long) robust, conical with slightly bulbous bases but they have often had their tips broken e.g. in QMF 12709. Eighteen teeth are present in the holotype. Teeth are ankylosed in shallow sockets along an inner shelf, with functional teeth usually interspersed with spaces previously occupied by functional teeth or containing developing teeth.

The supramaxilla is a very shallow splint of bone, lying along the top of the maxilla from near its posterior margin and thinning anteriorly to below the middle of the orbit, similar to that in *P. marathonensis*.

Lower jaw. The lower jaw is best known from its lateral and ventral aspects. It is relatively short and shallow.

The dentary comprises the major bone of the lower jaw, occupying some 70% of its estimated total length. The symphysis has not been preserved. The oral margin is straight or slightly dished, and posteriorly diverges slightly from its ventral margin; the anterior is gently shallowed, not abruptly so as in *P. marathonensis*. In ventral view, the dentary has greater lateral curvature along its dorsolateral edge than along its ventrolateral edge. Its ventral flange is shallow and is strongly inflected medially, giving the ventrolateral aspect of the bone a squared, solid appearance. Laterally, the dentary posteriorly overlies the angular, except immediately below the low coronoid process where reverse overlap with the angular occurs. As with the maxilla, there is a thin, dorsolateral flange of bone present supporting the lateral edges of the marginal teeth. Teeth are ankylosed in shallow sockets along an interior shelf of the dentary. The teeth vary in number but are fewer than in the maxilla with 13 present in F 15585. The bases preserved in F 12709 suggest the dentary teeth in that specimen were larger than would have been expected. Unfortunately, dentary teeth are not visible in the holotype.

The angular occupies about 30% of the length of the lower jaw. Dorsolaterally, it underlies a thin, anteriorly fused but posteriorly unfused part of the articular that provides the surface of the mandibular articulation. The post-articular process is poorly developed and not greatly elevated.

The tip of the post-articular process is contributed by the unfused but firmly united part of the articular.

The retroarticular is present as an unfused, posteroventral nugget of bone, sometimes separated dorsally from the main body of the post-articular process by a shallow notch. Its internal extent is not well exposed.

There is no gular plate.

Circumorbital series. The circumorbital series is incompletely preserved in the holotype and is imperfectly preserved in other specimens. Ornamentation is of longitudinal grooves separating broad, flat surfaces, terminated distally by pointed or rounded margins.

The supraorbital is well developed in the holotype, curving anteriorly from above the centre of the orbit to above the anteroventral orbital limit. It is relatively broad, increasingly so anteriorly. In F 48769, the supraorbital posteriorly meets the dermosphenotic.

The antorbital is poorly preserved but is relatively small, lying anteroventral to the supraorbital and anterodorsal to the front of the first infraorbital. It contributes to the basal margin of the olfactory capsule and the anterior margin of the orbit.

The first infraorbital is expanded anteriorly, providing the anteroventral margin of the orbit. It extends posteriorly as a thin sliver of bone tapering below the middle of the orbit and extending posteriorly above the dorsal margin of the surmaxilla. As in *P. marathonensis,* the second infraorbital wedges above the back of the first and contributes the posteroventral orbital margin. It deepens slightly posteriorly and extends to about the middle of the external surface of the quadrate and is slightly longer in F 48769. However, both Io1 and Io2 in the holotype differ from those in *P. marathonensis* where they are both more elongate reaching across the bottom of the cheek area further to near the back moiety of the quadrate. The third, fourth and fifth infraorbitals cover the bulk of the cheek region and provide most of the posterior margin of the orbit. They extend in F 48769 over the anterior of the preoperculum and in F 48770, those of Io5 reach well onto the operculum. The bones deepen posteriorly and are ornamented by longitudinal grooves. The fifth infraorbital dorsally reaches the base of the dilatator fossa.

The dermosphenotic wraps over the autosphenotic spine from its anterior junction with the supraorbital and covers at least the anterior of the dilatator fossa, tapering posteroventrally.

Opercular series. The opercular series is best preserved in the holotype and this together with other referred specimens enables most of the series to be described, showing it to be relatively more elongated and shallower than in *P. marathonensis.* Fig. 9 shows the relative differences in shape of the series to that in *P. marathonensis.*

The preoperculum is relatively large, being posteriorly expanded in the ventral moiety, more so than in *P. marathonensis*. It is reasonably strongly curved anteromedially over its lower one-third and is pointed dorsally. The bone is produced into a solid, sharply pointed spine that follows the line of the quadrate and is inturned ventrally. Further minor spikes are rarely present posterior to the major spine. A large opening for the preopercular sensory canal is present above the anteroventral spine, while lesser pores are associated with variable sweeping but very muted ridges in the ventral expansion of the preoperculum. The anterior margin of the preoperculum is thickened and is multilayered, with the layers ventrally rotated and broadened, overlying and adhering to one another but thinning posteriorly.

The interoperculum is incompletely preserved along the ventral margin of the preoperculum.

The operculum is relatively large and relatively more elongated than that in *P. marathonensis*, with a posterodorsally angled lower margin that is indented to a lesser degree.

The suboperculum is also reasonably large and elongated, angled posterodorsally with a curved lower margin.

The supratemporal and post-temporal is too crushed in the holotype to be described.

Pectoral girdle and fin. These elements are not well represented, with only the dorsal part of the cleithrum present. This has an anterodorsal, solid margin that would have extended well above the ventral margin of the supracleithrum. The posteroventral margin is excavated for insertion of the pectoral fin. The posterior margin is expanded and rounded, possibly by expansion of the ventral postcleithral element. The eroded base of the first fin ray in the holotype shows it to have been a very solid element.

Vertebral column. Vertebrae are amphicoelous and slightly spool-shaped in lateral view. Only anterior abdominal centra are known. These are somewhat shorter than deep and, in posterior view, are slightly flattened dorsally and rounded ventrally with a small opening for the notochord. The dorsal surface is deeply pocketed to accommodate the divided and separate neural arch components, while lateral walls are ornamented by anastomosing, slender ridges and grooves and rare foramina.

Other osteological elements are either not preserved or are too poorly preserved to be described.

Discussion. The features that distinguish *P. grawi* sp. nov. from *P. marathonensis,* as well as the detail of the skeletal anatomy of the two species, have been noted in the above descriptions. *Pachyrhizodus grawi* is by far the smaller of the two species, attaining approximately 55-60% the total length of the larger species. The more gracile nature of the neurocranium of *P. grawi* is illustrated in Figs. 8 and 9. Its cranial depth compared with its length is ca. 55%, while that in *P. marathonensis* is ca. 70%. The orbit in *P. grawi* is relatively larger (ca. 17.5% of cranial length) compared with ca. 14.5% in *P. marathonensis.* The lower flange of the dentary is much more strongly inflected in *P. grawi* while its lower jaw articulation with the quadrate is just below the back of the orbit, not well posterior as in *P. marathonensis.* The maxilla is relatively shallower in *P. grawi* (4.5% of neurocranial length c.f. 5.6% in the larger species) and is much more laterally convex. *P. marathonensis* has a large fenestra developed in the anterior of the dilatator fossa into the front of the post-temporal fossa, a feature not seen in the available sample of *P. grawi.* The post-temporal fossa is much narrower and laterally inclined in the latter species (Fig. 11A). The hyomandibular shaft in *P. grawi* is inclined and posteriorly curved in *P. grawi,* while the lateral ethmoid is much less developed in the smaller species. The anteromedial wing of the metapterygoid in *P. grawi* is pronounced and pointed, compared with the more flattened and rounded wing in *P. marathonensis.* The pterosphenoids exclude the orbitosphenoid from the dorsal margin of the opening for the optic nerves. In keeping with its more elongated neurocranium, the opercular bones are more elongated in *P. grawi.*

It is not considered unusual for two species within the genus *Pachyrhizodus* to co-exist in the same area at the same time in the relatively shallow-water, environments that developed in the Queensland Lower Cretaceous (latest middle to late Albian) marine transgression into the Eromanga Basin portion of the Great Artesian Basin. Co-existing species of *Pachyrhizodus* are preserved in both English (and European) and North American Cretaceous marine sediments. Sexual dimorphism is not considered likely to explain the differences in the Queensland material. Both overall body form and apparent differences in numbers of individuals within the preserved samples confirm this view. Because the Queensland material is derived from a relatively isolated zoogeographical situation and is generally somewhat older than the North American species, although broadly comparable in age with some of the European taxa, it would be anticipated that more primitive character states might be more evident in both species now recognised.

Forey (1977), in his consideration of pachyrhizodontoids, based his analysis on 45 character states of the genera *Notelops, Rhacolepis* and *Pachyrhizodus* that he believed useful in adding to the interpretation of the evolution of this early teleost group. Particular emphasis was given to the circumorbital series and the caudal fin anatomy in his conclusion that the group of genera is monophyletic. The presence of an antorbital in both Queensland species of *Pachyrhizodus* is at variance with Forey's (1977) statement that this element is lacking in pachyrhizodontoids. A separate antorbital is shown in the illustrations for *P. marathonensis* (Fig. 4A, B) and is here believed to represent retention of an additional primitive character state in the Queensland material. Similarly, separation of the second and third infraorbitals in both Queensland species is considered another retained primitive state that varies from Forey's statement that these are fused in pachyrhizodontoids. Indeed, the close association of the antorbital with the supraorbital in the Queensland taxa suggests that absence of the antorbital in other species of *Pachyrhizodus* may have resulted from its fusion with that element rather than with any other of the neurocranial elements or from actual loss.

It is unfortunate that no *P. marathonensis* or *P. grawi* specimens with associated post-cranial (especially caudal elements) are present in the Queensland Museum collections. However, a disassociated partial caudal specimen, QML 754, with morphological characters compatible with described pachyrhizodontoids is available and is illustrated in Fig. 12, while a second disassociated caudal fin (F 49171) is present in the part of the collection held in the Stonehouse Museum in Boulia, CWQ. An almost complete *Pachyrhizodus* specimen, probably of *P. grawi,* showing nearly all elements of the post-cranial skeleton as well as the body outline, has been collected and prepared by the Kronosaurus Korner in Richmond, NCQ. A photograph of this specimen, numbered RFM 500 in that collection, was provided to the author (P. Stumkat pers. comm.). This has been used to confirm reference of QML 754 and F 49171 to *Pachyrhizodus* sp.

The skeleton of the Queensland pachyrhizodontoid caudal fin retains similarities with those seen in *Notelops* (Forey 1977, Figs. 10). It also shares some character states with those in the Italian examples of *Pachyrhizodus* sp. (Taverne 1987, Figs. 4-5) and *P. caninus* Cope, from the Upper Cretaceous of North America (Forey 1977, Fig. 36; Nelson 1973, Fig. 8A). In general and where represented, those skeletal caudal fin characters in pachyrhizodontoids that are considered by Forey (1977) to represent a more advanced situation than in the elopoids, at least appear present in *Pachyrhizodus* sp. The parhypural bears a small hypurapophysis, similar to that shown by Taverne (1987, Fig. 5) in *Pachyrhizodus* sp. and is fused with the first preural centrum. This is also seen in the caudal fin of *P. caninus* (Forey 1977, Fig. 36). Unfortunately, the proximal end of the lower hypurals is not visible in QML 754 but is visible in F 49171, showing its fusion with the first ural centrum. All hypurals in QML 754 are imperfectly preserved and are present as 'strap'-like remnants. Those in F 49171 are fused to one another, similar to that illustrated by Forey (1977) for *P. caninus* and by Taverne

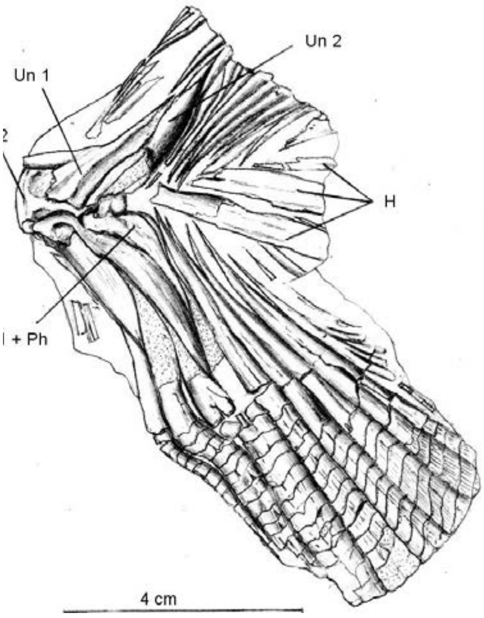

FIG. 12. *Pachyrhizodus* sp. F 55459, partial caudal fin, drawing in left lateral aspect.

(1987, Fig. 5) as *Pachyrhizodus* sp. However, as noted by Forey (1977), hypural fusion patterns vary and may even be an ontogenetic phenomenon. As in *P. caninus,* there are two uroneurals present, the first of which is strongly forked proximally, a feature of *Pachyrhizodus* noted by Forey (1977) and interpreted as possibly present to strengthen the skeleton. A quite strong anterior expansion of the base of Un 1 extends anteriorly along the dorsal moiety of the third preural centrum but probably not to the extent of that figured by Taverne (1987, Fig. 4) in *Pachyrhizodus* sp. The second uroneural is elongated and, although broken proximally, would have extended over the lateral face of the first preural centrum. There is no evidence to support the presence of a neural spine on the second preural centrum.

The lack of complete fusion of the articular and angular in the posterior lower jaw elements and the unfused retroarticular in both Queensland species of *Pachyrhizodus* (as in *Notelops*) were considered to be a primitive teleostean state by Forey (1977). The contribution of the separate articular with exclusion of the angular, at least to the dorsal part of the articulatory facet in the Queensland material (unlike *Notelops* where both separate parts of the angular and articular form the facet, with the articular excluded from the dorsolateral margin) is also at variance with the recorded observations of Nelson (1973) for *P. caninus,* where *Notelops* was stated to be more primitive than most 'lower teleosts'. Apparently, the American species of *Pachyrhizodus, Rhacolepis,* the euteleosts, the clupeomorphs and possibly the elopomorphs, have fusion of the angular and articular contributions to the facet and a separate retroarticular (Forey 1977).

It appears likely that the two species of *Pachyrhizodus* recorded from Queensland were both fast swimming, predatory carnivores of the Lower Cretaceous epeiric sea of the Eromanga Basin, particularly in the area close to the inflow over the basement Euroka Ridge. *Pachyrhizodus marathonensis,* in particular, is preserved more widely in the coquinas of the Toolebuc Formation, deposited especially along the shallow margins as far west as the Boulia area. This suggests that distance from the major inflow area into the Basin may represent a factor influencing their distributions. It is interesting that, although globally widespread and successful, unlike some of the contemporaneous but no more significant fishes of that time, *Pachyrhizodus* (and the group as a whole) did not apparently survive beyond the Cretaceous.

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