

A Review of the Plio-Pleistocene Crocodylian Genus *Pallimnarchus*

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The Plio-Pleistocene crocodylian genus *Pallimnarchus* is revised and new material is included in this revision including some material previously assigned to *Crocodylus porosus*. Species of *Pallimnarchus* inhabited most of northern Australia, extending as far south as northern New South Wales and South Australia, and as far west as Windjana Gorge in northern Western Australia. A new species of *Pallimnarchus* is recognised from Plio-Pleistocene deposits of northern Queensland.

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INTRODUCTION

The genus and species *Pallimnarchus pollens* has a chequered history. The name was first coined by De Vis (1886) as a cabinet name for particularly large and robust crocodylian fossils from the Darling Downs. The name gained acceptance through popular and scientific literature (eg. Longman 1925a, 1925b; Anderson 1937). It was not until Molnar (1982) revised the genus that types were nominated and the species and genus formally diagnosed and described.

Pallimnarchus was first suggested to be part of the Australian Tertiary radiation of crocodiles by Willis et al. (1990) and subsequent analyses (Willis 1993, 1995; Megirian et al. 1991) confirmed this. *Pallimnarchus* was formally included in the Mekosuchinae when that taxon was established by Willis et al. (1993).

SYSTEMATICS

Order Crocodylia Gmelin, 1700
Suborder Eusuchia Huxley, 1875
Family Crocodylidae Cuvier, 1807
Subfamily Mekosuchinae Balouet and Buffetaut 1987

Pallimnarchus (De Vis 1886)

The new species, *P. gracilis*, is similar to *P. pollens* and should be included in the genus *Pallimnarchus*. Because only a single species was assigned to *Pallimnarchus*, separate generic and specific diagnoses were not given. Molnar's (1982) specific (and generic) diagnosis for *P. pollens* is; "Symphyseal portion of mandibles broader than in any living species of *Crocodylus*; angle between ramus of mandible and plane of symphyseal surface greater than in either *C. porosus* or *C. johnstoni*." (Molnar 1982:659). Of

these features, the first cannot be assessed on any of the type material of *P. gracilis* and, with the inclusion of *P. gracilis*, the second is now recognised as of dubious value as a diagnostic feature of *Pallimnarchus* (see below).

Generic Diagnosis

Mekosuchines with a short, broad symphyseal region; symphyseal portion of mandibles broader than in any other Mekosuchine; low alveolar process on the dentary; low but very broad snout; small supratemporal fenestrae; quadratojugal-quadrato contact in ventral view extends anterolaterally from lateral quadrato condyle; distance from medial quadrato condyle to exoccipital buttress exceeds width of quadrato condyles. These latter two characters cannot be seen on any material referred to *P. gracilis* and thus may be specific characters of *P. pollens*.

Discussion

Of the two characters given by Molnar (1982) for the generic (and specific) diagnosis of *P. pollens*, the first cannot be seen in any material of the new species described here and the second becomes of dubious diagnostic value. The second character is: "angle between ramus of mandible and plane of symphyseal surface greater than in either *C. porosus* or *C. johnstoni*." Molnar measured this angle for 2 specimens of *Pallimnarchus* and 18 specimens of *Crocodylus porosus*. From this data the average measurement of this angle in *P. pollens* is 24.5 degrees ($n = 2$, s.d. = 2.1 degrees) while for *C. porosus* the average measurement is 17.3 degrees ($n = 18$, s.d. = 2.4 degrees). This measurement on QM F17069 (*P. gracilis*) is 20.5 degrees. While it would be imprudent to attempt statistical comparisons from such a small data set, it is apparent that QM F17069 could well fall within two standard deviations of the average measurements of both *P. pollens* and *C. porosus*. Such a continuous set of measurements makes this feature ambiguous as a generic diagnostic feature. This judgement should be reviewed when a larger data set becomes available. However, until then we regard this part of Molnar's original diagnosis as a specific diagnostic feature for *P. pollens*.

Molnar (1982) referred the large crocodylian snout from Lansdowne Station (QM 1752) to *C. porosus* for the following four reasons. (1). The breadth was not outside the range of variation of *C. porosus* contrary to Longman's (1924) belief. (2). The posterior part of the narial margin was inclined as in *C. porosus* rather than transversely directed. (3). Although the region was crushed and lachrymal ridges were not apparent, the sulci thought to have bounded them were seen. (4). The form of the snout did not match that of a mandible (QM F2025) of *P. pollens*. A reassessment of the snout by the authors revealed that it has two characteristics of the mekosuchine radiation: it lacks the anterior palatine process and shows a marked disparity in the sizes of the alveoli.

With this in mind Molnar's original features were re-examined and the first was obviously inconclusive (both *C. porosus* and *Pallimnarchus* have broad snouts). The second feature was also shown to be inconclusive by comparison of the premaxillae of the Geoff Vincent specimen (a collection of skull fragments from a single, large individual, collected by Mr Geoff Vincent and currently housed in the Queensland Museum), QM F11626, QM F1151 and QM F1154. These all matched in three features, robustness, size of alveoli (and sequences of size differences) and disparity in alveolar size, and so all are referred to *Pallimnarchus*. Two of them however had inclined posterior narial margins (Geoff Vincent's and QM F11626) and the other two had transversely directed margins. The third feature, the sulci, do seem to be present but are here considered — unlike the lachrymal ridges — to be of no taxonomic value (and lachrymal ridges are clearly absent in the Lansdowne snout regardless of the crushing). Finally the discrepancy with the mandible of *P. pollens* is to be expected because the Lansdowne snout derived not from that species but from *P. gracilis*.

In 1982 Molnar referred Longman's (1924) *Crocodylus nathani* to *C. porosus* in view of the apparent absence of distinguishing characteristics. This is now considered incorrect (in part; QM F11609 is still referred to *Crocodylus*) because QM F1512 and QM F1513 both show two diagnostic features of *P. gracilis* (a step in the posterior margin of the symphysis and a fossa behind the ventral part of the symphysis). Both specimens are now referred to *P. gracilis*.

We do not accept that *C. nathani* is the senior synonym of *P. gracilis* for four reasons. (1) *C. nathani* was established on a collection of specimens representing at least two taxa with no clear designation of a holotype specimen. (2) Molnar (1982) did designate QM F1513, a dentary fragment, as a lectotype but proceeded to place *C. nathani* into junior subjective synonymy with *C. porosus*. The holotype of *P. gracilis* is a premaxilla with an associated dentary fragment. This material allows the unambiguous definition of the new taxon and comments on the association of cranial and dentary characters. Reversion to *P. nathani* would entail the renomination of a lectotype specimen that is of limited taxonomic value. (3) Characters used in the definition of *P. gracilis* are completely different from those originally used in the definition of *C. nathani*. (4) Because of the fragmentary nature of both QM F1513 and the holotype material of *P. gracilis*, there is minimal overlap of bones represented with no shared diagnostic features. Thus there could be true synonymy between *C. nathani* and *P. gracilis* but we cannot be certain. We therefore maintain that *C. nathani* does not constitute an appropriate senior synonym of *P. gracilis* and that recognition of the new taxon avoids taxonomic confusion that could arise from redesignating uninformative lectotype specimens.

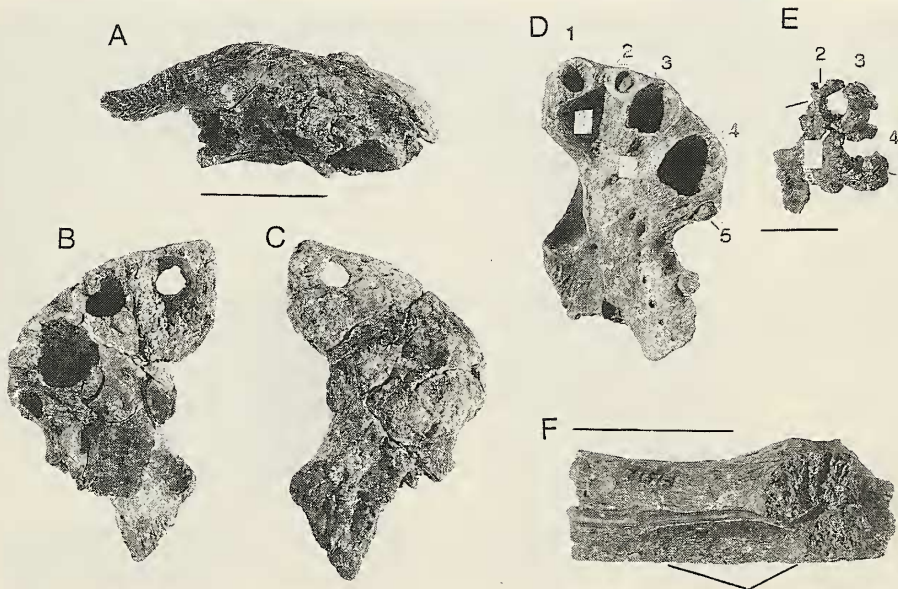


Figure 1. A-C. Right premaxilla of *Pallimnarchus gracilis*, sp. nov. (QM F17065, holotype), from Terrace Site, Riversleigh, Qld. (A) lateral view, (B) ventral (palatal) view, (C) dorsal view. Scale bar 50 mm. (D-E) comparison of Windjana crocodylian premaxilla (E, CPC 17122) with that of *Pallimnarchus pollens* (D, QM F11626), to identify the alveoli and accommodation pits for dentary teeth in the Windjana premaxilla. Numerals along the margins designate the alveoli, all 1-5 in QM F11626, but only 2-5 (2 and 5 have only the medial walls preserved) in CPC 17122. Italic numerals designate accommodation pits for the 1st and 2nd dentary teeth in both specimens. The patterns of both alveoli and accommodation pits are the same in both specimens, indicating that CPC 17122 is referable to *Pallimnarchus*. Scale bar 50 mm. (F) anterior dentary piece of *Crocodylus nathani* (QM F1512) showing two diagnostic features of *P. gracilis*, the medial fossa located ventral to the Meckelian groove (indicated on figure with lines) and the 'stepped' posterior margin of the symphysis. Scale bar 50mm.

Pallimnarchus gracilis sp. nov. (Fig 1)**Diagnosis**

Pallimnarchus gracilis has a broadly ovate first dentary alveolus, the width of which is approximately equal to the depth of the symphysis; symphysis extending backward to the fourth or fifth dentary alveolus; the posterior margin of the symphysis with a distinctly stepped profile such that the portion dorsal to the Meckelian canal extends posterior to that ventral to the Meckelian canal by about twenty percent of the length of the symphysis; regular spacing of the fifth to seventh alveoli; a shallow concavity on the medial surface of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; a splenial contact on the dentary that is poorly marked and difficult to delineate; a flattened premaxilla with the anterior part of the dorsal surface at a low angle to the palate; larger supratemporal fenestrae than *P. pollens*; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf.

Differential diagnosis

Differential diagnosis for *P. pollens* and *P. gracilis*: *Pallimnarchus pollens* is more robust than *P. gracilis*. *Pallimnarchus pollens* has a subcircular first dentary alveolus; the width of this alveolus is less than half the depth of the symphysis; symphysis extends posteriorly to the fifth or sixth dentary alveolus; the posterior margin of the symphysis lacks a distinctly stepped profile; bunching of the fifth to seventh alveoli; no concavity on the medial surface of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; a splenial contact that is well marked and incised into the dentary; a bulbous premaxilla with the anterior dorsal surface set at a high angle to the palate; smaller supratemporal fenestrae than *P. gracilis*; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf. Figure 3 clearly shows the separation of *P. pollens* and *P. gracilis* by the depth relative to the width of the premaxilla. This difference in snout depth is also shown by a comparison of QM F17065 (*P. gracilis*) with QM F11626 (*P. pollens*) (Fig. 5).

Etymology

The specific name is derived from the Latin *gracilis* and refers to the less robust nature of this animal.

MaterialHolotype

QM F17065, right premaxilla, Terrace Site, Riversleigh, Qld (Fig. 1 A-C).

Paratypes

QM F17066, left dentary fragment. Terrace Site, Riversleigh; QM F17069, left dentary, Leichhardt River; QM F1752, snout, Lansdowne Station; QM F1512, left dentary. Tara Creek; QM F1513, left dentary, Tara Creek; Mirani Museum 89-1072, Mirani shire skull.

Discussion

The association of the distinctive premaxilla, QM F17065, with the even more distinctive dentary, QM F17066, indicates that both probably derived from the same taxon and quite probably the same individual. This is important because it is the only association of cranial with mandibular material among the *P. gracilis* specimens, and so allows identification of both cranial and mandibular material.

Material designated as belonging to *P. gracilis* has previously been assigned to three other species. The Lansdowne snout (QM F1752, Fig. 6) was originally assigned to *P. pollens* by Longman (1925a). Molnar (1982) disagreed with Longman's designation and ascribed this specimen to *Crocodylus porosus*. QM F1512 and QM F1513 both formed part of the type material of *C. nathani* (Longman 1924). Molnar (1982) recognised this taxon as a junior synonym of *C. porosus* and explained how Longman had confused specimens of both *C. porosus* and *P. pollens* in his taxon. Molnar identified QM F1512 and QM F1513 as *C. porosus*.

Localities, sediments and associated faunas

Terrace Site, Riversleigh, Qld (Fig 2)

The "Terrace Site" is a perched and dissected river terrace deposit 5 km downstream from the crossing of the Gregory River and the Lawn Hill road, along the west bank of the Gregory River, Riversleigh Station, northwestern Queensland. The unnamed sediments at this site are freshwater fluvial deposits containing mostly unconsolidated sands, clays and conglomerates but which are locally indurated with a light carbonate cement.

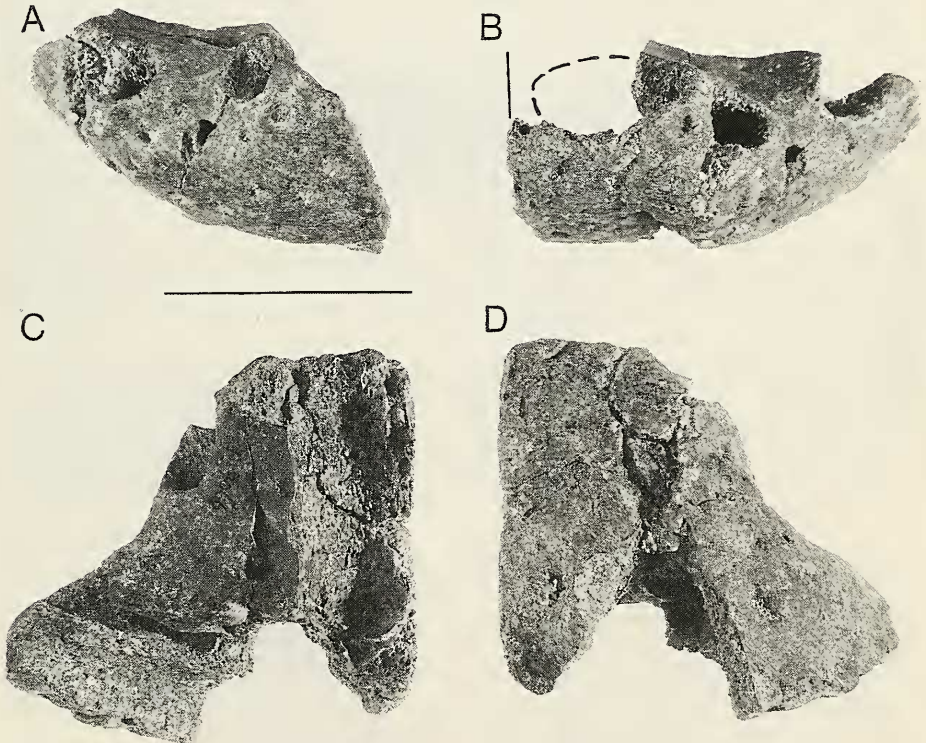


Figure 2. Anterior fragment of the left dentary referred to *Pallimnarchus gracilis*, sp. nov. (QM F17066), from Terrace Site, Riversleigh, Qld. (A) lateral view, (B) anterior view, (C) dorsal view, (D) ventral view. Scale bar 50 mm. Bar in B represents the midline and the presumed form of the 1st alveolus is dotted in to make the elongate form of the first alveolus more clear. This form can also be seen in C.

Two species of crocodile are known from fossils recovered from Terrace Site: *Crocodylus johnstoni* (Willis and Archer 1990) and the new species *P. gracilis*. The Terrace Site material is referred to the Terrace Site Local Fauna (Archer et al. 1989) that also includes freshwater molluscs, *Emydura lavarackorum* (White and Archer 1994), a varanid, *Palorchestes* sp. cf. *P. azael* (Davis in press), *Diprotodon optatum*, unidentified macropodids, and an unidentified rodent.

Leichhardt River, Qld (Fig 4)

A relatively complete left dentary, QM F17069, comes from "Ernie's Croc Jaw Site", part of a dissected flood plain of the Leichhardt River. It is located on Floraville Downs Station, 13 km south of the homestead and 500m west of the river. The unnamed fluviatile sediment is mostly sands and conglomerates with calcrete and ferrocrete concretions.

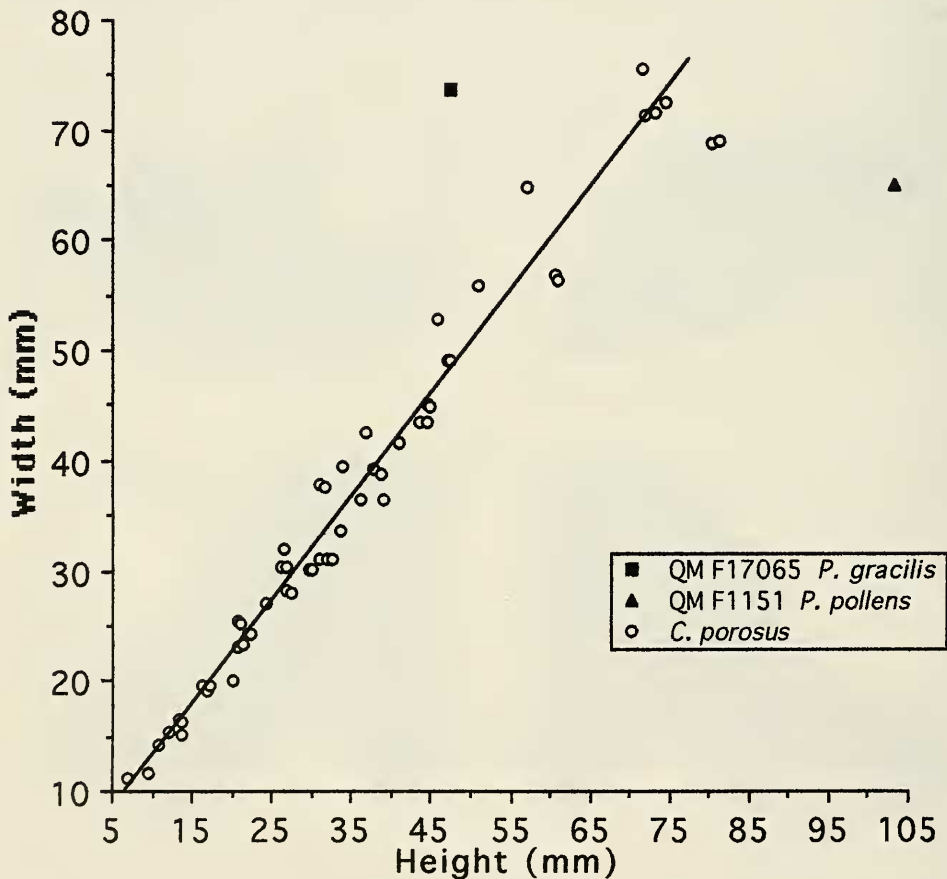


Figure 3. Comparison of the snout depths at the snout notch; *P. gracilis*, *P. pollens* and *C. porosus*.

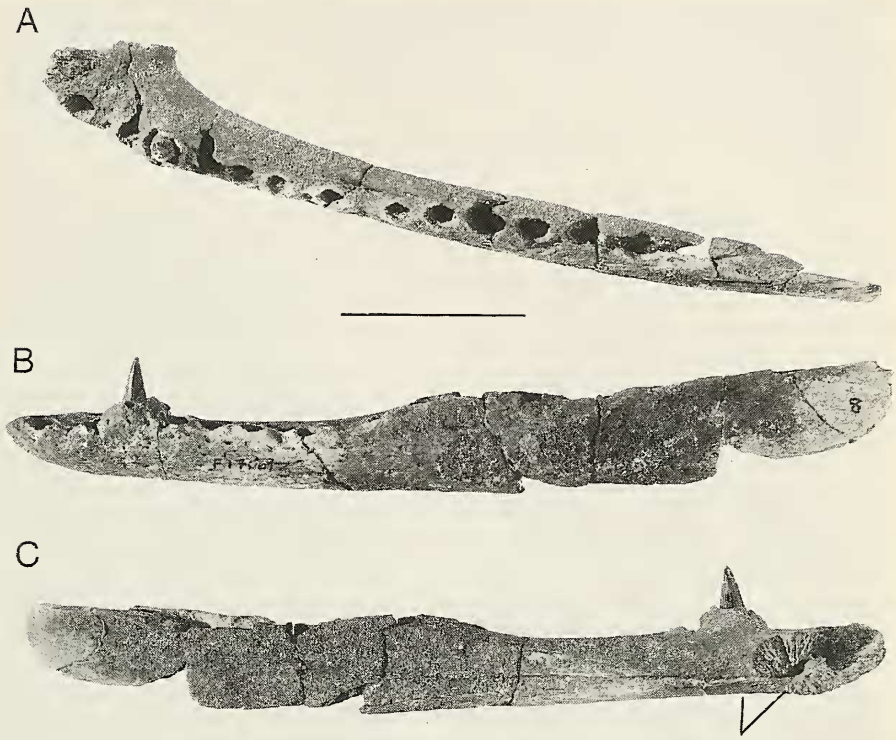


Figure 4. Juvenile left dentary referred to *Pallimnarchus gracilis*, sp. nov. (QM F17069) from the Leichhardt river. (A) dorsal view, (B) lateral view, (C) medial view. Scale bar 50 mm. The characteristic fossa below the Meckelian groove is indicated on C and the 'step' in the posterior margin of the symphysis may also be seen.

Molnar (1982) refers some specimens from the Leichhardt River, northwestern Queensland, to *P. pollens*. Other unidentified crocodylian material was collected in 1987 and a dentary of *C. johnstoni* has also been collected from the Leichhardt River (Willis and Archer 1990). All the crocodylian material is referred to the Floraville Local Fauna along with crustaceans, varanids, snakes, turtles and mammals.

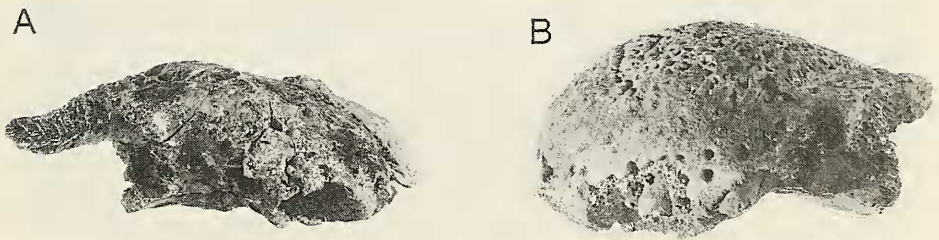


Figure 5. Premaxillae of (A) *Pallimnarchus gracilis*, sp. nov. (QM F17065, holotype) and (B) *P. pollens* (QM F11626) in lateral view to show the lower, more flattened form in *P. gracilis* and the higher more robust form in *P. pollens*. Anterior to the right in A, but to the left in B.

Lansdowne, Qld (Fig 6)

The Lansdowne snout (QM F1752) was collected from Lansdowne Station near Tambo, south central Queensland (Longman 1925b, Molnar 1982a). It was found during excavation for a dam from clays overlying a soft sandstone (Longman 1925a) but more precise geological information is not available. Fossils of *Palorchestes azael* and *Protetnmodon anak* were also collected during the excavations (Longman 1925b).

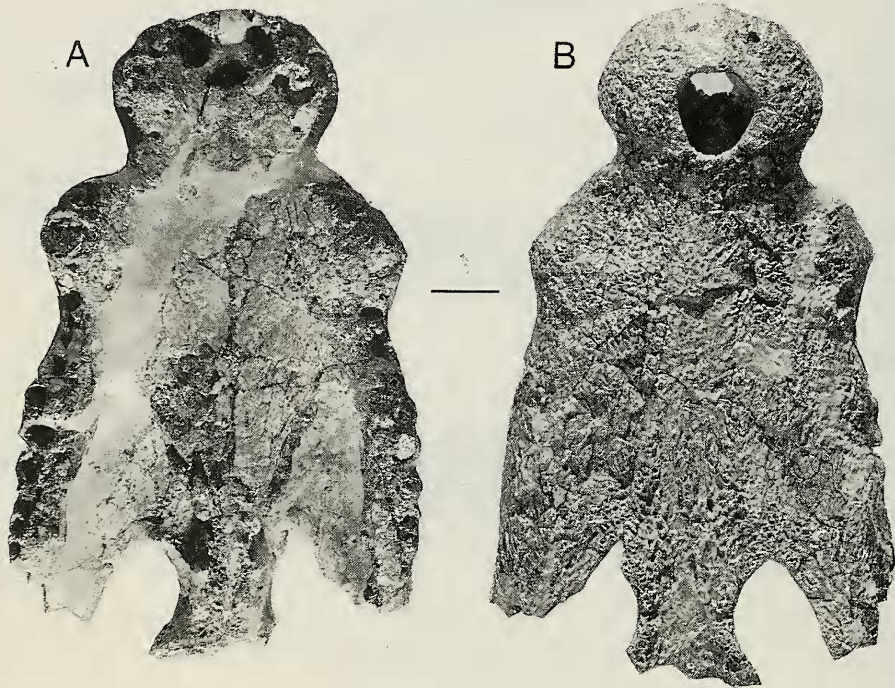


Figure 6. The Lansdowne snout (QM F1752), here referred to *Pallimnarchus gracilis*, sp. nov., in ventral (palatal) (A) and dorsal (B) views. Scale bar 50 mm.

Tara Creek, Qld

Material collected from Tara Creek, inland of Townsville, north Queensland, was recorded only as having come from sediments under the Nulla Basalt. The only comment Longman made regarding the geology here was that these were probably alluvial deposits, based on the grit adhering to the specimens.

Longman (1924) reported turtle and crocodilian fossils from Tara Creek. He referred the turtle material to *Chelodina insculpta* and erected a new taxon, *Crocodylus nathani*, for the crocodilian material. Some unidentified diprotodontids have also been reported from Tara Creek (Rich et al. 1983).

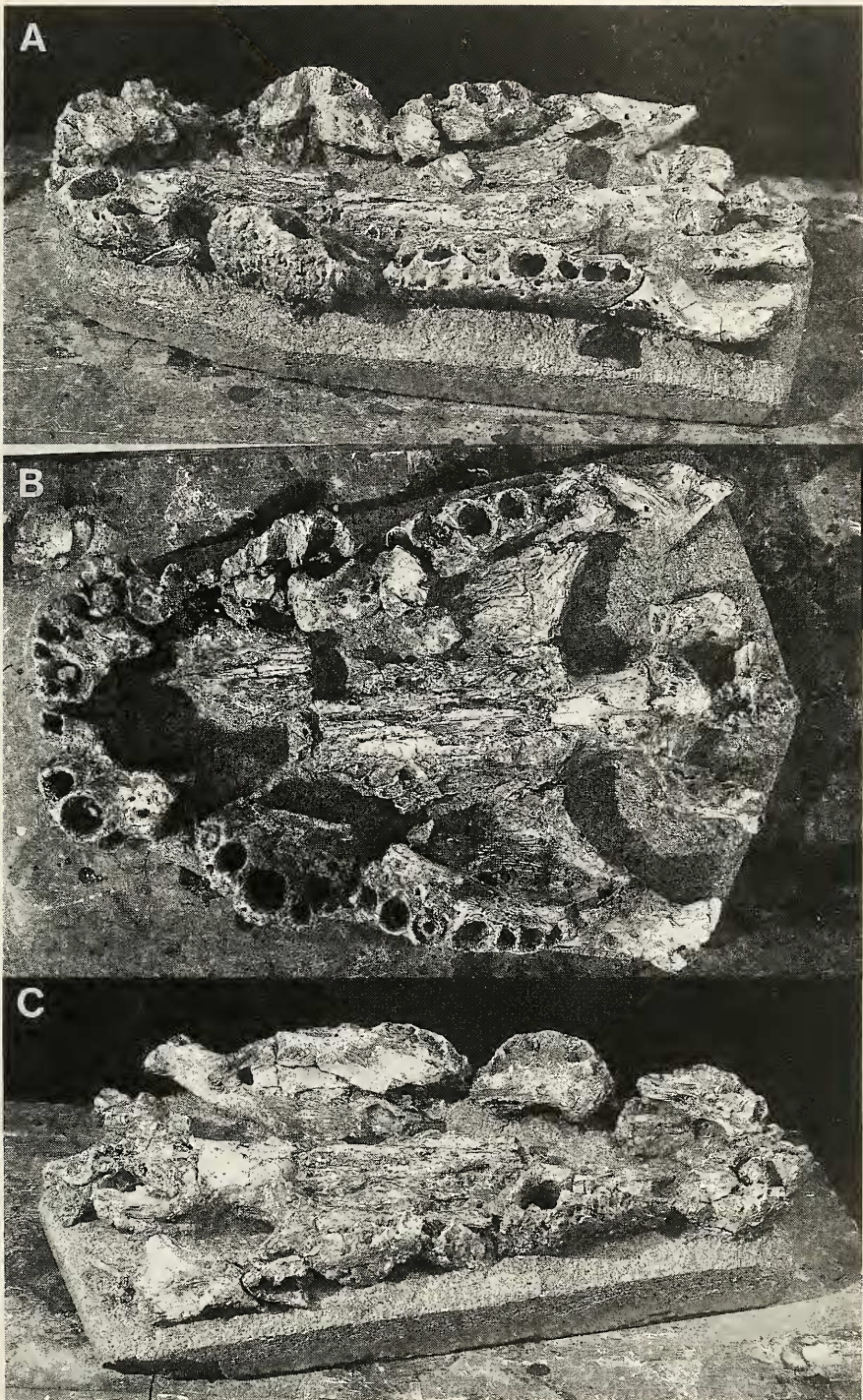


Figure 7. The Mirani Museum skull of *Pallinnarchus gracilis*, sp. nov. (Mirani Museum 89-1072). (A) right lateroventral view (skull inverted), (B) ventral (palatal) view, (C) left lateroventral view (skull inverted).

Mirani Shire, Qld (Fig 7)

Mirani Museum 89-1072 is probably the most complete skull referred to this species, but was encased in concrete (to prevent damage) by its previous owner (Fig. 7). The specimen was purchased by the Mirani Shire Council for the Mirani Museum as part of the collection of Mr J. Williams. It derives from the Nebo district, near Mackay, and is believed to have been found near the top of Mt Robert. Mt Robert consists of Permian sandstones capped with a Tertiary basalt (Malone 1969). The basalt however appears to be a plug (J. Draper, pers. comm., 1996) of Oligocene age (Sutherland et al. 1978). Thus we believe it unlikely that the skull did come from Mt Robert. It may derive from the Sutton Formation, a late Tertiary fluvial deposit.

Age

The oldest site from which material referred to *P. gracilis* has been collected is Tara Creek, dated at 4.0–4.5 Ma (Rich et al. 1983). The youngest site that has been reliably dated is the Terrace Site, Riversleigh. Carbon from this site has given a C^{14} date of 23,900 years (+4,100, -2,700 years; Angela Davis pers. comm.). It seems, therefore, that *P. gracilis* has a Plio-Pleistocene distribution.

Terrace Site is interpreted as Pleistocene based on the presence of premolars and molars of *Diprotodon optatum*, a taxon that is restricted to Pleistocene deposits (Archer 1984). Charcoal and shell material suitable for radiocarbon dating was retrieved from the level containing the vertebrates and gave a C^{14} date of 23,900 years (+4,100, -2,700 years; Angela Davis pers. comm.). However, there is some doubt as to the accuracy of this date and a more accurate one is expected from shell material obtained from the site (Davis pers. comm.). The Terrace Site deposit can be referred to as late Pleistocene pending further radiocarbon dates.

The age of the Floraville Local Fauna is ambiguous due to the lack of fossil taxa suitable for age correlation. This fauna is tentatively accepted as Plio-Pleistocene (Archer 1982, Archer and Hand 1984), and geological data suggests an early Pleistocene age for this locality (Grimes and Douth 1978).

Material from Lansdowne Station is suggested to be Pleistocene due to the presence of *Palorcheses azael* and *Protemnodon anak* (Longman 1925b).

The Nulla Basalt has been dated at between 4.0 and 4.5 Ma (Wyatt and Webb 1970) and hence the Tara Creek fauna is regarded as Pliocene (Rich et al. 1983).

Description

Because QM F1752 has previously been described (Molnar 1982), only new characters seen on this specimen will be described here. The Mirani Shire skull has been set in concrete with only its ventral surfaces visible. Thus this specimen is of limited descriptive value.

Premaxillae

QM F17065 (Fig. 5A) is an almost complete right premaxilla of a large, shallow-snouted, brevirostrine crocodile. The palatal portion, part of the internal wall of the narial canal, and a small piece near the dorsal side of the premaxilla-maxilla suture are missing. The specimen is extensively fractured and calcarenitic matrix adheres to some surfaces. The specimen shows some slight crushing.

The premaxilla has five alveoli. The first and second alveoli has small and of subequal size. The third alveolus is twice as large as the first two but the fourth alveolus is huge, about 1.5 times as large as the third. The fifth alveolus is intermediate in size between the third and second. All alveoli are more or less circular in cross section. The margins of the third, fourth and fifth alveoli are built up into collars that interconnect to

form a low alveolar process.

The pit for the reception of the first dentary tooth is large and penetrates through to the dorsal surface of the premaxilla. This pit separates the first and second premaxillary teeth. Pits for the second and third dentary teeth are less distinct and do not occlude between the upper series by the massive fourth premaxillary alveolus. There is a constriction at the premaxilla-maxilla suture for the reception of the fourth dentary tooth. A distinct nutrient foramen occurs slightly lingual to the constriction for the fourth dentary tooth.

The external naris is tear-shaped and pointed posteriorly. The nasals participated in the external nares which reached posteriorly past the anterior termination of the maxilla.

The sculpture consists of indistinct pits, better defined toward the margins.

Other Cranial Elements

The following cranial features are noted: all elements are heavily built, but not as heavily as in *P. pollens*; the supratemporal fenestrae (seen on the Mirani Shire skull only in ventral view) are small, but not as small as in *P. pollens*; there is a wide shelf of bone between the anterior margins of the supratemporal fenestrae and the base of the postorbital bar.

Dentaries

QM F17066 (Fig. 2) is an anterior fragment of dentary representing the symphyseal region from the first to the fourth alveoli. Most of the dorsal surface is missing as is part of the medial portion of the symphyseal region. Its proportions are consistent with being part of the lower jaw of the same individual represented by QM F17065. QM F17069 (Fig. 4A-C) is the left dentary of a juvenile. It is generally complete except for a portion of the symphyseal region antero-medial to the first alveolus and much of the ventral surfaces posterior to the twelfth alveolus. QM F1512 and QM F1513 are left dentary fragments. QM F1512 (Fig. 1F) is complete from the third to the seventh alveolus and QM F1513 is complete from the third to the eighth alveolus.

The mandibular body is moderately developed and the dentary becomes more shallow in the symphyseal region. The symphyseal region is sub-triangular in dorsal aspect.

Fifteen alveoli are preserved on QM F17069 representing the complete complement of lower teeth. The first and fourth alveoli are huge but the second and third alveoli are much smaller and subequal in size. The first alveolus is compressed and presumably held a flattened, spade-like tooth. The sequence of tooth enlargement is typically mekosuchine and strongly pseudoheterodont. The alignment of dentary teeth shows a distinct angle about the fourth tooth. Anterior alveoli are nearly circular but they become progressively more ovate posterior to the eighth alveolus in a typically mekosuchine manner.

The fourth tooth is preserved in its alveolus on QM F17069 (Fig. 4), the only tooth preserved in situ in the specimens studied. This tooth has distinct anterior and posterior carinae and the lingual surface has prominent vertical ridges. Less prominent ridges adorn the labial surface. The tooth is slightly compressed to an ovate cross section.

Pits for the reception of maxillary teeth are poorly developed. They indicate that the posterior dentary teeth partially interlock on the lingual side of the upper series. There are no pits for the reception of premaxillary teeth.

The symphysis extends posteriorly to the mid-line of the fourth alveolus in QM F17069 and to between the fourth and fifth alveoli on both QM F1512 and QM F1513. The splenial contact is difficult to delineate on some specimens but reaches anteriorly to the sixth alveolus on QM F17069. The splenial contact can not be determined on either QM F1512 or QM F1513.

The symphysis in medial aspect is quite distinctive. The position of the symphysis ventral to the Meckelian canal ends more anteriorly than does the dorsal portion. Thus the dorsal portion extends more to the posterior than the ventral portion by about twenty percent of the total length of the symphysis. Immediately posterior to the symphysis and

ventral to the Meckelian canal there is a shallow concavity on the medial surface of the dentary.

Sculpture consists of well spaced pits and grooves aligned antero-posteriorly.

Comparisons

Except for the overall shallowness and the specific differences mentioned above, QM F17065, the premaxillae of QM F1752 and the Mirani Shire skull are similar to QM F1151, a premaxilla designated as *P. pollens* by Molnar (1982). Another difference between the premaxillae of *P. gracilis* and *P. pollens* is the shape of the external nares. Molnar stated that QM F1151 has a round external narial opening that does not taper posteriorly. The external narial opening of QM F17065 does taper posteriorly and thus apparently differs from *P. pollens*. However, inspection of the specimen Molnar described reveals that the external nares do taper posteriorly in the same manner as they do in QM F17065 but not to the extent seen in *C. porosus*. This difference in interpretation is a result of misinterpreting the correct orientation of the specimens. Slight rotation in the horizontal plane produces the apparent taper. Such rotation is justified if the vertical suture posterior to the nares is interpreted as contacting the tapering end of the nasals. Another problem in orientating QM F1151 is that it is incomplete both anteriorly and posteriorly. Regardless of the differing interpretations of the correct orientation of the premaxilla, it is apparent that the form of the external nares is similar in both specimens. Further, the shape of the external nares varies considerably within *P. pollens*, as discussed below.

Pallimnarchus pollens

Molnar (1982) discussed the occurrence of *P. pollens* within Queensland. The following introduces material referable to this species from South Australia and new material from Queensland.

Revised diagnosis

Pallimnarchus pollens is a species of *Pallimnarchus* that has: robust proportions; subcircular first dentary alveolus; width of that alveolus less than half the depth of the symphysis; symphysis extending to the fifth or sixth dentary alveolus; the posterior margin of the symphysis without a distinctly stepped profile; bunching of the fifth to the seventh alveoli; no concavity on the medial portion of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; splenial contact well marked and incised into the dentary; a bulbous premaxilla with the anterior dorsal surface inclined at a high angle to the palate; small supratemporal fenestrae; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf.

Material

As given in Molnar (1982) plus the material given below.

South Australia

A number of specimens recovered from Pleistocene sediments in South Australia can be referred to *Pallimnarchus* cf. *P. pollens*.

1). Dentaries. Two dentary fragments in the collections of the South Australian Museum are identified as *Pallimnarchus* cf. *P. pollens*. SAM P17352 is the anterior portion of the left dentary of a large individual. This specimen is from Coopers Creek in South Australia and is thought to be Pleistocene. It is generally robust and of massive proportions. SAM P17353 is a dentary fragment of a smaller individual than that represented by SAM P17352. It is from the Warburton River in South Australia. Only four

alveoli are present, the sixth through to the ninth. The bases of the seventh and ninth teeth are preserved within their alveoli. These alveoli are subequal in size.

The first eight alveoli are preserved in SAM P17352 but no teeth except for the bases of the first, fourth and seventh. The alveoli indicate that this crocodile was strongly pseudoheterodont with the first and fourth teeth greatly enlarged and subequal in size. There is a slightly developed alveolar process corresponding in development to tooth size. The mandibular symphysis reached anteriorly to the level of the fifth alveolus. The extent of the splenial contact cannot be determined.

2). Other material. The palaeontological collection of Flinders University, Adelaide, SA, includes an anterior snout and a posterior cranium with posterior mandibles both collected from the Tirari Formation, Warburton River. Both are crushed and distorted and their preservation obscures many details. However, both can be referred to *Pallimnarchus* cf. *P. pollens*. Both specimens are currently being studied by Dirk Megirian. Other specimens in the vertebrate palaeontological collections of Flinders University that may be referred to *Pallimnarchus* include: P 25086 and P25087, two large teeth from the Katipiri Formation of Coopers Creek; P 25212 a right dentary fragment, P 25213 and P 25214 are posterior maxillary fragments, P25215 a small skull fragment from the Tirari Formation at Waralamanko on Coopers Creek; P 25490 a posterior fragment of a left maxilla, P 25481 a fragment of skull deck including the right parietal and squamosal, and P 25482 an anterior fragment of skull deck including parts of the left postorbital, frontal and parietal, all from the Tirari Formation at Pompapillina on the Warburton River.

Swinton (ca 1924) identified crocodylian remains recovered by Gregory from Central Australia as *Crocodylus* or *Crocodylus porosus* (sic). This material can also be referred to *Pallimnarchus* cf. *P. pollens*.

A specimen of a crocodylian snout and anterior mandible in the collections of the Australian National University (ANU Geol 49071) also appears to be *P. pollens*. Its provenance is unknown but is believed to be from South Australia (Tim Munsum pers. comm.). Portions of the specimen are rebuilt in plaster and many details are obscured by crystal growth and poor preservation.

The Geoff Vincent specimen

Fragments of the skull of a large specimen of *P. pollens* were recovered by Mr Geoff Vincent and are currently housed in the Queensland Museum. These fragments relate to the same individual. They were collected from a site not far from Chinchilla. The following is a brief description. It is unclear whether this specimen derived from the early to medial Pliocene Chinchilla Sands or the Pleistocene sediments of the Darling Downs. *Pallimnarchus pollens* has been recorded from both of these sediments (Molnar 1982).

Fragments recovered include both premaxillae, the anterior portions of both maxillae, anterior fragment of nasals, posterior portions of nasals, posterior fragment of left maxilla, small fragment of the posterior of the right maxilla, anterior fragment of the left jugal, anterior process of the frontals, left lacrimal, left quadrate, half of the skull deck (includes left frontal, left postorbital, left parietal and left squamosal) and a basiocranial fragment (including the basioccipital, exoccipital, opisthotics and basisphenoid). There may be more of this specimen in the deposit that has not yet been recovered.

The supratemporal fenestrae are small and enclosed, elliptic and angled to the mid-line. The skull deck is basically flat or slightly concave with no raised margin around the supratemporal fenestrae. The margins of the orbits are slightly raised. The jugal fragment is larger and deep anteriorly. The jugal-postorbital bar contact does not have a distinct step.

The lateral sutured margin on the quadrates for the quadratojugal is very deep dorso-ventrally. The medial condyle of the mandibular articulation is half the width of the lateral. The squamosal contact of the quadrate forms a distinct plinth.

On the left maxilla the first and second alveoli are inside (medial to) the fourth dentary tooth reception pit.

Gregory River, Qld

Anderson (1937) described an anterior mandibular fragment of a large crocodylian from the Gregory River, north Queensland, as *Pallimnarchus pollens*. This specimen (AM F36947) is of uncertain provenance but the preservation suggests that it is not from the Terrace Site on the Gregory River at Riversleigh. Examination of the specimen confirms Anderson's original identification as *P. pollens*.

Pallimnarchus sp.

The following material can be identified as *Pallimnarchus* but not to species. This material comes from Queensland, Western Australia and New South Wales.

Bluff Downs, Qld

Queensland Museum specimens QM F 17067 and QM F11623 and a specimen collected by Brian Mackness (QM F23240), all from Bluff Downs, north Queensland, are different from both *Pallimnarchus pollens* and *P. gracilis*. However, insufficient material is available to quantify these differences and erect a new species. Until such material is available, the *Pallimnarchus* material from Bluff Downs is referred to *Pallimnarchus* sp.

A mature dentary from Bluff Downs (QM F11623) has a symphysis extending to the posterior margin of the fourth tooth. A more juvenile dentary from this locality (QM F17068) has a symphysis that extends to between the fourth and fifth teeth. Mackness's specimen (QM F23240) has the symphysis extending to the fifth alveolus. In *P. gracilis* the symphysis extends to the fourth or fifth alveolus and in *P. pollens* it extends to the fifth or sixth alveolus. In general proportions the Bluff Downs *Pallimnarchus* is similar to *P. pollens* and is not as lightly built as *P. gracilis*. However, the Bluff downs *Pallimnarchus* differs from *P. pollens* in details of the symphysis and alveolar grouping (see the next section for more details).

Description

The following description is based on the Mackness specimen (QM F23240). This specimen is a fragmentary right dentary. It lacks the extent anterior to the second alveolus and posterior to the tenth alveolus. It is a robust, heavily built dentary similar to that of *P. pollens*. However, it has a slightly stepped symphysis (not as strongly stepped as *P. gracilis*), a splenial contact that is distinct but not incised into the dentary and a shallow concavity on the ventral part of the medial surface immediately posterior to the symphysis. The symphysis is relatively deep, it extends posteriorly to the fifth alveolus and there is no bunching of the fifth, sixth and seventh alveoli. In the expression of these characters, the Mackness specimen (QM F23240) could be seen as being a structural intermediate between *P. gracilis* and *P. pollens*.

Windjana Gorge, WA

Gorter and Nicoll (1977) described crocodylian and turtle material from Windjana Gorge, north Western Australia. Among the crocodylian material was CPC 17122 (Commonwealth Palaeontological Collections, BMR, Canberra), an incomplete left premaxilla (Fig. 1E). Gorter and Nicoll (1977) also described some scutes (CPC 17113 and CPC 17114) and fragmentary crocodylian bones. However, when comparing the Windjana Gorge crocodylian to other crocodylians, they appear to have confused dentary tooth reception pits with alveoli in the comparative specimens of *Pallimnarchus*. Thus they describe *Pallimnarchus* as having six (not five) premaxillary alveoli and use this character to exclude the Windjana Gorge specimen from that genus. Significantly Gorter and Nicoll used the large difference in alveolar size as a character excluding the Windjana Gorge crocodylian from extant species of *Crocodylus*. Understandably con-

fused, Gorter and Nicoll finally relegated the premaxilla to “?*Crocodylus* sp. indet.”

Gorter and Nicoll (1977) identified CPC 17113 as a dorsal scute and CPC 17114 as a collection of ventral scutes. They considered that these scutes were distinct from those of members of the *Crocodylinae* and from Gavials but were more similar to *Alligatorinae* (except *Alligator*). They also considered that these scutes could be distinguished from those of all extant crocodylians.

Gorter and Nicoll (1977) provided the following diagnosis for the Windjana Gorge crocodylian: “Diagnosis: a brevirostrine form, with five premaxillary teeth, pseudo-heterodont, a premaxillary-maxillary notch, mandibular teeth occluding inside the upper series, dorsal and ventral scutes, scutes without crests or angulations but having an anterior bevelled edge and laterally sutured edges.”

Study of this material reveals that it can be referred to *Pallimnarchus* and it appears to be very similar to *P. pollens*. However, the premaxilla is very fragmentary and it is difficult to assign it to this species with confidence. Its overbite dentition and huge tooth disparity demonstrate mekosuchine affinities and the massive proportions identify it as *Pallimnarchus*. Until more crocodylian material is recovered from this site, this crocodylian can only be identified as *Pallimnarchus* sp.

Cuddie Springs, NSW

Numerous large crocodylian teeth from Cuddie Springs, New South Wales are held in the collections of the Australian Museum. These can all be referred to either *Pallimnarchus* sp. or (the ziphodont teeth) to *Quinkana* sp.

Myrtle Vale, NSW

Thompson (1980) reported on two Pleistocene river bank deposits in western New South Wales, one of which (Myrtle Vale) contained a crocodylian tooth. Thompson (1980) describes the conical tooth as being 15mm across the base. Based on the size as described this tooth could represent a large *C. porosus* but would more likely represent *Pallimnarchus* sp. The present location of the fossils Thompson collected is unknown and the Myrtle Vale site has been submerged under the waters of a weir. Thus there appears to be little chance of correctly determining the identity of this crocodylian or of collecting more material.

PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

At Cuddie Springs isolated teeth of *Pallimnarchus* and *Quinkana* have been recovered suggesting sympatry between these two species. The ecomorphic forms of these two taxa suggest a clear niche separation; *Quinkana* was a ziphodont, terrestrial carnivore whereas *Pallimnarchus* was a broad-snouted, semi-aquatic or aquatic ambush predator.

The occurrence of *P. gracilis* at the Terrace Site, Riversleigh coincides with the occurrence of *Crocodylus johnstoni* (Willis and Archer 1990), both being found very close to each other in the same deposit. The deposits on the Leichhardt River at Floraville Downs have also produced both *C. johnstoni* (Willis and Archer 1990) and *P. gracilis*. At Macalister on the Darling Downs (Molnar 1982) *P. pollens* and *C. porosus* coincide and at Bluff Downs *Pallimnarchus* sp. and *C. porosus* (Molnar 1979) also occur together. This suggests sympatry between a species of *Pallimnarchus* and *Crocodylus* at each of these sites.

At Terrace Site and on the Leichhardt River the coexistence of *P. gracilis* and *C. johnstoni* can be explained by the differing ecomorphs. *Pallimnarchus gracilis* is a broad snouted crocodylian, an ecomorph usually associated with a generalised diet, whereas *C.*

johnstoni is a longirostrine crocodylian with a piscivorous diet.

The occurrence of *P. pollens* and *C. porosus* at Macalister and the occurrence of *Pallimnarchus* sp. and *C. porosus* at Bluff Downs are more problematic. Both crocodylians have the broad snout of generalist crocodylians, although the snout of *Pallimnarchus* is considerably more broad than that of *C. porosus*. It is not clear how a particularly broad snout can separate the niche occupation of *Pallimnarchus* species from *C. porosus* but the occurrence of these species in the same deposits suggests sympatry and some form of niche separation must have occurred. Meyer (1984) concluded that niche separation in sympatric crocodylians is reflected in snout form. The heavily-built, broad snout of *Pallimnarchus* species would be particularly useful to a semi-aquatic or aquatic ambush predator that includes particularly large and heavy prey species in its diet. Macalister has produced fossils of *Diprotodon optatum*, the largest known marsupial with masses up to an estimated 1500 kg. The Bluff Downs fauna includes mammals that range in size up to 1,000 kg (*Euryzygoma*). However, modern individuals of *C. porosus* have been known to take prey items such as water buffalo, horses and cattle up to 700kg in mass. Thus it appears likely that *C. porosus* was capable of taking larger prey items known from these fossil faunas.

Previously, *Pallimnarchus* was known as a single species restricted to numerous Plio-Pleistocene sites throughout Queensland. Two species are now recognised and a third is suggested. The recognition of the new material described here extends the range of the genus into Western Australia (Windjana Gorge), South Australia (Coopers Creek and Warburton River) and New South Wales (Cuddie Springs and possibly Myrtle Vale). The temporal range for the genus is pushed back to the early Pliocene deposits of Bluff Downs and established from sites as young as a 20–30 thousand years at Cuddie Springs and Terrace Site (Dodson et al. 1993, Davis in press).

Both Coopers Creek and the Warburton River drain into Lake Eyre. It is likely that the Pleistocene waterways inhabited by these crocodiles also drained into a large inland lake. *Pallimnarchus pollens* has previously been recognised from the inland drainage basins of eastern Australia from localities such as the Darling Downs, Lansdowne and Chinchilla (Molnar 1982). However, the South Australian specimens push the geographic range of this species much further west. The identification of the Windjana Gorge specimens as *Pallimnarchus*, possibly *P. pollens*, suggests an even greater geographic range for this species but certainly for the genus.

There does seem to be a clear geographic separation between *P. pollens* and *P. gracilis* (Fig. 8). *Pallimnarchus pollens* is known from the northern portions of the Darling River drainage and the Diamantina-Coopers Creek drainage whereas *P. gracilis* appears to be confined to drainage systems associated with the Gulf of Carpentaria. However, this is not entirely the case. The Mirani Shire skull of *P. gracilis* and Anderson's specimen of *P. pollens* attributed to the Gregory River may be exceptions to this geographic division.

The temporal distributions of the species of *Pallimnarchus* (Fig. 8) is generally uninformative. Both *P. pollens* and *P. gracilis* have been recovered from sediments dated from early Pliocene through to late Pleistocene. The Bluff Downs species appears to be restricted to the early Pliocene and undesignated material referred to *Pallimnarchus* occurs in mid to late Pleistocene deposits. Clarifying the apparent geographic relationships and temporal patterns of the species of *Pallimnarchus* will require better information on the exact location of these specimens and more refined dating of all *Pallimnarchus* material. Neither of these requirements are likely to be immediately fulfilled.

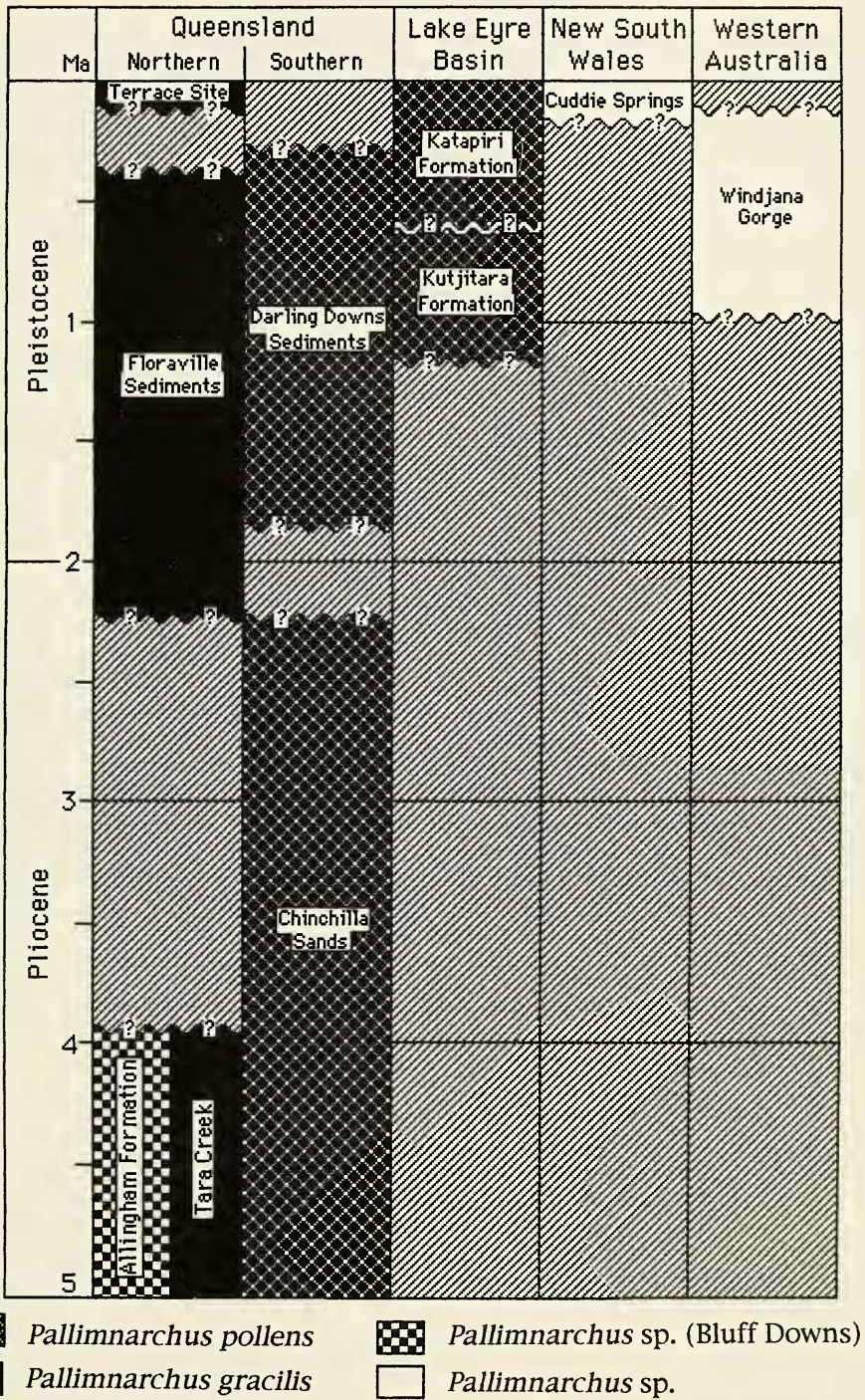


Figure 8. Biocorrelation of sites containing *Pallinnarchus* species.

FUNCTIONAL MORPHOLOGY

Pallimnarchus exhibits certain unusual features that suggest an unusual lifestyle, at least for Australasian crocodylians. The Mirani Shire skull, which includes the snout, jugal arches and dorsal braincase (with skull deck) in articulation, differs from other crocodylian skulls in that the jugals are orientated in the horizontal, rather than the parasagittal, plane. This is also the case on the (uncrushed) right side of the Lansdowne snout. Thus the orbits are directed dorsally rather than dorsolaterally. Together with the very broad, low snout these features give different — broader and flatter — aspects to the skull of *Pallimnarchus* than those of most other crocodylians. Such an appearance is matched by the skulls of the extant *Crocodylus palustris* of India and *Caiman neivensis* from the late Miocene of Colombia (Langston 1965) with *C. neivensis* having the most similar skull. *Caiman neivensis* was the largest species of *Caiman* and Langston (1965) estimated its length as 7–9 metres with a skull comparable in size to that of *Pallimnarchus*. Unfortunately *C. neivensis*, like *Pallimnarchus*, is extinct so its lifestyle cannot be directly observed. *Crocodylus palustris* is, of course, a different matter. It inhabits lakes, rivers, marshes and swamps including, rarely, coastal marshes (Neill 1971) and feeds on fish, water birds, turtles and mammals as large as pigs, goats and deer (Guggisburg 1972). If the similarity in cranial proportions implies a similarity in feeding habits, we might expect *Pallimnarchus* to have fed on fish, turtles, birds and moderately large marsupials. The habitat of *Pallimnarchus* seems to have corresponded to that of *C. palustris*, as *Pallimnarchus* are unknown from coastal regions similar to those inhabited today by *C. porosus*.

The small supratemporal fenestra in both species of *Pallimnarchus* relative to most other crocodylians suggests that the internal and external adductors were less extensively developed than the pterygoid musculature. This in turn suggests that the jaws were capable of being powerfully closed from a fairly wide gape. We suggest that *Pallimnarchus*, like many crocodylians, was an aquatic or semi-aquatic ambush predator. The flat skull and dorsally directed orbits suggest that it lay in wait on the bottom of shallow water bodies, and the robust mandible (in *P. pollens*) and large teeth suggest that it was capable of feeding on relatively large prey. The function of the (presumably) flattened first dentary tooth of *P. gracilis* remains unknown, but the more gracile mandibles and relatively larger supratemporal fenestrae than found in *P. pollens* suggests that this species was less specialised in this direction (although more so than either of the native species of *Crocodylus*).

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