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PLEISTOCENE ZIPHODONT CROCODILIANS OF QUEENSLAND

R. E. MOLNAR

Queensland Museum
Fortitude Valley, Qld. 4006

SUMMARY

The rostral portion of a crocodylian skull, from the Pleistocene cave deposits of Tea Tree Cave, near Chillagoe, north Queensland, is described as the type of the new genus and species, *Quinkana fortirostrum*. The form of the alveoli suggests that a ziphodont dentition was present. A second specimen, referred to *Quinkana* sp. from the Pleistocene cave deposits of Texas Caves, south Queensland, confirms the presence of ziphodont teeth. Isolated ziphodont teeth have also been found in eastern Queensland from central Cape York Peninsula in the north to Toowoomba in the south. *Quinkana fortirostrum* is a eusuchian, probably related to *Pristichampsus*. The environments of deposition of the beds yielding ziphodont crocodylians do not provide any evidence for (or against) a fully terrestrial habitat for these creatures. The somewhat problematic Chinese *Hsisosuchus chungkingensis* shows three apomorphic sebecosuchian character states, and is thus considered a sebecosuchian.

INTRODUCTION

The term ziphodont crocodylian refers to those crocodylians possessing a particular adaptation in which a relatively deep, steep sided snout is combined with laterally flattened, serrate teeth (Langston, 1975). Although such crocodiles were described in the nineteenth century (Cuvier, 1824; Marsh, 1871) little attention was paid them until Colbert (1946) redescribed *Sebecus icaeorhinus* from Argentina. The nearly contemporaneous description of *Baurusuchus pachecoi* (Price, 1945) in which the ziphodont condition reaches its most extreme expression, also attracted interest toward these forms. Langston (1956) demonstrated that there were two phylogenetically distant forms of ziphodont crocodile, the mesosuchian sebecoids and the eusuchian pristichampsines. Although Colbert (1946) had proposed that sebecosuchians deserved subordinal status, this was not widely accepted until the study of Gasparini (1972).

Sebecosuchians appear first in the Chinese Jurassic (Young and Chow, 1953; Langston, 1956), and are most numerous in South America, ranging from the Upper Cretaceous to the Miocene (Molnar, 1978), although two reportedly sebecosuchian genera derive from the Eocene of Europe (Berg, 1966; Antunes, 1975). Pristichampsines first appear in the Paleocene of China (Li, 1976) and are widely distributed through Europe and North America in the Tertiary (Langston, 1975; Steel, 1973). They became extinct in the northern continents with the end of the Eocene (Molnar, 1978), but may have survived in Africa into the Miocene (Andrews, 1914).

Prior to 1970, only isolated ziphodont teeth had been reported from Australasia, from two localities of the Otibanda Formation in New Guinea (Plane, 1967). During exploration of Tea Tree Cave near Chillagoe, north Queensland, in 1970 Lyndsey Hawkins, of the Sydney Speleological Society, discovered the snout of a ziphodont crocodylian. In 1975 Michael Archer discovered a second ziphodont crocodylian in the deposits at The Joint, one of the Texas Caves in southern Queensland. Soon afterwards ziphodont teeth and fragments were recognised from several other Australian localities, all but one in Queensland. The single South Australian ziphodont crocodylian, from the Pliocene of Lake Palankarinna (Hecht and Archer, 1977) is not treated here.

The discovery of ziphodont crocodylians in Australia, is of interest zoogeographically (cf. Molnar, 1977) and stratigraphically. While ziphodont crocodylians elsewhere became extinct at the end of the Miocene, the Australian forms survived well into the Pleistocene (Molnar, 1978; Hecht and Archer, 1977).

COLLECTION DESIGNATIONS:

AM — Australian Museum, Sydney

FMNH — Field Museum of Natural History, Chicago

ME — Museum für Erdgeschichte-Geiseltalsammlung, Halle

QM — Queensland Museum, Brisbane

UCMP — Museum of Paleontology, University of California, Berkeley

YPM — Peabody Museum of Natural History, Yale University, New Haven

Order CROCODYLIA

Suborder EUSUCHIA Huxley, 1875

Family CROCODYLIDAE Cuvier, 1807

Genus **Quinkana**, nov.

Species **Quinkana fortirostrum**, nov.

ETYMOLOGY: The generic name is from *Quinkan*, a term, probably from the Gugu-Yalanji tribe, denoting a spirit (Trezise, 1971). Quinkans are associated with crocodiles in at least one of the rock art sites in southeastern Cape York. This name is given neuter gender. The specific name is from Latin, *fortis*, strong, and *rostrum*, beak, here used in the sense of snout.

TYPE SPECIMEN: Australian Museum F.57844: a cranial rostrum lacking anterior end and teeth.

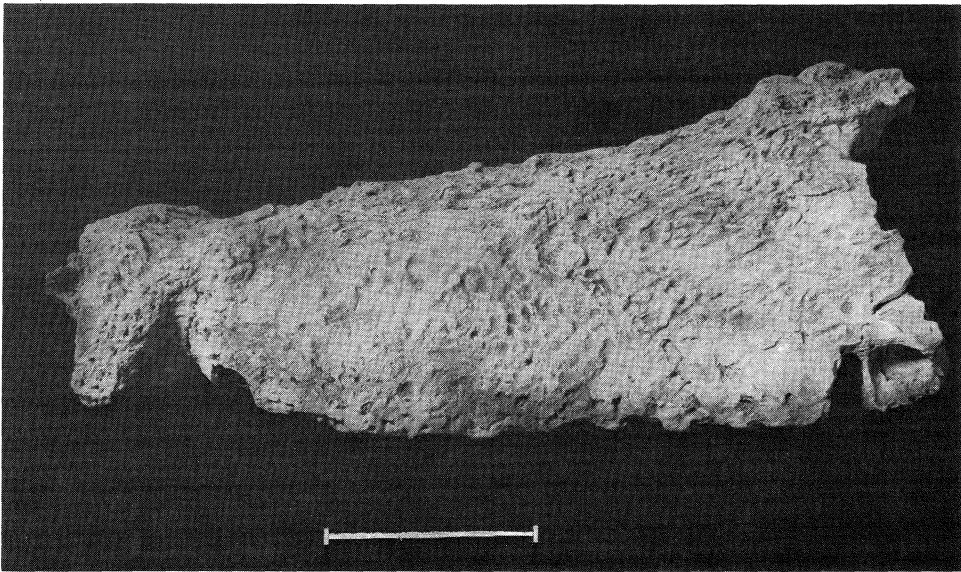
LOCALITY: Tea Tree Cave, near Chillagoe, north Queensland.

AGE: Pleistocene (Molnar, 1978).

DESCRIPTION OF TYPE SPECIMEN: The illustrations (Fig. 1, 2, 3, 4) show the features of the type specimen of *Quinkana fortirostrum*. A brief description has already appeared (Molnar, 1977), hence this description will emphasize those features important for taxonomic analysis or not previously noted.

Premaxilla: Both premaxillae are present, with the right almost complete. A raised rim surrounds the confluent external nares. Extending posteriorly from the dorsal body of the premaxilla, a short posterior process separates the anterior portion of the nasal from the anterior portion of the maxilla. On the palate, the maxillary-premaxillary junction is U-shaped with the convexity directed posteriorly. That portion preserved of the incisive foramen suggests that this foramen was broader transversely than long. From the incisive foramen a shallow trough extends posteriorly across the premaxillae and into the maxillae.

Four alveoli are present in the right premaxilla, in an alveolar process. The posterior two are elongate in form, while the third from the back is more nearly circular. A deep pit,



1. *Quinkana fortirostrum*, AM F.57844. Snout in lateral aspect. Scale 5 cm. Note that portions of three alveoli can be seen at the lower right.

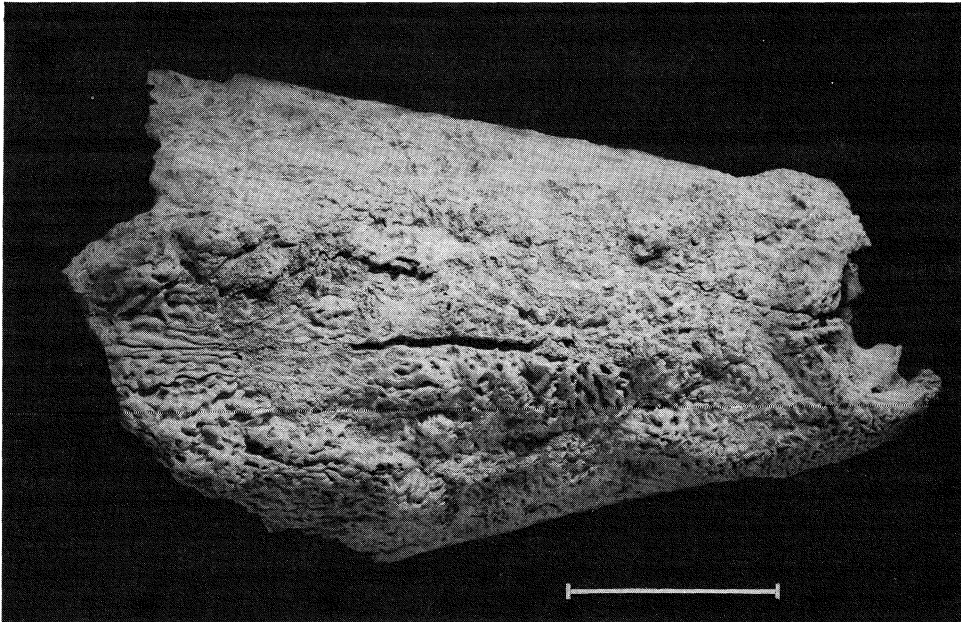


Fig. 2. *Quinkana fortirostrum*, AM F.57844. Snout in dorsal aspect. Scale 5 cm.

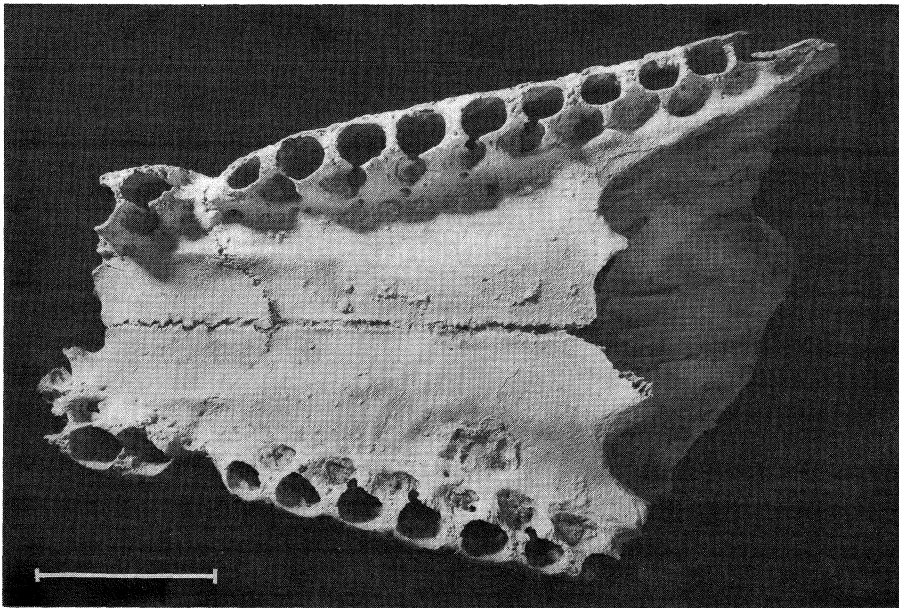


Fig. 3. *Quinkana fortirostrum*, AM F.57844. Snout in ventral aspect. Scale 5 cm.

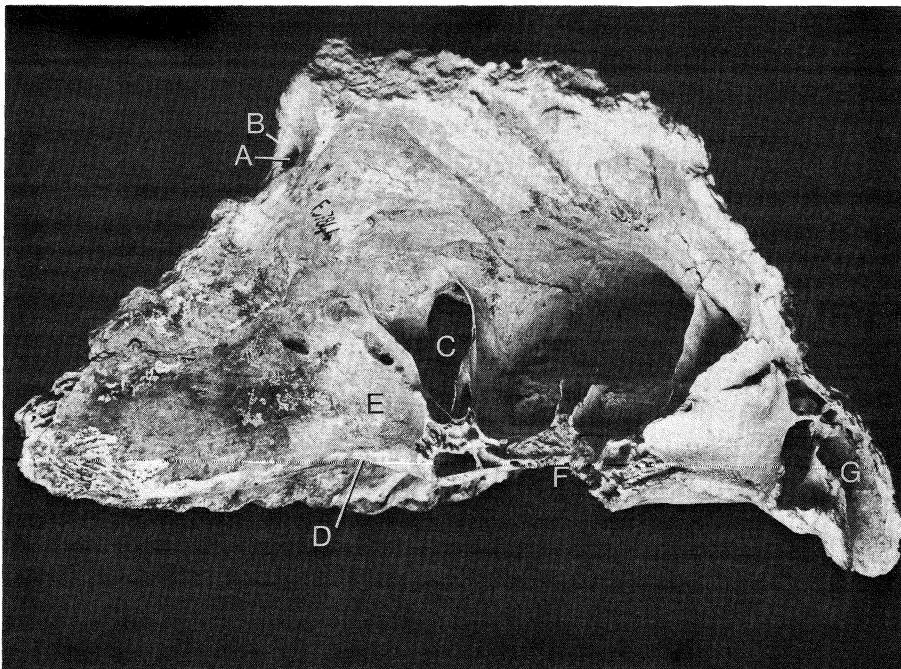


Fig. 4. *Quinkana fortirostrum*, AM F.57844. Right oblique posterior view, into nasal cavity. A. nasolachrymal canal, B. orbital margin, C. lateral chamber, D. anterior margin of palatal fenestra, E. anterior rim of palatal fenestra, F. palate, G. alveolus in section.

lacking the posterior wall of an alveolus, lies between the remnant of the anteriormost alveolus preserved and the incisive foramen (Fig. 3). Fossae for the reception of dentary teeth lie just medial to the alveolar process.

Nasal: Both nasals are complete, but have separated slightly along the midline. Their sides are parallel, tapering markedly anteriorly and slightly posteriorly. The nasals separate the two premaxillae anteriorly and project as a posterior nasal spine into the external nares. The corresponding portion of the premaxilla is not preserved, hence it cannot be determined if an internarial bridge was present.

The nasals are but slightly arched in the coronal plane, and lie wholly on the dorsum of the snout, unlike those of sebecosuchians which form a median crest (Colbert, 1946). They are heavily sculptured.

Maxilla: The left maxilla is nearly complete, while the right lacks the posterolateral portion. The lateral wall of the maxilla inclines upward at an angle of from 45 degrees (posteriorly) to 60 degrees (anteriorly) to the horizontal, and is lightly sculptured. A distinct, blunt ridge crowns the anterior portion of the maxilla above the first alveolus.

The suborbital portion of the maxilla shows that the jugal did not extend in front of the anterior margin of the orbit. This condition is uncommon among crocodiles. The suborbital portion of the maxilla is of such depth as to suggest that the infraorbital bar was markedly deeper than usual among crocodilians. Although little of the palatines is preserved much of the maxillary contact for these elements is present. This indicates that the anterior process of the palatine, usually found in crocodilians, was absent from *Q. fortirostrum*. The ventral margin of the maxilla is weakly convex, without any sign of the festooning typical of most crocodilians.

A high, posteriorly concave partition dorsally bounds the anterior margin of the palatal fenestra. A similar, but less well developed partition is found in *Crocodylus johnstoni*, *C. novae-guineae* and *C. porosus*, where, however, it is placed well anterior to the margin of the fenestra, and is restricted to the lateral portion of the snout cavity. In *Q. fortirostrum* the maxilla is excavated anterior to this partition, forming lateral chambers that open posteriorly. Above the junction of the palatal processes of the two maxillae rise two thin, nearly vertical flanges, which together form a narrow trough along the floor of the snout cavity (Fig. 4).

Nine complete and three incomplete alveoli are found in the alveolar process of the left maxilla (the three incomplete alveoli can be seen in Fig. 1). The alveoli are elongate and subequal in size (Fig. 5). The elongate shape of the alveoli suggests that the teeth were laterally compressed (Molnar, 1977). The long axes of the alveoli parallel one another but are inclined both to the long axis of the snout and to the margin of the snout, giving the alveolar row a distinctive appearance (Fig. 3). Medially the alveolar process bears fossae for the reception of the dentary teeth. These indicate that the dentary teeth closed medial to the upper teeth, unlike the situation in the Crocodylinae where the teeth interlock.

Frontal: Only the anterior extremities of the frontals remain. They are heavily sculptured, and extend two cm further anterior on the ventral than on the dorsal surface.

Prefrontal: The anteriormost portions of both prefrontals are present. They are narrow, heavily sculptured, and bear a distinct knob above the anterior extremity of the orbit.

Lachrymal: Almost the entire left, and a portion of the right lachrymal are preserved. The lachrymal, lying on the lateral wall of the snout, makes an angle of about 45 degrees

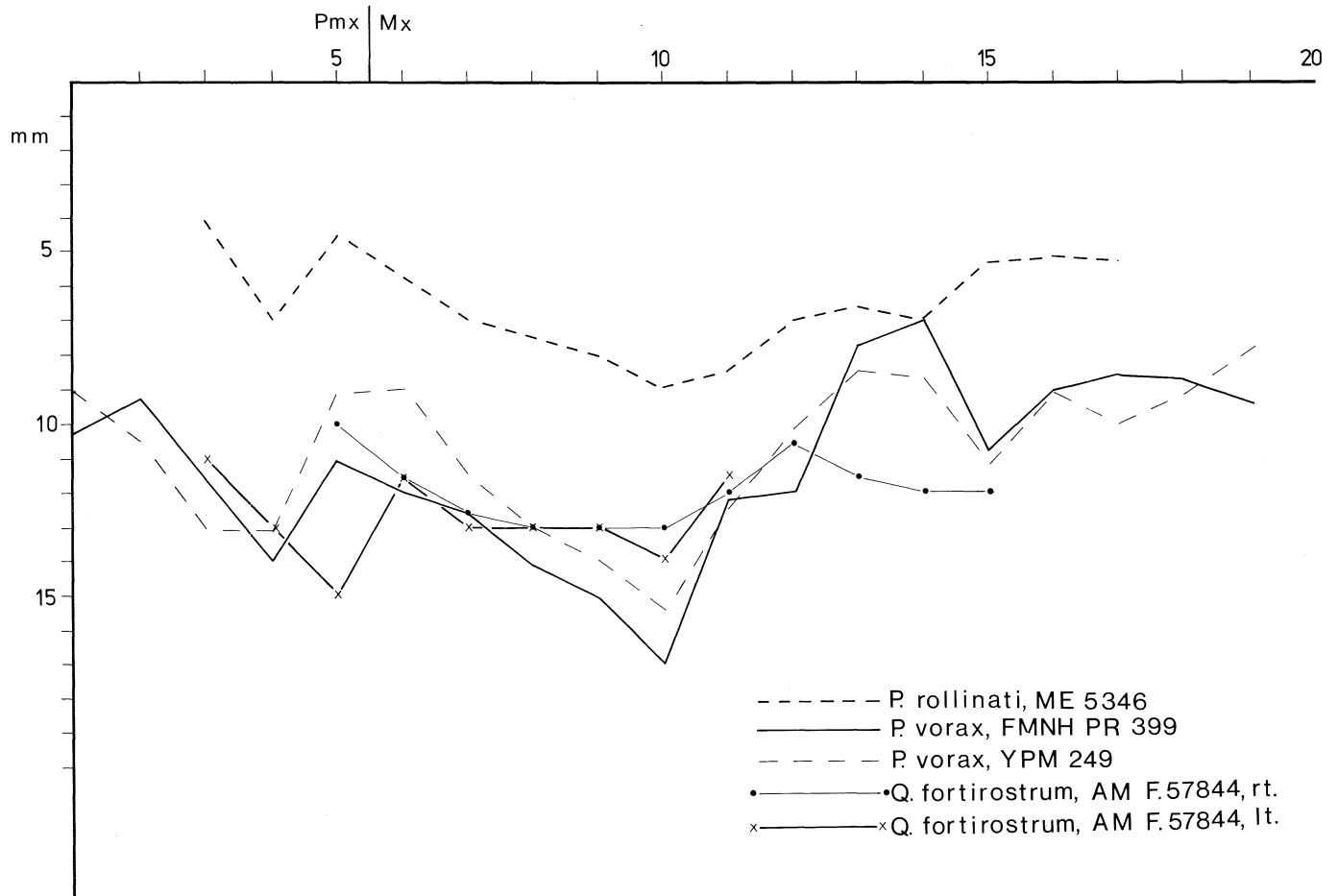


Fig. 5. Alveolar size (anteroposterior diameters) of *Quinkana fortirostrum* (AM F. 57844) compared with *Pristichampus rollinatus* (ME 5346) and *P. vorax* (FMNH PR 399 and YPM 249). (A, B, and C after Langston, 1975.)

with the prefrontal, which lies on the roof of the snout. The orbital margin of the lachrymal shows that the orbit faced laterally. Opening into the anterior margin of the orbit is the nasolachrymal canal, which is continued posteriorly along the dorsal margin of the orbit as a broad sulcus. The canal opens anteriorly on the medial surface of the lachrymal about one-third of its length back from the anterior margin.

The lachrymal exhibits two knobs along its dorsal edge, the first just anterolateral to the prefrontal knob, and the second 1.5 cm directly in front of the prefrontal knob. Although lachrymal ridges are present in some crocodylians, none known to me show knobs like those of *Quinkana*.

Palatine: Two small pieces of palatine are present on the dorsal surface of the palatal process of the maxilla.

Snout form: The snout proportions of *Q. fortirostrum*, together with those of selected comparable taxa (cf. Molnar, 1977) are given in Table 1. The snout of *Quinkana* is broader than that of *Pristichampsus*, and the sebecosuchians, and deeper than in the Crocodylinae and Alligatorinae: in the terminology proposed in the character analysis of this paper, *Quinkana* can be described as having a broad, moderately deep snout. No other crocodylians show this combination of character states.

TABLE 1. Snout proportions of *Quinkana* and comparable crocodylians.

Taxon	H/L	H/W	W/L
<i>Sebecus icaeorhinus</i>	0.39	1.37	0.28
<i>Pristichampsus vorax</i>	0.24	0.51	0.48
<i>Quinkana fortirostrum</i>	0.36	0.51	0.70
<i>Osteolaemus tetraspis tetraspis</i>	0.35	0.35	1.00
<i>Osteolaemus tetraspis osborni</i>	0.31	0.41	0.74
<i>Paleosuchus palpebrosus</i>	0.29	0.48	0.60

L is the distance from the anterior extremity of the orbit to the posterior extremity of the external nares, H is the maximum depth of the snout at the fifth maxillary alveolus, and W is the maximum breadth of the snout at the fifth maxillary alveolus. Values for the taxa other than *Quinkana* are taken from published illustrations, *Sebecus* from Colbert (1946), *Pristichampsus* from Langston (1975), and the modern taxa from Wermuth and Mertens (1961).

DEFINITION: Snout broad and moderately deep; alveoli elongate and arranged in a distinctive pattern; maxillary alveoli subequal in size; distinct alveolar process; palatal portion of maxillary-premaxillary suture U-shaped with convexity directed posteriorly; anterior process of palatine very short or absent in ventral aspect; rim superiorly adjacent to anterior margin of palatal fenestra; no portion of jugal extending anterior to the orbit; three knobs present on lachrymal and prefrontal dorsal to the anterior margin of the orbit. Because *Quinkana* is a monotypic genus, no distinction can be made between the generic and the specific diagnosis. The referred specimen (QM F.7898) suggests that ziphodont teeth were present.

THE TEXAS CAVES CROCODYLE (QM F.7898): A second Pleistocene ziphodont crocodile, found at The Joint, a cave near Texas, southeast Queensland, was described by Hecht and Archer (1977). The specimen was found in a typical late Pleistocene vertebrate assemblage (Archer, 1978), in intimate association with mammalian remains: the right

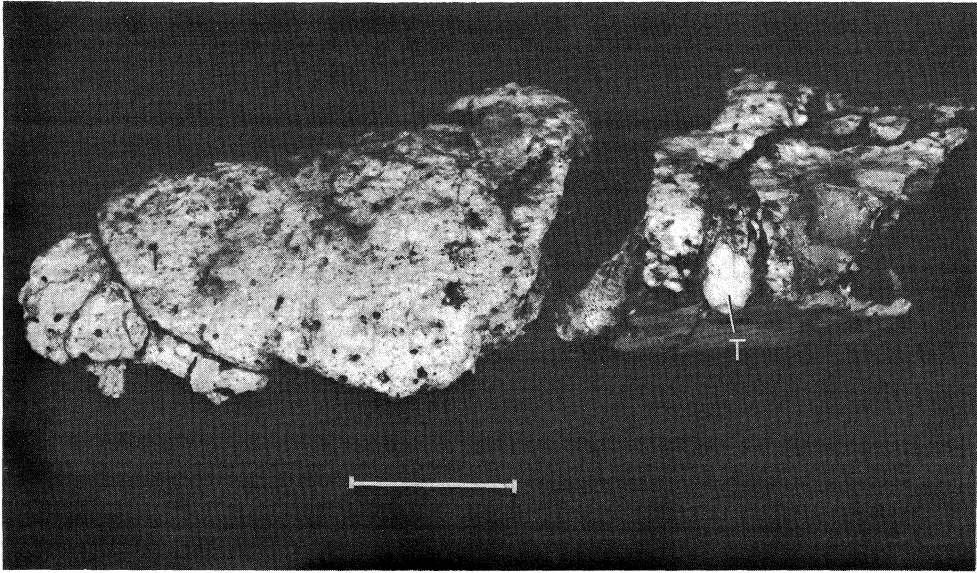


Fig. 6. *Quinkana* sp., QM F7898. Snout in lateral aspect. Scale 1 cm. **T**, ziphodont tooth *in situ*.

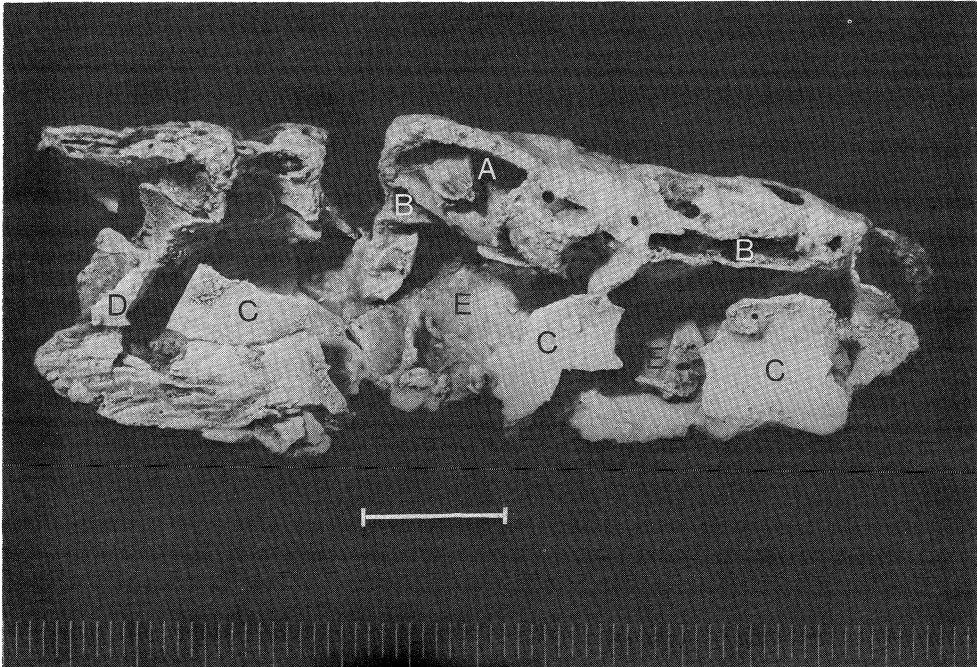


Fig. 7. *Quinkana* sp., QM F7898. Snout in medial aspect. Scale 1 cm. **A**, niche dorsal to alveolar part of maxillary wall, **B**, narrow chamber between niche and alveolar part of wall, **C**, remnants of partition dividing nasal cavity from lateral chamber, **D**, anterior rim of palatal fenestra, **E**, alveolar process.

upper molar of a small macropodine was found within the snout.

The specimen consists of the greater portion of a left maxilla, and two smaller fragments, one a flake of bone with the crown of a tooth adherent.

The palatal portion of the left maxilla is nearly complete, the lateral is less complete, with some portions of the internal partitions present (Fig. 6). The lateral wall makes an angle with the palate of 60 degrees, and appears relatively thinner and more lightly sculptured than that of AM F.57844. Six elongate alveoli are present in the same distinctive pattern as in AM F.57844.

The delicate internal partitions preserved indicate that the lateral maxillary wall was separated from the nasal cavity by an elongate chamber (4 in Fig. 9) extending almost the length of the maxilla. The alveoli extend almost to the dorsal margin of the maxilla anteriorly (for the first two present), but are surmounted by a niche (1 in Fig. 9) posteriorly. A second, narrow chamber (2 in Fig. 9) extends the length of the maxilla lying dorsomedial to the alveolar portion anteriorly and superiorly adjacent to that portion (and hence flooring the niche) posteriorly. The niche opens medially into the elongate lateral chamber, which, in turn, opens posteriorly into the nasal cavity as in AM F.57844. At least one small opening perforates the ventral edge of the partition separating the lateral chamber from the nasal cavity. This thin partition inclines dorsolaterally at 30 degrees to the plane of the palate.

Similar lateral chambers are present in the skulls of *Alligator mississippiensis*, *Crocodylus johnstoni*, *C. novae-guineae* and *C. porosus*, although the chamber is much reduced in *C. johnstoni* relative to the others. The niche surmounting the alveolar portion of the maxillary wall is absent in these forms, and thus is presumably related to the snout depth of *Quinkana*. Apparently the maxillary wall is deeper than need be to accommodate the roots of the teeth, and a similar, but more marked condition is present in *Sebecus icaeorhinus*.

The anterior margin of the palatal fenestra is present, and is bounded dorsally by a curved rim, as in AM F.57844. The contact surfaces for the palatines indicate that these elements dorsally overlapped the palatal portions of the maxillae, again as in AM F.57844.

A ziphodont crown is preserved in the fifth alveolus from the front: it is serrate posteriorly, but no serrations could be seen on the poorly preserved anterior margin. The isolated crown likewise is serrate posteriorly but obscured anteriorly. The delicate state of the specimen precludes any further preparation of either tooth for the present.

The form and orientation of the alveoli, and the presence and form of the partition anteriorly rimming the palatal fenestra indicate reference to *Quinkana*. But the specimen is too incomplete for assessment of its specific allocation, and will be referred to *Quinkana* sp. Its smaller size and relatively thinner bone suggest a juvenile individual. The presence of a ziphodont tooth *in situ* in the left maxilla supports the inference that the type specimen of *Q. fortirostrum* also possessed a ziphodont dentition.

THE CROYDON SPECIMENS: At "Alehvale" Station, near Croydon, north Queensland, Archer collected three isolated ziphodont crowns (QM F.9220, QM F.9225 and QM F.9226) in 1976, and two fragments of maxilla, each with a single ziphodont tooth *in situ*, in 1977 (QM F.10141). All specimens were collected from the top of the wall of a dam constructed on "Alehvale". During excavation for the construction of the dam, fossil crocodylian material was reportedly encountered 6 to 12 metres below ground level.

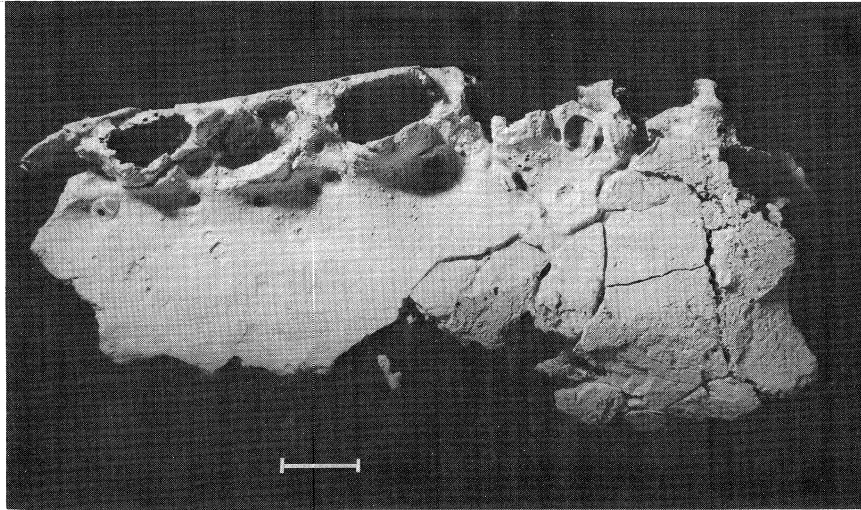
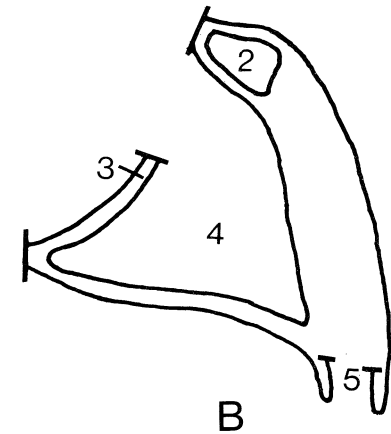
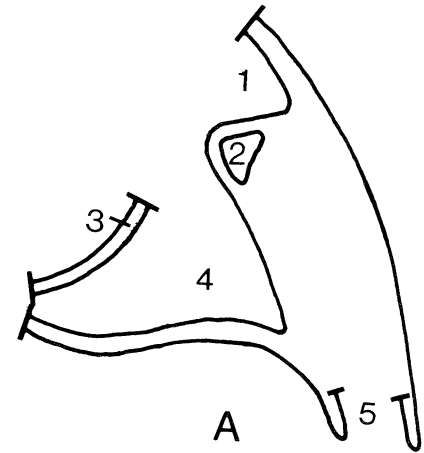


Fig. 8. *Quinkana* sp., QM F7898. Snout in ventral aspect. Scale 1 cm.

Fig. 9. Diagrammatic cross-sections of the snout of *Quinkana* sp., QM F7898. **A.** section at level of the first preserved maxillary alveolus, **B.** section at fourth preserved maxillary alveolus. Labels: **1.** niche dorsal to alveolar part of wall, **2.** narrow chamber between niche and alveolar part of wall, **3.** partition dividing nasal cavity from lateral chamber, **4.** lateral chamber, **5.** alveolus. Scale 1 cm.



Most of this material appeared referable to *Crocodylus* or some closely related genus (Archer, pers. comm., 1978). The occurrence near the top of the dam suggests that the ziphodont crocodilian material was encountered near the bottom of the excavation.

Both maxillary fragments represent the extreme posterior ends of that element, the more complete from the left side and the other from the right. Comparison with the corresponding portions of the maxillae of AM F.57844 has revealed differences of proportion, but from so few and incomplete specimens the significance, if any, of this variation cannot be determined.

The crown present in the right fragment is more compressed than most of the isolated crowns from this locality (Table 2), and is medially flexed. Without a complete tooth row the import of this change in crown form cannot be assessed. This tooth also shows a shallow, vertical sulcus in the medial surface of the root (also found in teeth of a ziphodont crocodilian from the Paleocene of New Mexico, UCMP 100029). Such sulci have been thought to be characteristic of theropod teeth, and absent in those of crocodilians (cf. Langston, 1956). The tooth tip is well worn, and gives the appearance that the tip was broken off prior to the wear.

THE "ROSELLA PLAINS" AND OTHER NORTH QUEENSLAND TEETH: Two isolated teeth (AM F.25227 and AM F.25228), found while excavating a well at "Rosella Plains" Station, north Queensland, were figured and described by Anderson (1930) as *Megalania* teeth. Hecht (1975) recognised these as crocodilian. Another ziphodont crown (QM F.1515) was received with teeth assigned by Longman to *Crocodylus nathani*, from the head of Tara Creek, near "Maryvale", north Queensland. This material may be Pliocene in age (Archer, pers. comm. 1978). None of the *C. nathani* type material appears to be distinct from the corresponding elements of *C. porosus*, so it is unlikely that this tooth derives from *C. nathani*. Two more teeth (QM F.10507) have recently been found at "Glen Garland" Station, central Cape York Peninsula (Fig. 14). All teeth closely resemble those from Croydon.

TABLE 2. Ziphodont teeth from Croydon

Specimen	Maximum length of crown (L)	Maximum width of crown (W)	W/L	Serrations per 5 mm	
F9220	16.0	10.3	0.64	18 ant.	19 post.
F9225	11.6	7.2	0.62	27 ant.	worn
F9226	12.9	7.1	0.55	worn	worn
Right maxillary	8.0	4.3	0.54	25 ant.	27 post.

THE DARLING DOWNS TEETH: Ziphodont crowns have also been collected from Pliocene deposits of the western Darling Downs (Fig. 13), at Chinchilla (QM F10204, QM F10205), as well as from Pleistocene deposits of the eastern Darling Downs, at Westbrook or Gowrie Creek (Toowoomba) (AM F.2876). These teeth, like those from north Queensland, are not sabre-like in form as are those from Pliocene of South Australia reported by Hecht and Archer (1977).

THE CHINCHILLA JUGAL: An isolated crocodilian jugal (Figs 11 and 12) from the Pliocene deposits at Chinchilla (QM F1152) bears sculpture much like that of the maxillae of the type of *Q. fortirostrum*. This jugal is very deep, much more so than that of *Crocodylus*. As discussed previously, the jugal of *Quinkana* must also have been deep,

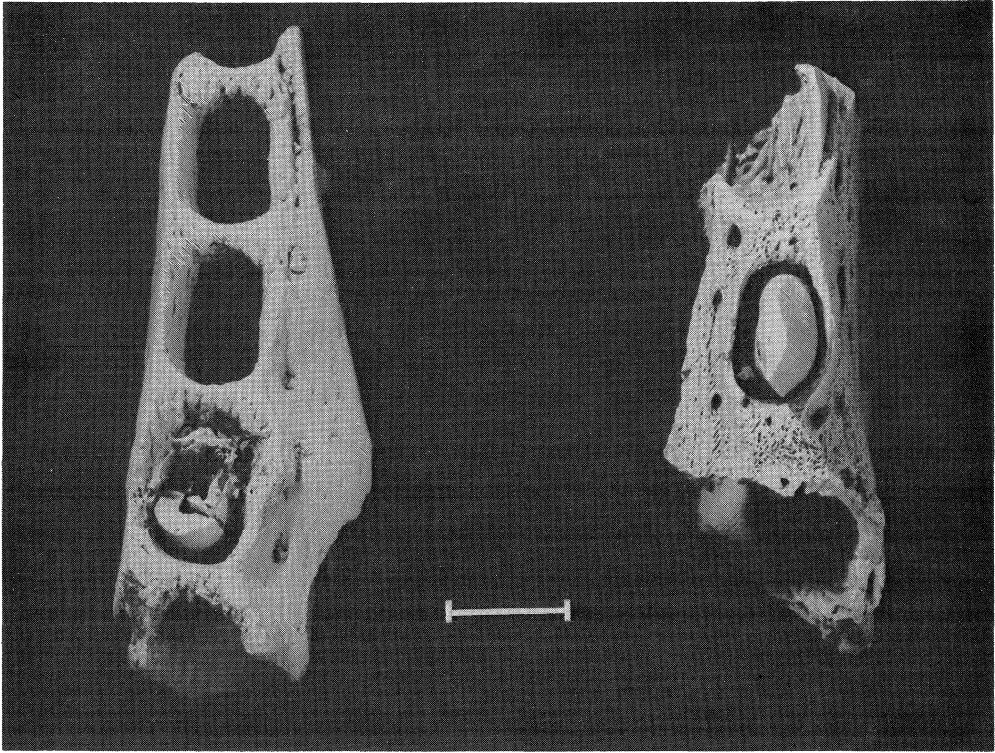


Fig. 10. Two fragments of the maxillae of a ziphodont crocodilian from near Croydon, north Queensland, QM F10141 in ventral view. Scale 1 cm.

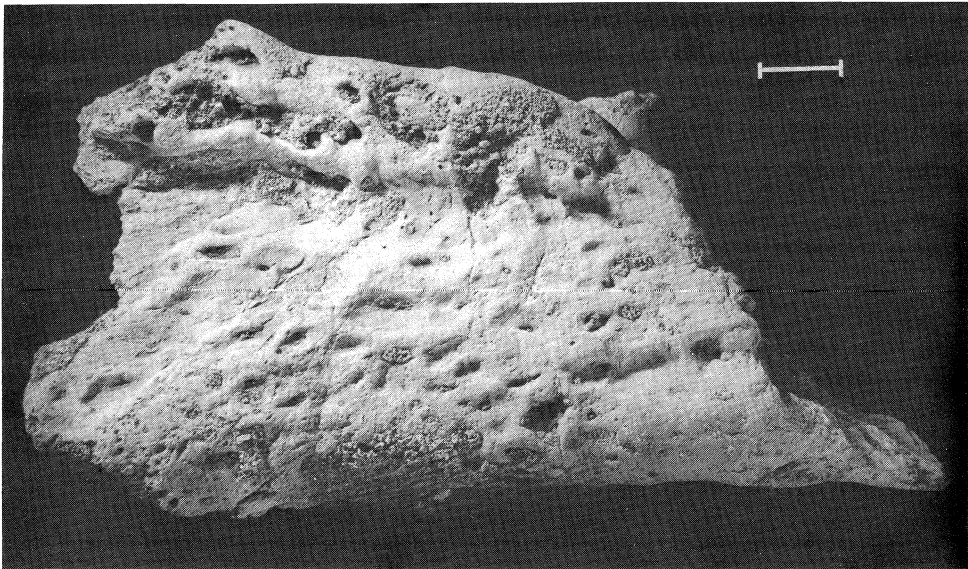


Fig. 11. Crocodilian jugal, QM F1152, from Chinchilla, in lateral view. Scale 1 cm.

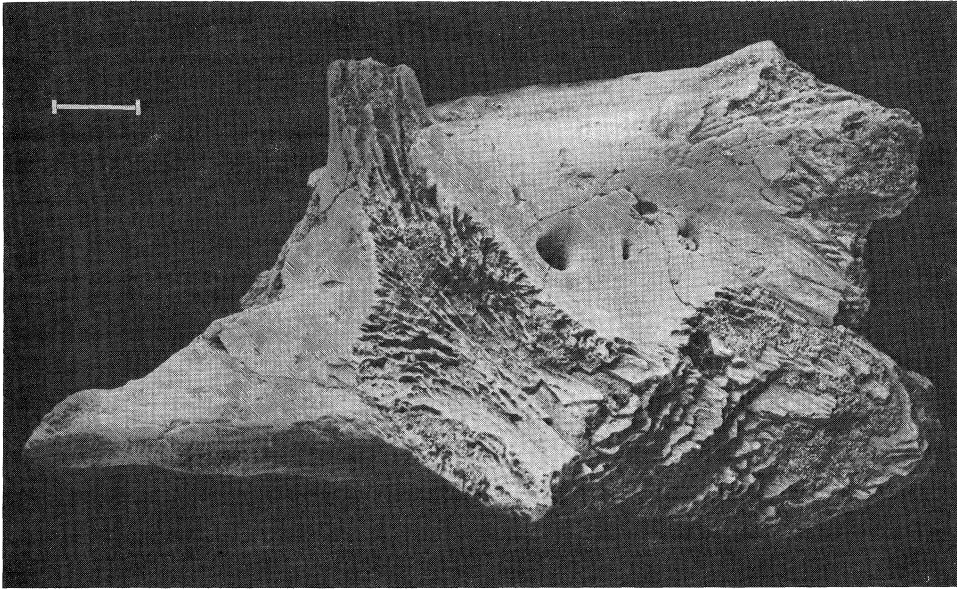


Fig. 12. Crocodilian jugal, QM F1152, from Chinchilla, in medial view. Scale 1 cm.

and the Chinchilla jugal would agree in size and in such proportions as can be deduced with what would be expected of *Quinkana*.

Ventrally the sculptured external surface is flexed to face downwards. Thus a ventral surface, reminiscent of the pitted ventral surface of the jugals of *Alligator mississippiensis*, but unlike those of any Australasian species of *Crocodylus*, was present. The postorbital bar is inset from the lateral surface, which bears a deep, longitudinal sulcus below the inferior orbital margin. The posterior process is unusually short and slender compared to the suborbital portion of this element (Fig. 11).

CHARACTER ANALYSIS

CHARACTERS USED: The characters used to analyse the taxonomic relationships of *Quinkana fortirostrum* have been grouped into three suites: first, those related to the ziphodont condition; second, those related to the sebecosuchian and eusuchian conditions (i.e. infraordinal characters), and; third, a miscellaneous suite. The system of Hecht (1976) and Hecht and Edwards (1976) has been used as a guide in assessing the significance of these characters. These workers have divided all possible character states into five classes. These are:

- I. Shared, derived states that result from loss.
- II. Shared, derived states that result from simplification or reduction of complex structures.
- III. Shared, derived states that result from age or size dependent processes, such as growth.
- IV. Shared, derived states that make up some functional complex. These would be highly integrated and co-evolving.
- V. Derived states "that are unique and innovative in determining new dichotomies and lineages" (Hecht, 1976, p. 344).

The states of these characters for thirty-four crocodilian genera, determined from the literature and available specimens are presented in Table 4. This information has been

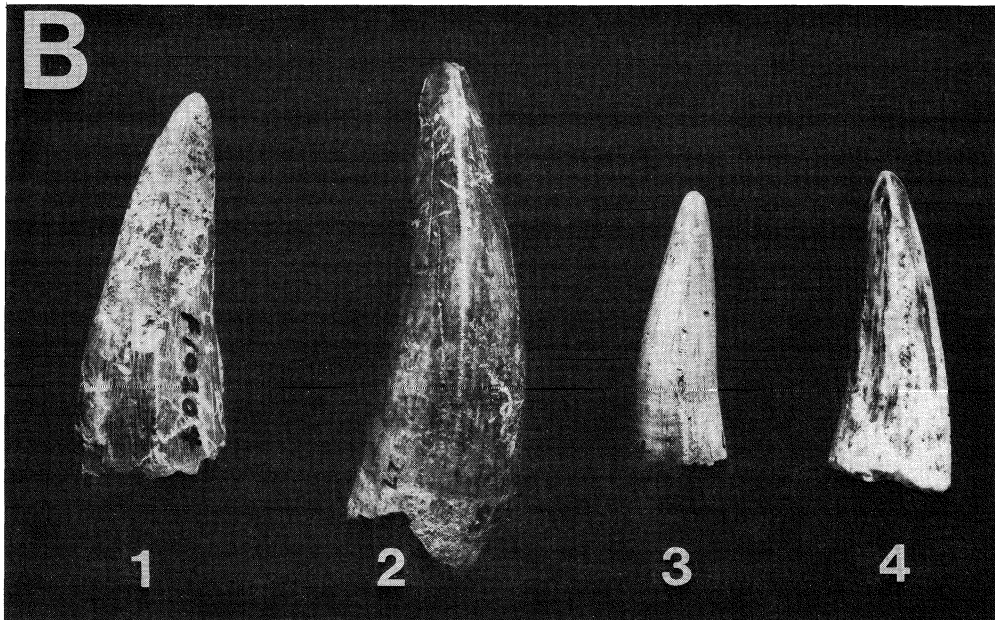
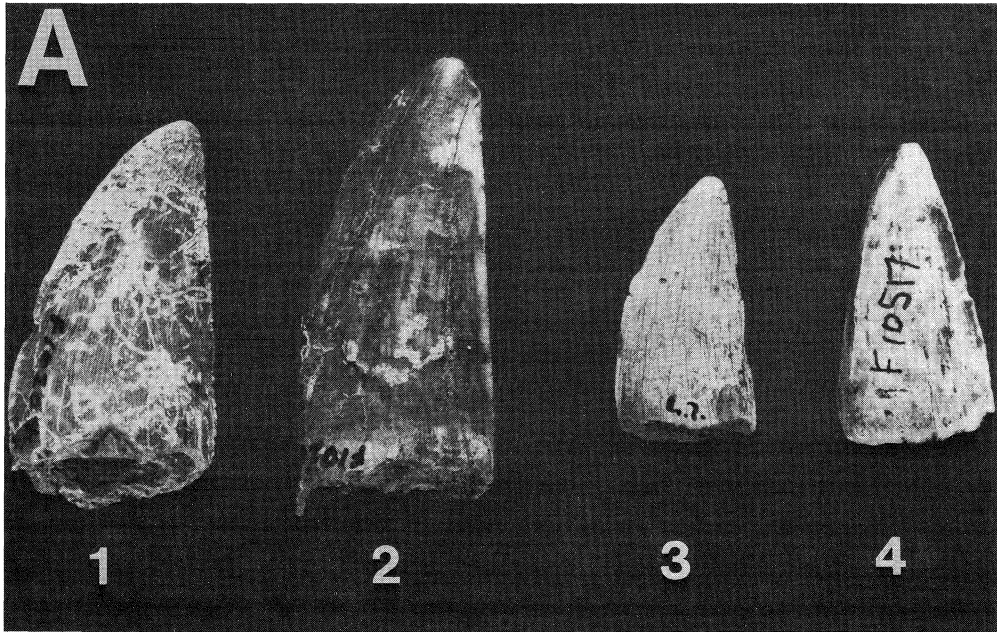


Fig. 13. Four isolated ziphodont teeth in lateral view (A) and anterior or posterior view (B). 1, QM F10204; 2 and 3, QM F10205, all three from Chinchilla, and; 4, QM F10517, from "Glen Garland". Scale 1 cm.

used to determine plesiomorphic states, based on the commonality of the state except where otherwise noted.

The first suite of characters, falling into Hecht's group IV (characters participating in an adaptive complex), clearly indicates the reference of *Quinkana* to the ziphodont crocodylians, but does not differentiate between the sebecosuchian and pristichampsine ziphodonts.

1. Snout depth. Crocodylian snouts are here arbitrarily classified into three categories of depth: low, those with a depth by width ratio (Table 3) less than 0.5; moderately deep, those for which this ratio is greater than or equal to 0.5 and is less than 1.0; and deep, those for which this ratio is greater than or equal to 1.0. Both this set of terms and those introduced for snout breadth agree with general usage. Low snouts are plesiomorphic for both mesosuchians and eusuchians.

2. Snout breadth. Crocodylian snouts are also here classified into three categories of breadth: broad, those with a length by breadth ratio (Table 3) greater than or equal to 0.66; moderately narrow, those in which this ratio is less than 0.66 and greater than 0.33; and narrow, those in which this ratio is less than or equal to 0.33. The broad snout is here considered plesiomorphic, although it is recognised that narrow snouted marine crocodylians, such as the teleosaurs, occur as early or earlier in the fossil record than broad snouted forms. These forms are not ancestral to later broad snouted taxa however and are usually considered specialised for a marine existence (cf. Kálin, 1955; Langston, 1973; Steel, 1973).

The genus *Crocodylus* includes species (e.g. *C. cataphractus* and *C. johnstoni*) with narrow snouts, suggesting that snout breadth considered in isolation might be regarded as variable. Among ziphodont crocodylians, however, snout breadth usually correlates with the presence of a ziphodont dentition and with snout depth. Non-Australian ziphodont crocodylians have narrow to moderately narrow deep to moderately deep snouts (cf. Berg, 1961; Langston, 1975).

3. Maxillary wall inclination. The inclination of the maxillary wall is related to the breadth and depth of the snout, narrow, deep snouts having a steep inclination, while low, broad snouts have a shallow inclination. For intermediate conditions, for example, a moderately deep, moderately narrow snout, variation in inclinations is conceptually possible. Since both low and broad snouts are plesiomorphic, it follows that shallow inclinations are also plesiomorphic. Only one non-ziphodont crocodile, of the thirty-four crocodylians for which information was available, shows a steep inclination, and that is *Paleosuchus palpebrosus*.

4. Dorsal margin of snout. All ziphodont crocodylians hitherto known possess a straight or slightly convex dorsal margin to the snout. Almost all other crocodylians have a dorsal margin concave in lateral view, and thus this condition is taken as plesiomorphic.

5. Laterally compressed dentition. The term ziphodont refers to crocodylian teeth that are laterally compressed and serrate. Because some crocodylian teeth are serrate but not laterally compressed these traits will be treated as two separate characters. It should be noted that some crocodylians (e.g. *Uruguaysuchus*) have laterally compressed teeth that are not ziphodont. But such brevirostrine crocodylians are unlike any known ziphodont crocodylians. The plesiomorphic condition is a tooth of sub-circular or oval cross-section.

6. Serrations. Other than among ziphodont crocodylians, the only dental serrations known to me among crocodylians occur in large teeth of rounded cross-section referred

TABLE 3. Characters and character states.

	Character	Character states	Condition
1	Snout depth	low moderately deep deep	plesiomorphic apomorphic apomorphic
2	Snout breadth	broad moderately narrow narrow	plesiomorphic apomorphic apomorphic
3	Maxillary wall inclination	shallow steep	plesiomorphic apomorphic
4	Dorsal margin snout	straight concave dorsally	apomorphic plesiomorphic
5	Lateral compression of teeth	present absent	apomorphic plesiomorphic
6	Serrations of teeth	present absent	apomorphic plesiomorphic
7	Relation of tooth rows during closure	lower medial to upper interlocking	plesiomorphic apomorphic
8	Enlarged maxillary alveoli	present absent	plesiomorphic apomorphic
9	Festooning	present absent	plesiomorphic apomorphic
10	Maxillary tooth count	less than 12 12-15 greater than 15	apomorphic plesiomorphic apomorphic
11	Positions of nasals	dorsal dorsolateral (nasal crest)	plesiomorphic apomorphic
12	Nasal form	flared posteriorly tapered posteriorly	plesiomorphic apomorphic
13	Posterior process of premaxilla	present absent	plesiomorphic apomorphic
14	Post-fenestral alveoli	present absent	apomorphic plesiomorphic
15	Lachrymal-prefrontal knobs	present absent	apomorphic plesiomorphic
16	Anterior process of palatine	present absent	plesiomorphic apomorphic
17	Palatal premaxillary-maxillary contact	angulate non-angulate	apomorphic plesiomorphic
18	Antorbital portion of jugal	present absent	plesiomorphic apomorphic

(dubiously) to *Pallimnarchus*. Thus the non-serrate condition is taken to be plesiomorphic.

7. Relation of tooth rows during closure. As among alligatorines, in ziphodont crocodylians the lower tooth row lies medial to the upper when the mouth is shut. This is presumably related to the efficiency of shearing, necessitating the passage of one tooth row past the other. The condition of crocodylines in which the teeth interlock is usually assumed to be primitive, although this condition is less widespread than that of the medial lower tooth row. The "overbite" of alligatorines is thus here taken as plesiomorphic.

8. Single or few enlarged maxillary alveoli. Most eusuchians and non-marine mesosuchians possess one or two enlarged maxillary teeth (and hence alveoli), usually the fourth, fifth or sixth maxillary teeth. Longirostrine forms, especially marine forms, have teeth of nearly equal size throughout the anterior part of the tooth row, gradually decreasing in size posteriorly. This tendency also appears among ziphodont crocodylians, and may be related to the shearing action of the dentition. The possession of one or two enlarged maxillary teeth is considered plesiomorphic.

9. Festooning. Festooning, resulting in a vertically undulating tooth row, might also interfere with the shearing action of the dentition. Colbert (1945) related differences in form of the jaw margins and their relation to the quadratomandibular articulation between theropod and hadrosaurid dinosaurs to the shearing and "nutcracker action" occurring with the closure of the jaws. A working model of the skull and jaws of *Crocodylus rhombifer*, showed that marked festooning results also in "nutcracker action" over much of the tooth row (although some shear does occur). During "nutcracker action" upper and lower teeth come together almost simultaneously, while during shear the point of contact of the upper and lower tooth rows travels anteriorly along these rows during closure. A similar model of the skull of *Sebecus icaeorhinus*, where the ventral margin of the maxilla forms a single convex curve, shows that the amount of tooth row involved in shearing is increased. Only the premaxillary teeth, which are not ziphodont, show "nutcracker action". Thus to increase shearing action festooning would be suppressed.

These characters constitute the first suite, probably related to the presence of a ziphodont dentition. Certain other characters, such as the alveolar process, which might also have been included were not used because of absence of relevant information in the literature. As shown in Table 4 there is independent variation among the states of these characters, not all occurring together in each taxon hence the characters are treated as independent in this analysis. Closure of the lower teeth medial to the upper tooth row, loss of an enlarged maxillary tooth (or teeth) and reduction of festooning may reasonably be related to increased efficiency of shearing action of the teeth.

Character 9 points up an ambiguity in the use of the scheme of weighting proposed by Hecht (1976). The state present in ziphodont crocodylians is clearly the loss of festooning, and hence would fall in Hecht's group I (losses) and thus render minimal phylogenetic information. Nonetheless, as demonstrated previously, this loss is part of the development of "a highly integrated functional complex" (Hecht and Edwards, 1976), and thus falls into group IV, which is considered of "great information content if properly evaluated" (Hecht, 1976). The problem is that a given character state may fall into more than one category, and that no priority of categories is presented. I shall here consider that such states are not simply losses and shall count them as falling into group IV.

The second suite of characters is:

10. Maxillary tooth count. A relatively low count of 12 to 15 maxillary teeth is plesiomorphic for mesosuchians and eusuchians (*vide* Table 4), although some genera of both groups have more. All known sebecosuchians (and notably *Baurusuchus*) have fewer than 11 maxillary teeth, and this low count is apparently apomorphic. This state distinguishes sebecosuchians from pristichampsines, which have at least 12 maxillary teeth.

11. Position of nasals. Sebecosuchians are distinguished by the possession of a nasal crest (Colbert, 1946), by virtue of which the nasals are broadly visible in lateral aspect. The plesiomorphic condition, found in other crocodylians, restricts the nasals to the dorsum of the snout.

12. Nasal form. Sebecosuchians and non-marine mesosuchians, have nasals that flare posteriorly. The majority of eusuchians have nasals that taper posteriorly: only the aberrant *Mourasuchus* departs from this condition. Since eusuchians derive from mesosuchians, the mesosuchian condition, i.e. flaring nasals, is here taken to be plesiomorphic, even though it is not the most widespread character state.

13. Posterior process of premaxilla. Most eusuchians and many mesosuchians have a short process projecting posteriorly from the premaxilla on the dorsum of the snout. This process separates the anterior portion of the nasals from the anterior portion of the maxillae. It is lacking in few crocodylians (among them the Sebecosuchia) and this absence is taken as apomorphic.

14. Relation of maxillary tooth row to palatine fenestra. All eusuchians known to me have a maxillary tooth row that extends well posterior to the front of the palatine fenestra. This condition is unknown among sebecosuchians and non-marine mesosuchians (excepting *Eutretauranosuchus*).

Characters 10, 11 and 13 have unique states among the sebecosuchians, while characters 12 and 14 have unique states among the eusuchians. Thus this suite of characters is useful in determining the infraordinal allocation of *Quinkana*.

The third suite of characters is:

15. Lachrymal-prefrontal knobs. These knobs are found only in *Quinkana*, and thus are autapomorphic (and perhaps variable from individual to individual). The lachrymal knobs may be related to the lachrymal ridges of *Crocodylus porosus* but, as all autapomorphs, reveal nothing about the taxonomic relations of *Quinkana*.

16. Anterior process of palatine. Except for *Brachyuranochampsa* and *Quinkana*, eusuchians, mesosuchians and sebecosuchians all have an anterior process of the palatine. Hence the presence of the process is considered plesiomorphic.

17. Form of premaxillary-maxillary contact on palate. *Quinkana* shows an unusual form of palatal premaxillary-maxillary contact. Only *Brachyuranochampsa*, *Kentisuchus* and *Osteolaemus* also show a U- or V-shaped contact of similar form, and in *Osteolaemus* this seems to be variable (cf. Kälin, 1933, with Wermuth and Mertens, 1961). The sporadic, non-systematic appearance of this character suggests that it is best considered apomorphic, appearing independently in several lines.

18. Relation of anterior margin of jugal to that of orbit. *Quinkana* again differs from almost all other crocodylians in that the jugal cannot have extended anterior to the front of the orbit. This condition is also found in *Paralligator* and *Osteolaemus*, and, for the

same reasons as given for character 17, is considered autapomorphic.

RESULTS OF ANALYSIS: Using the characters listed in Table 3, *Quinkana* was compared with those genera previously determined to most closely resemble it (Molnar, 1977), and being sufficiently complete for comparison. The character states of *Sebecus*, *Pristichampsus*, *Quinkana*, *Paleosuchus* and *Osteolaemus* are given in Table 4. Many characters used to differentiate eusuchians from mesosuchians and sebecosuchians are not included because they are restricted to the postorbital region of the skull, not preserved in any known material of *Quinkana*.

Quinkana agrees with *Sebecus* in seven of the eighteen states (all of which are apomorphic states associated with the ziphodont condition), with *Pristichampsus* in ten of the eighteen, and with *Paleosuchus* and *Osteolaemus* in seven of the eighteen. Four of the states in which *Quinkana* agrees with *Pristichampsus*, *Paleosuchus* and *Osteolaemus* are apomorphic eusuchian states.

The seven states in which *Quinkana* agrees with *Sebecus* are all related to trophic adaptation and thus fall into Hecht's group IV (co-evolving, functionally integrated states). Of the ten states shared with *Pristichampsus* six are ziphodont adaptations, and fall into group IV, while the other four are derived states shared with the other eusuchians. The state of character 14, concerning the extension of the tooth row posterior to the front of the palatine fenestra, seems likely related to the development of the trophic apparatus (although not a part of the ziphodont adaptation), and hence may be put into group IV. The other three states do not obviously fall into any of Hecht's categories. The dorsal position of the nasals (character 11), the posterior taper of the nasals (character 12), and the posterior process of the premaxilla (character 13) do not seem to be losses (group I) or reductions (group II). Perhaps one could stretch a point and regard the tapered nasals as a reduction of flared nasals. But one could equally regard this as an increase in relative size of the lachrymals, and thus not a reduction at all. None of these states obviously falls into the category of highly integrated, coevolving functional complexes (group IV) and cannot fall into group V (which are derived but not shared character states), and thus seem by default to fall into group III. Since all character states would seem to be the result of allometric or other ontogenetic processes it would appear that any shared, derived state could fall into this group. Considering these states to fall in group III, the four states shared with *Pristichampsus* (and other eusuchians) carry sufficient import to determine that *Quinkana* is an eusuchian.

These states are also the majority of states by which *Quinkana* agrees with *Paleosuchus* and *Osteolaemus*. Of the other two such states, one is uncommon and variable (character 17, form of palatal maxillary-premaxillary contact) and thus considered to have been independently derived, and the other (character 2, snout breadth), although part of the feeding mechanism, appears to be part of two different adaptive complexes in the different forms. The broad snout of *Osteolaemus* and *Paleosuchus* is not related to any other ziphodont features in those forms, while *Quinkana* is admittedly the only ziphodont crocodylian to have a broad snout. The absence of any other features in common, however, compels abandonment of any hypothesis that *Quinkana* was an aberrant alligatorine that developed the ziphodont habitus independently of the other ziphodont crocodylians. Thus the application of Hecht's method supports the assessment of *Quinkana* as a crocodylid.

DISCUSSION OF ANALYSIS: The first suite of nine characters are all related to the ziphodont condition, and thus corroborate the suggestion that *Quinkana* was a ziphodont crocodylian. Each of these states falls into Hecht's group IV which he considers as quite informative. But care must be taken with this kind of analysis, as Hecht himself

comments, for *Sebecus* and *Pristichampsus* agree in almost as many characters (nine out of eighteen) as *Quinkana* and *Pristichampsus* and of the former pair each belong to different infraorders. Such characters can be misleading if, as here, they pertain to adaptive complexes evolving independently, but which because of the environmental constraints and selection for optimal function come to closely resemble one another. If there is only one optimal way to do something, all optimal structures developed will closely resemble one another. The classical example of this is streamlining in large, fast-swimming fish, ichthyosaurs and cetaceans. In the example discussed here the effect is emphasized by the absence of postorbital and postcranial characters from the analysis.

Characters 8 and 9 which have shared states between *Quinkana* and *Sebecus*, but not between *Quinkana* and *Pristichampsus*, I regard as indicating no closer relationship of *Quinkana* to *Sebecus* than to *Pristichampsus*. *Quinkana* shares four of the five eusuchian character states with *Pristichampsus*, and none with *Sebecus*. (Obviously: had *Sebecus* these states it would be considered a eusuchian.) This indicates that *Quinkana* was a eusuchian, and a later one than *Pristichampsus* (cf. Molnar, 1978), and hence could have evolved a more efficient feeding mechanism than *Pristichampsus*. These differences cannot be taken at face value.

Since the states of the second suite are common to most eusuchians it is neither surprising nor indicative of special affinities that *Quinkana* also shares four of the five states with *Osteolaemus* and *Paleosuchus*.

The first suite of characters indicates that *Quinkana* is ziphodont, and the second that it is eusuchian. The third suite is those diagnostic of the genus *Quinkana*. Only one state present in *Quinkana* is shared with any of the other taxa used in the comparison, the angulate form of the palatal premaxillary-maxillary suture, shared with some specimens of *Osteolaemus tetraspis*.

All previously known ziphodont eusuchians (i. e. *Pristichampsus*) are classified in the subfamily Pristichampsinae Kuhn, 1968. Kuhn's definition of the subfamily, translated from the German and with description of the postcranial character states omitted, reads:

For the narrow- and long-snouted genera *Pristichampsus* and *Weigeltisuchus*, that according to Berg are very probably synonymous, I suggest this new subfamily. The teeth are unmistakably dinosaur-like, compressed, with anterior and posterior serrations, (and) shearing bite; eusuchian . . . From the position of the fourth dentary tooth (it is) a crocodyline, from which it diverges in bite and tooth form. The teeth of the lower jaw bite lingual to those of the upper. (Kuhn, 1968, p. 40).

Of the four character states distinctive of pristichampsines given, *Quinkana* probably possessed two: it did not have a long nor a narrow snout. Because no other eusuchians are ziphodont and because *Quinkana* probably was, I consider that *Quinkana* probably will prove, when more material is found, to belong to this subfamily.

COMMENTS ON OTHER ZIPHODONT CROCODILIANS

In view of the unexpected geographic and temporal occurrence of *Quinkana*, some comments on the palaeozoogeography and taxonomy of ziphodont crocodylians are in order. Langston (1956, 1975) has long worked in this area, and recently Buffetaut (1978) and Molnar (1978) have offered short reviews of ziphodont crocodylian palaeogeography.

In spite of the description of thirteen nominate genera of ziphodont crocodylians (not all here considered valid), only four genera are represented by material more

complete than that known for *Quinkana*. These genera are *Baurusuchus*, *Hsisosuchus*, *Pristichampsus* (= *Limnosaurus* Marsh, non Nopcsa = *Planocrania* = *Weigeltisuchus*), and *Sebecus*. The others (*Bergisuchus*, *Cynodontosuchus*, *Doratodon*, *Iberosuchus* and *Ilchunaia*) are represented by less complete material.

Hsisosuchus chungkingensis (Young & Chow, 1953) is the sole species of a monotypic family usually considered to be mesosuchian (e.g. Steel, 1973). Langston (1956) suggested that *Hsisosuchus* was an ancestral sebecosuchian, an interpretation that finds support in the presence of several apomorphic sebecosuchian character states, and the absence of any apomorphic non-sebecosuchian states. Like other sebecosuchians, *Hsisosuchus* has relatively few maxillary teeth (9 to 10), a nasal crest, and apparently lacks maxillary teeth posterior to the front of the palatal fenestra (Young and Chow, 1953, Fig. 7). *Hsisosuchus* differs from later sebecosuchians, such as *Sebecus*, in having a low, moderately broad snout. I interpret this as suggesting that the acquisition of a ziphodont dentition may have preceded the development of a laterally compressed, deep, narrow snout.

The occurrence of the earliest known, and structurally most primitive sebecosuchian in China, while most of the other taxa derive from South America, supports Langston's (1956) contention of a cosmopolitan sebecosuchian radiation. Since *Hsisosuchus* dates from the Jurassic, the possibility must be considered that sebecosuchian teeth have been collected from later Mesozoic beds and misidentified as theropod. The Cretaceous Austrian ziphodont *Doratodon carcharidens* is now considered to be closely related to *Hsisosuchus* (Buffetaut, 1979).

Buffetaut (1979) has argued that hsisosuchians constitute a third group of ziphodont crocodylians unrelated to sebecosuchians or pristichampsines. Buffetaut cites the greater compression of the teeth of hsisosuchians than of primitive members of the other groups as evidence for the absence of any close relation. However this may simply remove the two known hsisosuchian species from ancestry, but does not, I feel, eliminate some unknown hsisosuchian species from ancestry of the sebecosuchians: this unknown hsisosuchian would have to have retained a less-specialized dentition than *Hsisosuchus chungkingensis* or *Doratodon carcharidens*.

Much of the material currently referred to the Sebecosuchia is quite incomplete. While this material is clearly referable to ziphodont forms, its position in the Sebecosuchia is uncertain due to the absence of diagnostic characters in the material preserved. Such forms as *Bergisuchus* are best regarded as *incertae sedis*.

Molnar (1977), Hecht and Archer, (1977) and Buffetaut (1978b) showed that the monotypic genus *Planocrania* (Li, 1976) was not sebecosuchian. This genus lacks the nasal crest and maxillary tooth number of sebecosuchians, and shows a eusuchian palate (Li, 1976). No character states are reported in the type (and only described) specimen of *Planocrania datangensis* that are absent in the known species of *Pristichampsus* (Berg, 1966; Langston, 1975) and thus this species is to be regarded as *Pristichampsus datangensis*, new combination.

Hecht and Archer, (1977) suggest that the Palankarina crocodile probably represents a sebecosuchian. *Quinkana* does not. Although it remains to be determined by what route sebecosuchians reached Australia (perhaps via Antarctica), pristichampsines would most likely have come from Asia. It is known that pristichampsines were spread throughout the northern hemisphere in the early Tertiary (Langston, 1956; Molnar, 1978), including south China (Li, 1976). Presumably like other forms that relatively recently reached Australia, they migrated through Indonesia and

New Guinea. The Otibanda teeth (which include no sabre-shaped crowns as are often found among sebecosuchians) may represent a vestige of this migration. The coexistence of sebecosuchians and pristichampsines would seem unusual, although this apparently occurred in Europe as well.

RANGE: Fossils of ziphodont crocodilians have been found in Queensland from central Cape York Peninsula in the north to the New South Wales border in the south. The sites fall into two groups (Fig. 14), one in the north and one in the south. Most of the localities are closely associated with the Great Dividing Range, with the exception of Croydon (at the end of the Gregory Range) in the north, and Chinchilla (on the Darling Downs) in the south. None of the localities is greatly removed from a modern watercourse, the most distant being Chillagoe which is approximately ten miles from the Walsh River, and through which runs a large creek. Croydon is also removed from a major modern watercourse, but there is geological evidence for a local watercourse at the time the fossils were deposited (Archer, pers. comm., 1978).

I feel that insufficient work on fossil crocodilians in Australia has been done to be sure that ziphodont crocodilians did not occur elsewhere. The collections of the Australian Museum and the Geological and Mining Museum in Sydney were searched for evidence of ziphodont crocodilians in New South Wales without success.

Although the evidence is scanty there is no suggestion of any change in range with time, as the Pliocene occurrences (Tara Creek and Toowoomba) are among both the northern and the southern group of sites.

ASSOCIATED FAUNAS: One of the localities that produced ziphodont teeth, "Rosella Plains" has yielded no other vertebrate remains. Each of the other localities has produced one or more additional tetrapod taxa. At "Glen Garland" teeth of three terrestrial mammals have been found with the ziphodont teeth. At Tara Creek and Croydon the ziphodont was found with remains referable to *Crocodylus porosus* or a very similar species. At Chinchilla a fauna of terrestrial mammals is known (Archer and Bartholomai, 1978), as well as at least two other forms of crocodile, currently under study, one of which is probably *C. porosus*. The Toowoomba area (Gowrie Creek especially) has produced a terrestrial Pleistocene fauna (Owen, 1877). At Texas Caves and Tea Tree Cave, faunas consisting largely of mammals have been found with the ziphodont crocodilians (Archer, 1978; Molnar, 1978). No other crocodilians were found at these localities, nor were other aquatic or amphibious forms represented.

Since the Queensland ziphodont crocodilians have been found both in association with apparently terrestrial faunas and with faunas that include amphibious elements, no conclusion as to the possible habitats of the ziphodonts themselves can be drawn from the faunal associations.

OCCURRENCE OF ZIPHODONT CROCODILIAN FOSSILS: The Chillagoe and the Texas Caves crocodile represent two of the few ziphodont crocodilian specimens that were found in cave deposits. The description of the deposits in The Joint at Texas Caves (Archer, 1978) describes equally well the deposits in Tea Tree Cave. There is some evidence that the bones in Tea Tree Cave all lie in one relatively narrow level, but this has yet to be confirmed.

The other Queensland ziphodont material was either collected from the surface (Chinchilla, Toowoomba and Tara Creek) or from excavations (Croydon, "Rosella Plains"). The environment of deposition of these latter sites has not been determined, although there is some suggestion that the Croydon material accumulated in the bottom of a stream channel or billabong (Archer, pers. comm., 1978).

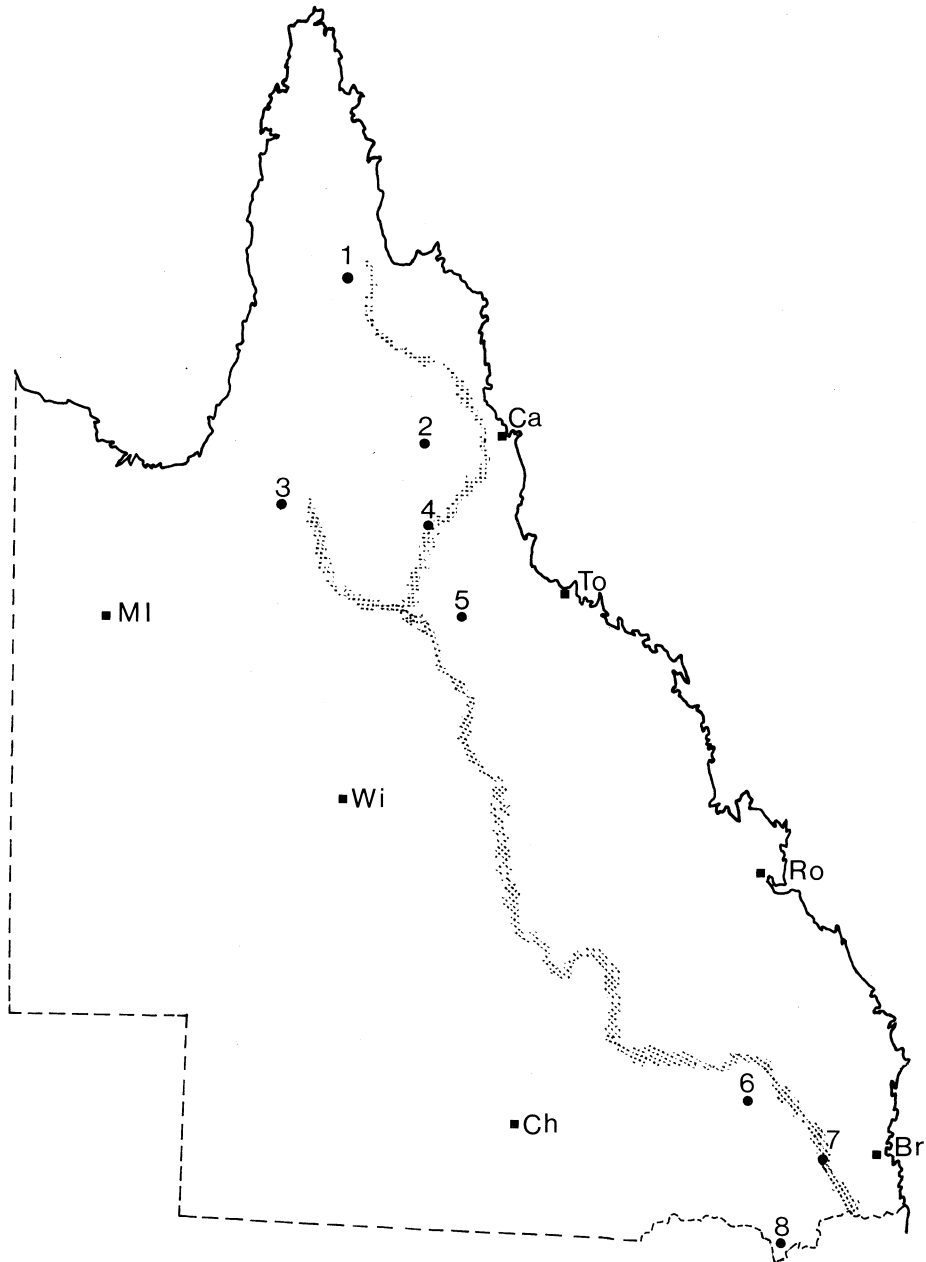


Fig. 14. Map of Queensland showing the distribution of known fossils of ziphodont crocodilians. 1, "Glen Garland"; 2, Chillagoe; 3, "Rosella Plains"; 4, Croydon; 5, Tara Creek; 6, Chinchilla; 7, Toowoomba; 8, Texas Caves; Br, Brisbane; Ca, Cairns; Ch, Charleville; MI, Mount Isa; Ro, Rockhampton; To, Townsville; Wi, Winton.

In view of the unusual occurrence of some of the Australian ziphodont material, and of the evidence suggesting terrestrial (as opposed to amphibious) habits of ziphodont crocodylians (Kuhn, 1938; Zappler, 1960), it is worth reviewing the conditions of deposition of beds bearing ziphodont crocodylian remains. Occurrences of isolated teeth will usually not be considered, because of the obvious possibility of transportation. The material is treated by continent.

South America. The type of *Sebecus icaeorhinus* derives from a pocket of the Casamayor Formation, associated with a fauna not elsewhere found in that formation (Colbert, 1946). This fauna includes a waterbird, turtles and a frog and hence suggests a near-water environment. The second specimen of *S. icaeorhinus* was apparently a surface find deriving from beds of Casamayorian age yielding a typical *Notostylops* fauna (Colbert, 1946). The Brazilian *Sebecus* sp. derives from Paleocene fissure or cave fills of the São José de Itaboraí Basin (de Paula Couto, 1953; Codevila Palma and Brito, 1974), but no further information is recorded. The type jaw of *Sebecus huilensis* derives from the La Venta fauna, from a unit ("Monkey unit") of the Honda Group (Langston, 1965). *Caiman neivensis* was also found at this locality, so a near-water environment is again possible. The Peruvian *Sebecus* cf. *S. huilensis*, from the Ipururo Formation is associated with a fauna containing turtles and other crocodylians (Buffetaut and Hoffstetter, 1977), suggesting a near-water environment.

Cynodontosuchus rothi derives from the "Estratos con Dinosaurios" (Upper Cretaceous) of Neuquen which has also produced a dinosaur fauna. *Ilchunaia parca* derives from the Divisadero Largo Fm. along with a fauna of snakes, turtles and various mammals (Báez and Gasparini, 1977; Simpson, Minoprio and Patterson, 1962). *Baurusuchus pachecoi* comes from the Baurú Series, which also yields the goniopholid *Itasuchus*, podocnemids, teleosts and fresh-water invertebrates (Price, 1955). Obviously this is an aquatic deposit: although no further stratigraphic details are given by Price (1945), Beurlen (1970) implies that *Baurusuchus* derives from the upper Baurú at Marília, which he describes as "lacustrine-limnic".

North America. The principle specimens of *Pristichampsus vorax* come from the Washakie and Bridger Basins (Langston, 1975). In the Washakie Basin the Green River Formation is a well-known fresh-water deposit, while the Washakie Fm. is also fluvial (Black, 1967; Roehler, 1973). The Bridger Fm. is predominantly fluviatile, with a large number of thin layers of lacustrine sediments. Much volcanic ash apparently fell during the deposition of this formation (Bradley, 1964).

Europe. Both *Pristichampsus rollinatti* and *Bergisuchus dietrichbergi* have been found in the Eocene near Messel, Germany, in association with much other crocodylian material (Berg, 1966). Matthes (1966) suggests a larger water system than presently exists, and gives evidence suggesting wooded or forested conditions.

P. rollinatti has also been found in the Geiselthal deposits. These are described as having been deposited in a forest with river and ponds (Kurten, 1971) and in a swampy forest with open swampland (Zappler, 1960): both cases presenting a near-water environment.

P. rollinatti and *Pristichampsus* sp. have also been reported in the Eocene of the Paris Basin and of southern France, and involve beds of fluvial or lacustrine origin, which have also yielded the remains of other types of crocodylians (Buffetaut, pers. comm., 1979). One tooth has been found in the phosphorites of Quercy (Berg, 1966), which are cave deposits.

Doratodon carcharidens from the Cretaceous Gosau Fm. of Austria derives from

fresh-water beds (Bunzel, 1871; Suess, 1881). *Iberosuchus macrodon* occurs at widely distributed localities on the Iberian Peninsula (Antunes, 1975). Antunes (1975) concludes that "Sedimentological and other evidence concerning the localities strongly suggests that, . . . *Iberosuchus* would be less strictly aquatic dwellers than most Crocodylia. They may equally have frequented high energy water courses, . . ." (p.290).

Asia. No relevant information is yet available for *Pristichampsus datangensis*. *Hsisosuchus chungkingensis* was found associated with *Plesiochelys*, but no further details are available (Young and Chow, 1953).

Pristichampsine material (Buffetaut, 1978b) has also been recently described from what appears to be a portion of the Kuldana Fm., in Pakistan. This material occurs together with other crocodylian remains in fluvial deposits (Buffetaut, pers. comm., 1979). Sahni, Srivastava and D'Souza (1978) have reported ziphodont teeth (that they attribute to a pristichampsine) from a calcareous shale in the Subathu Fm., of Jammu and Kashmir in northwest India. They suggest that the Indian ziphodonts were "river or river bank carnivores." Maw, Ciochon and Savage (1979) list ziphodont crocodylian remains (described as sebecid) from claystones in the Pondaung Fm. of Burma. From the same beds also come fish, turtles, other crocodylians, brontotheres, amynodonts and anthracotheres, so a subaqueous deposition of the beds is indicated.

In conclusion, there are only two known occurrences of ziphodont crocodylian fossils in caves, or fissure fills, other than in Queensland. Most, if not all other occurrences of ziphodont crocodylians are in deposits that formed under or near water. Hence there is no decisive indication of terrestrial habits for ziphodont crocodylians from the environments of deposition in which they were buried, nor any contradiction either, since most terrestrial tetrapods are buried in subaqueous deposits. The occurrence of some Australian specimens in caves strongly suggests that the crocodiles fell into the caves and died there. This, in turn, suggests that they wandered overland. Modern individuals of the genus *Crocodylus* however often wander overland some distance from water (Cott, 1961; Webb, pers. comm., 1978) so this does not constitute good evidence for terrestrial habits.

INFERRED HABITS OF AUSTRALIAN ZIPHODONT CROCODYLES: None of the Australian ziphodont crocodylian material is sufficiently complete to allow any biomechanical analyses, so that any speculation of the habits of these crocodiles must be extrapolated from knowledge of the other, better known ziphodonts. On the basis of two features of the postcranial skeleton of "*Weigeltisuchus geiseltalensis*" (here considered a synonym of *Pristichampsus rollinoti*), the hooflike unguals and the rounded, rather than laterally flattened, tail it has been suggested that this form was more terrestrial in habits than other crocodylians (Kuhn, 1938).

The discovery of the best two specimens of Australian ziphodont crocodylians in caves certainly does not contradict this, but neither (as previously noted) does it unambiguously support this suggestion. Nor does the occurrence of ziphodont crocodylians in the more usual kind of deposits shed light on this question.

The possession of ziphodont teeth and the associated lateral compression of the snout would seem to indicate predation upon larger prey than is usual for crocodylians, but does not indicate that this prey was terrestrial: they may have preyed upon other crocodylians, for example.

The relative absence of large terrestrial predators in the Tertiary and Pleistocene deposits of Australia (cf. Archer and Bartholomai, 1978, Fig. 2), other than the giant

varanid *Megalania*, leads to the suspicion that the role of large terrestrial predator may have been played by the reptiles, specifically *Megalania* and *Quinkana*. Only further discoveries will demonstrate whether or not this interesting hypothesis can be supported.

REVIEW

The Chillagoe crocodile, based on the rostral portion of a skull (AM F.57844), is described as the type specimen of the new genus and species, *Quinkana fortirostrum*. This species is characterised by a broad, moderately deep snout, a distinct alveolar process on the maxilla, the anterior process of the palatine very short or absent, and a jugal that does not project anterior to the orbit. The alveoli lie in a distinctive pattern and suggest the presence of ziphodont teeth. A second specimen (QM F7898), from Texas Caves, also referred to this genus, does have a single ziphodont crown *in situ*.

Ziphodont teeth have also been found isolated at "Alehvale" (with some cranial fragments), "Rosella Plains", "Glen Garland", and Tara Creek, in north Queensland, and near Chinchilla, and Toowoomba on the Darling Downs. An isolated, deep crocodilian jugal (QM F1152) found at Chinchilla may pertain to *Quinkana*.

A character analysis, modelled on the work of Hecht (1976) indicates the eusuchian nature of the specimen and suggests a relationship to *Pristichampsus*. Problems encountered in the use of this mode of analysis include ambiguity in the definition of the possible categories of character states, particularly in regard to losses or reductions, and discrimination of parallelism.

Hsisosuchus chungkingensis possesses several apomorphic sebecosuchian character states (few maxillary teeth, nasal crest, and absence of maxillary teeth posterior to the palatal fenestra) and is thus considered the oldest known sebecosuchian.

No information about ziphodont crocodilian habits can be drawn from stratigraphic occurrences, although the finding of the two most complete Australian specimens in caves suggested that at the very least they did wander overland.

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TABLE 4. Character States in Crocodylian Skulls. The following table enumerates the states of the eighteen characters used in the taxonomic analysis of *Quinkana fortirostrum*. This illustrates the commonality of the various characters, and was used to determine plesiomorphs and apomorphs.

The characters are designated by the same numbers used in the text. The genera included and the symbols used in the table are listed below. Two symbols separated by a slash indicates that both states are present in that genus.

List of symbols used in supplementary table.

For all characters:	For character 3:
? state not determinable from literature or specimens	nh less than 45 degrees
For characters 5 to 9 and 13 to 18:	nv greater than 45 degrees
+ present	For character 4:
- absent	s straight
For character 1:	c concave
l low	For character 11:
md moderately deep	d dorsal
d deep	dl dorsolateral
For character 2:	For character 12:
b broad	t tapered
mn moderately narrow	f flared
n narrow	o parallel

Genus	Character State																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Mesosuchia																		
Atoposauridae																		
<i>Alligatorellus</i>	l	b	?	s	-	-	?	+	-	13	?	t	?	?	-	?	?	?
<i>Alligatorium</i>	?	b	?	?	-	-	?	?	?	?	?	t	?	?	-	?	?	?
Goniopholidae																		
<i>Amphicotylus</i>	l	mn	nh	c	-	-	?	+	+	15	d	f	+	-	-	+	-	+
<i>Eutreuranosuchus</i>	?	mn	?	?	-	-	?	+	?	18	d	f	?	+	-	+	?	?
<i>Goniopholis</i>	?	mn/b	nh	?	-	-	?	?	?	?	d	f	+	?	-	+	?	+
Paralligatoridae																		
<i>Paralligator</i>	l	b	nh	c	-	-	+	+	+	14	d	t	-	?	-	?	?	-
Bernissartiidae																		
<i>Bernissartia</i>	?	mn	?	?	-	-	?	+	?	19/20	d	?	?	+	-	?	?	?
Sebecosuchia																		
Baurusuchidae																		
<i>Baurusuchus</i>	d	n	nv	s	+	+	+	+	-	5	d	?	+	-	-	?	?	+
Sebecidae																		
<i>Sebecus</i>	d	n	nv	s	+	+	+	-	-	10/11	dl	f	-	-	-	+	-	+
Hsisosuchidae																		
<i>Hsisosuchus</i>	l	mn	?	?	+	+	+	+	-	9	dl	?	?	-	-	?	?	?
Eusuchia																		
Nettosuchidae																		
<i>Mourasuchus</i>	l	mn	nh	c	-	-	+	?	?	?	d	f	+	?	-	?	?	+
Crocodylinae																		
<i>Asiatosuchus</i>	?	b	nh	?	-	-	+	+	?	14	d	t	+	+	-	+	-	?
<i>Brachyuranochampsa</i>	?	mn	?	?	-	-	?	+	?	14	d	t	+	+	-	-	+	+

<i>Crocodylus</i>	l	n-b	nh	c/s	-	-	-	+	+	14/15	d	t	+	+	-	+	+/-	?	
<i>Kentisuchus</i>	l	n	?	?	-	?	-	+	-	15?	d	t	+	?	-	?	+	+	
<i>Leidyosuchus</i>	l	mn	nh	c	-	-	-	+	+	19/20	d	t	+	+	-	+	-	?	
<i>Navajosuchus</i>	l	b	nh	c	?	?	?	+	+	14/15	d	o	+	+	-	+	-	+	
<i>Orthogenysuchus</i>	?	mn	?	?	-	-	-	?	?	?	?	t	+	?	-	?	?	+	
Alligatorinae																			
<i>Albertochampsa</i>	l	b	nh	?	-	-	?	+	+	15	d	t	+	+	-	+	-	+	
<i>Alligator</i>	l	b	nh	c	-	-	+	+	+	12/14	d	t	+	+	-	+	-	+/-	
<i>Allognathosuchus</i>	l	b	nh	s	-	-	+	+	+	13	d	t	+	?	-	?	?	+	
<i>Brachychampsa</i>	?	b	?	?	-	-	+	+	?	14	d	t	+	+	-	?	-	+	
<i>Caiman</i>	l	mn/b	nh	c	-	-	+	+	+	12/15	d	t	+/-	+	-	+	-	+	
<i>Ceratosuchus</i>	?	b	?	?	-	-	+	+	?	14?	d	?	?	?	-	+	?	?	
<i>Diplocynodon</i>	l	b	nh	c	-	-	+	+	+	16/17	d	t	+	+	-	+	-	+	
<i>Hispanochampsa</i>	?	b	?	?	?	?	+	?	?	16	d	t	+	+	-	+	?	+	
<i>Melanosuchus</i>	l	b	nh	c	-	-	+	+	+	13	d	t	+	+	-	+	-	+	
<i>Osteolaemus</i>	l	b	nh	c	-	-	-	+	+	12/13	d	o/t	+	+	-	+	+/-	-	
<i>Paleosuchus</i>	md	mn/b	nv	c	-	-	+	+	+	14/15	d	t	+	+	-	+	-	+	
<i>Procaimanoidea</i>	?	b	?	?	-	-	+	+	?	13	?	t	+	+	-	+/-	-	+	
<i>Prodiplocynodon</i>	l	b	nh	?	-	-	?	+	+	13/14	d	?	?	+	-	?	?	?	
Thoracosaurinae																			
<i>Maroccosuchus</i>	?	mn	?	?	-	-	?	?	?	?	d	t	+	?	-	?	?	+	
Pristichampsinae																			
<i>Pristichampsus</i>	md	mn	nv	s	+	+	+	-	-	13/16	d	t	+	+	-	+	-	+	
Subfamily incertae sedis																			
<i>Quinkana</i>	md	b	nv	s	+	+	+	-	-	12	d	t	+	+	+	-	+	-	

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NOTE ADDED IN PROOF

An incomplete maxilla with two teeth *in situ* (QM F10771) was recently collected from "Glen Garland" Station. While generally agreeing with the maxilla of *Quinkana fortirostrum* in form and sculpture, and particularly in the presence of pits for the reception of the dentary teeth between the maxillary alveoli, this maxilla differs in alveolar form and orientation. This suggests either a second Pleistocene ziphodont taxon, or that *Q. fortirostrum* is quite variable in alveolar morphology. The "Glen Garland" ziphodont material, kindly brought to our attention by Mr D. Ree, occurs in association with *Megalania*, chelonian, macropod and diprotodontan material.

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