

CRANIAL MORPHOLOGY AND ECOLOGY AMONG PHYTOSAURS

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Abstract - Three morphologies of phytosaur skulls are present at each stage of phytosaur evolution: (1) slender snouted with homodont dentition, (2) moderately slender snouted with heterodont dentition and (3) massive snouted. These represent probable ecological vicars of the three morphologies of modern crocodylians, the piscivorous (e.g. Gavialis), the generalist feeder (e.g. Caiman) and the predatory (e.g., Crocodylus niloticus).

INTRODUCTION

When complete cranial material of phytosaurs was first discovered it was immediately apparent that they displayed many morphological similarities to crocodylians. Indeed, for about 25 years it was actually believed that phytosaurs represented primitive crocodiles (Huxley, 1875; McGregor, 1906). Given the gross similarities in cranial morphology many authors have compared various crocodylian taxa with phytosaurs (e.g., Camp, 1930; Colbert, 1947). Camp (1930) noted that larger snouted phytosaurs are similar in morphology to broad-snouted crocodylians while the slender snouted forms compared favorably with piscivorous gharials.

There is a large variation in phytosaur cranial morphology which is probably due to ontogenetic, sexual dimorphic and taxonomic factors (Camp, 1930; Colbert, 1947; Gregory, 1962). The purpose of this paper is to review briefly the main morphologies of phytosaur skulls and their possible ecological implications.

THREE MORPHOLOGIES OF PHYTOSAUR SKULLS

Collecting by the author for the New Mexico Museum of Natural History has revealed that phytosaur skull morphology is related to faunal and facies context. One collecting area is at Revuelto Creek in Quay County, eastern New Mexico (Hunt and Lucas, 1989) where a rich biota is preserved in the Norian Bull Canyon Formation. In Revuelto Creek the faunal and sedimentologic context indicate that the preserved fauna is much more terrestrial than is common in other Late Triassic red beds of the Southwest. Most phytosaur remains from this area appear to represent one taxon. In 1947, J. T. Gregory collected the first phytosaur skull from this area (Yale Peabody Museum 3293). This skull has been referred to Nicrosaurus or Rutiodon [Machaeroprotopus] gregorii by most authors (Gregory, 1972; Lucas et al., 1985; Parrish and Carpenter, 1986). However, although this skull has the massive proportions of gregorii from the lower Chinle, it has a temporal structure identical to

Nicrosaurus/Pseudopalatus (Ballew, 1989; Murry and Long, 1989) from the upper Chinle. A similarly massive snouted taxon (Brachysuchus) is known from strata older than the lower Chinle in the Dockum of Howard County, Texas (Case, 1929). If we examine these three faunal levels (Howard County, Dockum and equivalents; lower Chinle and equivalents; upper Chinle and equivalents), it is possible to distinguish three broad types of phytosaur skull morphology that occur at each "grade" of phytosaur evolution (Fig. 1):

1. A form with a slender, elongate snout with homodont dentition consisting of cylindrical, usually, non-serrated teeth.

2. A relatively slender snouted form with a more robust rostrum, usually surmounted by a crest, with heterodont dentition including slicing blade teeth.

3. A massive skulled form with heterodont dentition and a proportionally short snout.

THREE MORPHOLOGIES OF CROCODYLIAN SKULLS

Although caution should be exercised in reconstructing the ecology of an animal based on a modern analogue, the truly remarkable convergence between phytosaurs and crocodiles indicates that such a comparison should be examined.

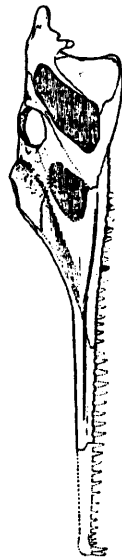
An interesting feature of modern crocodylian ecology is that "in each of the major areas of distribution there is a single large, dangerously predaceous.....species, and a number of freshwater dwellers that either feed on a general selection of smaller prey or which are piscivorous" (Dowling and Duellman, 1974, p. 118.2). There is much variation in modern crocodylian skull proportions (Fig. 2), but it is generally true that the large predaceous species (e.g., Crocodylus acutus, C. niloticus) have massive, moderately elongate snouts, the generalized feeders (e.g., Gavialis, Caiman) have broad, flattened snouts and the specialized piscivorous forms (e.g., Gavialis, Tomistoma) have narrow elongate snouts (Dowling and Duellman, 1974).

There are some obvious parallels between the three forms of crocodylian and phytosaur skulls (Figs. 1-2). The correspondence between the piscivorous crocodylians and the type 1 phytosaurs is obvious and has been noted before (e.g., Colbert, 1947). There is also a great similarity between the predatory crocodiles and the type 2 phytosaurs, also noted before (e.g., Camp, 1930). Type 2 skulls have elongate piscivorous-aspect snouts, but they are robust and contain a slicing dentition. The combination of these two features suggests that type-2-skulled animals were generalist feeders.

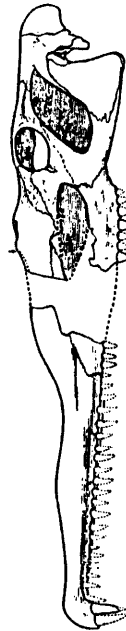
Thus it appears that the three ecomorphs of modern crocodylians had ecological vicars in the Late Triassic, with type 1 phytosaurs being dominantly piscivorous, like modern gharials, type 2 phytosaurs being generalist feeders like modern caimans and type 3 phytosaurs being more terrestrially predaceous like Nile crocodiles.

Intriguingly, although type 2 skulls do not resemble generalist crocodylians in gross skull form, there is a semi-aquatic group in the Late Triassic that does have a broad U-

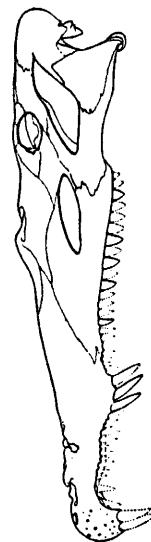
Type 1



Type 2



Type 3



Belodon buceros

Pseudopalatus

UPPER CHINLE: **pristinus**

**Revuelto Creek
taxon**

Rutiodon adamanensis

LOWER CHINLE: **Rutiodon zunii**

Rutiodon gregorii

LOWER DOCKUM: **Paleorhinus**

Angistorhinus

"Brachysuchus"

FIGURE 1. The three persistent morphologies of phytosaur skulls and examples of different ages (skulls after Camp, 1930).

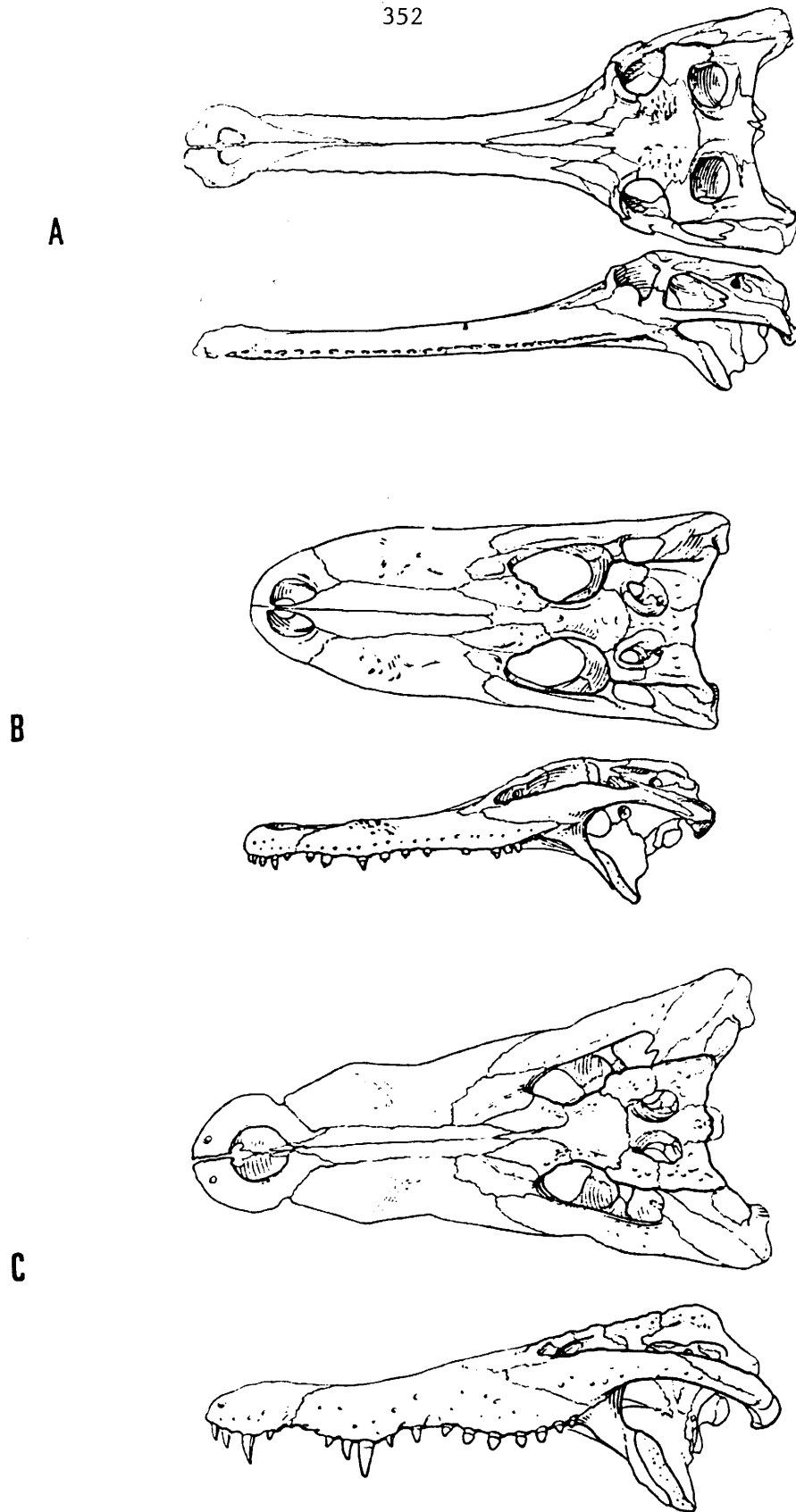


FIGURE 2. The three principal morphologies of modern crocodilian skulls, illustrated in dorsal and lateral view (from Mook, 1921). A, the piscivorous Gavialis. B, the generalist Alligator mississippiensis. C, The predaceous Crocodilus niloticus.

shaped skull analogous to a caiman, and that is the metoposaurs. Although metoposaurs had weak limbs and were presumably poor swimmers (Colbert and Imbrie, 1956), some generalist crocodiles have resting metabolic rates lower than chameleons and pursue very low energy foraging strategies (Coulson and Hernandez, 1983; Fitzgerald, 1988). Although faunal evidence from Revuelto Creek suggests that type 3 skulls were more terrestrial than other phytosaurs, which supports the above conclusions, caution must be applied in assessing the crocodylian analogue. Chatterjee (1978) described piscivorous-aspect phytosaurs with reptile remains in their stomach contents. Thus, three morphologies of phytosaur skull are present at all stages of phytosaur evolution. Comparison of these three morphologies with modern crocodylians suggests that they are analogous to the three ecomorphs of piscivorous, generalist and predatory forms.

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