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The Early Cretaceous Crocodylomorph *Hylaeochampsia vectiana* from the Wealden of the Isle of Wight

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ABSTRACT

Hylaeochampsia vectiana is the oldest known crocodylomorph with a eusuchian-type palate. We have had the holotype prepared further, clarifying an enigmatic feature but revealing several peculiarities. An opening in the palate previously considered to be either the suborbital fenestra or a foramen of unknown function actually comprises confluent alveoli for enlarged maxillary teeth. Although the incompletely preserved rostrum is constricted immediately anterior to the orbits, as in some longirostrine crocodylians, the missing portion was probably not elongate. The possession of a choana bordered anteriorly by the pterygoid indicates that *Hylaeochampsia vectiana* is a eusuchian, but other diagnostic eusuchian features are

not evident on the holotype. Three features may indicate *Hylaeochampsia vectiana* lies outside of the crocodylian crown group, but the conditions in the outgroups are unclear. Enlarged posterior crushing teeth may be a primitive feature of eusuchian crocodylomorphs, so that the presence of this feature in many alligatorids and in the extant *Osteolaemus tetraspis* appears to be plesiomorphic. The phylogeny of advanced neosuchians suggests that, during the course of their evolution, the movement of the choana posteriorly to a position within the pterygoids in Eusuchia was preceded by a posterior shift of the food-handling position in the mouth.

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INTRODUCTION

The Early Cretaceous *Hylaeochampsa vectiana* Owen, 1874, is of considerable interest to paleontologists as the oldest known crocodylomorph with a eusuchian-type palate. The holotype, a skull lacking the rostrum, was collected by the Rev. W. Fox from the Vectis Formation (Barremian) on the Isle of Wight. Although other specimens have been referred to this taxon, the type is today the only specimen that unquestionably pertains to this species, and the genus is monotypic.

Hylaeochampsa vectiana has been referred to the Eusuchia on the basis of its advanced palatal condition, with the choana bordered anteriorly by the pterygoids. The condition of other features is less clear in published descriptions and figures, and the holotype was, until recently, incompletely prepared. The original description by Owen is today the only detailed consideration of this taxon, supplemented by a brief discussion of the palate by Andrews (1913).

Although Mook (1934: 304) suggested that "its characters, together with its geologic horizon (Wealden), fit it admirably to serve as . . . ancestral to the later eusuchians," most authors have considered *Hylaeochampsa vectiana* too specialized to have been a eusuchian ancestor. These peculiarities, particularly an enigmatic opening in the palate, compelled some paleontologists to suggest that it evolved a eusuchian-type palate independent of Eusuchia (e.g., Buffetaut, 1975). A precise hypothesis of relationships, however, has never been offered.

The eusuchian palate is very similar to the plesiomorphic "mesosuchian" condition, differing only by the additional involvement of the pterygoids in the secondary palate. The functional morphology of the crocodylian secondary palate has received little attention, and the significance of the posterior shift that took place during the transition from neosuchians with the "mesosuchian" condition to those with the eusuchian condition has been virtually ignored.

We have had the holotype of *Hylaeochampsa vectiana* further prepared, exposing most of the sutures and revealing several remarkable features of the palate and braincase.

We provide a revised description of the specimen—concentrating on those characters that have proved to be useful in discovering the phylogenetic affinities of other neosuchian crocodylomorphs. A diagnosis based on apomorphic characters is also provided. We then discuss the phylogenetic relationships of this taxon, specifically addressing whether *Hylaeochampsa vectiana* is a member of the eusuchian clade and, if so, what its relationships are to other Eusuchia.

The Palatal "Foramen" of *Hylaeochampsa vectiana*

The palate of *Hylaeochampsa vectiana* has received much attention both for the posterior placement of its choana and for its peculiar arrangement of openings. Owen (1874) described two fenestrae lateral to the palatine beneath the orbit, separated by a process he believed to comprise parts of the pterygoid and palatine. He considered the lateral opening to be the suborbital fenestra, and he compared the medial fenestra with the interpterygoid vacuity of lizards (fig. 1a). Andrews (1913) reinterpreted the process separating the two openings: he considered it to be formed entirely by the ectopterygoid, and the lateral opening to be a foramen within the ectopterygoid (fig. 1b). He therefore interpreted the medial fenestra as the suborbital fenestra. This interpretation has been followed by subsequent authors (e.g., Kålin, 1955; Romer, 1956; Steel, 1973), and the idea that *Hylaeochampsa vectiana* is an aberrant form is based largely on the presence of this supposedly unique feature.

Preparation of the ectopterygoid "foramen" reveals that it is not so unusual. Rather than being a foramen, it is roofed dorsally by thin bone separating it from the orbit. Furthermore, although it has been previously illustrated as being widely separated from the dental alveoli of the maxilla (e.g., Andrews, 1913: fig. 1b), it is, in fact, juxtaposed with the posteriormost dental alveolus in the maxilla, and is separated from it only by a thin septum identical to the septum separating the two well-preserved alveoli. We therefore in-

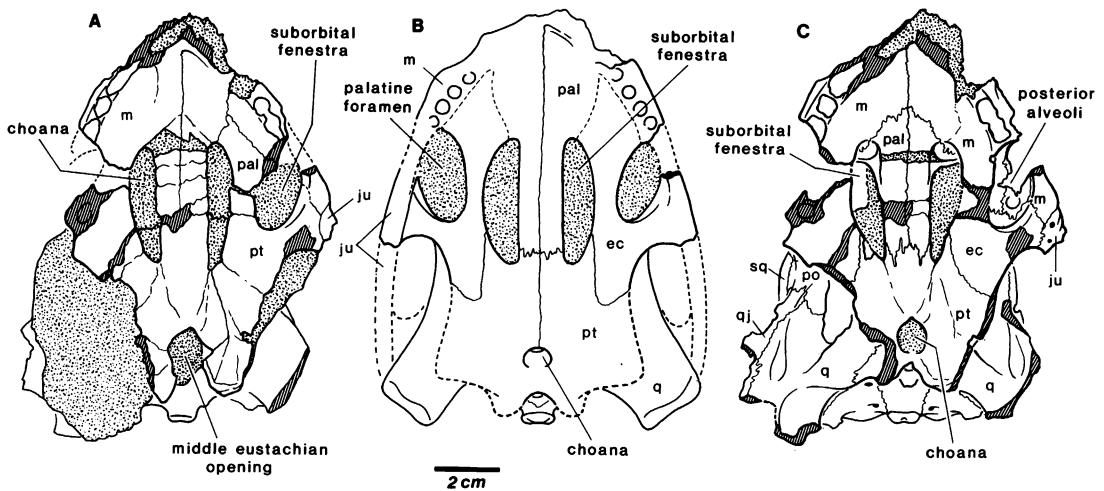


Fig. 1. The palate of *Hylaeochampsa vectiana* as interpreted by (A) Owen (1874), (B) Andrews (1913), and (C) Clark and Norell, this paper.

interpret this large depression as several confluent dental alveoli that housed greatly enlarged posterior maxillary teeth (fig. 1c).

The Status of *Heterosuchus valdensis*

A series of procoelous cervical and trunk vertebrae collected from beds roughly correlative with those from which *Hylaeochampsa vectiana* originated were designated the holotype of *Heterosuchus valdensis* Seeley, 1887, and the potential synonymy of the two taxa has been noted frequently (e.g., Lydekker, 1888; Romer, 1956; Steel, 1973; Carroll, 1988). The holotype of *Heterosuchus valdensis* is from the Hastings Sands of Hastings, Sussex, approximately 150 km from the type locality of *Hylaeochampsa vectiana*. A few fragmentary nonvertebral elements present in the hematite nodule containing the vertebrae have not been prepared and cannot be identified at present. Four isolated procoelous vertebrae from the Wealden of Cuckfield and Brook, England, were referred by Seeley to *Heterosuchus valdensis*.

The Hastings Sands are equivalent to the now subdivided Hastings Series and underlie the Weald Clays and Weald Marls (Anonymous, 1967). Only the Weald Marls and Clays (the upper part of the Weald series) are exposed on the Isle of Wight (Chatwin, 1960).

The holotypes of the two species therefore are not from precisely correlative strata, the Hastings Sands being slightly older than the Marls and Clays.

The synonymy of *Heterosuchus valdensis* with *Hylaeochampsa vectiana* rests upon the occurrence of the two taxa in roughly correlative beds and the expectation that a form with a eusuchian-type palate should have procoelous vertebrae. Because no elements are shared between the only known specimens of each species, the species cannot be synonymized with certainty (Buffetaut, 1983). It is unclear, furthermore, whether the vertebrae of *Heterosuchus valdensis* possess any characters diagnostic of a taxon more inclusive than Eusuchia, although the constriction of the centra noted by Seeley may prove to be diagnostic once appropriate comparisons are made. The possession of procoelous vertebrae is not by itself a sufficient basis for considering a taxon to be eusuchian (Norell and Clark, 1990), but the well-developed condyles on the trunk vertebrae indicate that if *Heterosuchus valdensis* is an advanced crocodylomorph (a neosuchian) then it is more closely related to the Eusuchia than is *Bernissartia*. Thus, we consider *Heterosuchus valdensis* to be a nomen dubium until unequivocal diagnostic features are delineated, and it cannot be synonymized with *Hylaeo-*

champsia vectiana until such characters are evident and a specimen is discovered with features diagnostic of both taxa.

Buffetaut (1983) has recorded the presence of another taxon with procoelous vertebrae, *Theriosuchus*, in the Wealden of the Isle of Wight, and he suggested that the isolated vertebrae ascribed to *Heterosuchus valdensis* may instead belong to *Theriosuchus*. We have not examined these vertebrae, but it should be possible to determine whether their condyles are prominent and their centra constricted, as in *Heterosuchus valdensis*, or whether instead they have low condyles and unconstricted centra as in *Theriosuchus*.

Abbreviations

Institutional

AMNH DH	Department of Herpetology, American Museum of Natural History
AMNH DVP	Department of Vertebrate Paleontology, American Museum of Natural History
BMNH	British Museum (Natural History), London
UCMP	University of California Museum of Paleontology, Berkeley, California
USNM VP	Vertebrate Paleontology, National Museum of Natural History, Washington, D.C.
USNM RA	Reptiles and Amphibians, National Museum of Natural History, Washington, D.C.

Anatomical

A	muscle scar A of Iordansky (1964)
B	paroccipital protuberance
ALV	alveolus
bo	basioccipital
bs	basisphenoid
cq	cranioquadrate passage
ect	ectopterygoid
eo	exoccipital
f	frontal
ju	jugal
la	lacrimal
LEUS	lateral eustachian opening
ls	laterosphenoid
m	maxilla
MEUS	median eustachian opening
n	nasal
p	parietal
pal	palatine
PCAR	posterior carotid foramen

po	postorbital
prf	prefrontal
pt	pterygoid
q	quadrate
qj	quadratojugal
soc	supraoccipital
SOF	suborbital fenestra
sq	squamosal
XII	hypoglossal foramina

SYSTEMATIC PALEONTOLOGY

EUSUCHIA HUXLEY, 1875

COMMENTS: We previously presented a revised diagnosis of the Eusuchia (Norell and Clark, 1990): (1) choana lies well within pterygoids positioned near their posterior ends; (2) trunk vertebrae procoelous, (3) cervical vertebrae procoelous (convergently evolved in *Theriosuchus*), (4) condyles on biconvex first caudal vertebra strongly convex, and (5) dorsal osteoderms lack smooth area anteriorly on dorsal surface where they imbricate. As we emphasized, however, many taxa of primitive Eusuchia cannot be assessed for all of these characters, including *Hylaeochampsia vectiana*. Only the first character is known to be present in this species.

FAMILY UNCERTAIN

The Hylaeochampsidae Andrews, 1913, was erected to include only *Hylaeochampsia vectiana*, because "the structure of the palate is so remarkable, and differs so widely from that found in the other Mesozoic crocodiles, and in some respects from the typical Eusuchia also, that it should certainly be placed in a distinct family" (p. 493). The only other taxon that has been included in this family, to our knowledge, is *Heterosuchus valdensis* (e.g., Williston, 1925), but if this species is distinct, and not synonymous with *Hylaeochampsia vectiana*, there is no evidence that the two species form a clade exclusive of other Eusuchia. The family is therefore monotypic; we consider monotypic taxa above the generic level to be uninformative, and therefore unnecessary (see de Queiroz and Gauthier, 1990).

Hylaeochampsia vectiana
Owen, 1874

HOLOTYPE: BMNH specimen R 177.

TYPE LOCALITY: Isle of Wight.

STRATIGRAPHIC OCCURRENCE: Vectis Formation, Barremian.

DIAGNOSIS: A eusuchian possessing the unique derived features of an extensive ectopterygoid bordering extremely broad posterior maxillary teeth and contacting the palatine anteriorly, a flat surface on the occipital faces of the quadrate and pterygoid, an unusually prominent process on the occipital surface of the paroccipital process medial to the cranioquadrate passage, a vertical posterior wall to the supratemporal fossa, a relatively long skull table with a narrow, elongate supratemporal fenestra, a posterior process of the jugal that is twisted dorso-medially around its longitudinal axis, a short distal portion of the quadrate, and an extremely broad prefrontal pillar. Uniquely possesses the combination of a preorbital constriction, enlarged posterior maxillary teeth, and an apparently short rostrum. Derived characters shared with some Eusuchia (but not necessarily synapomorphic)—prominent boss on ventral surface of quadrate (also in primitive alligatorids), lower temporal bar strongly arched dorsally, posterior ectopterygoid process absent (also in some crocodylids), and palatines very narrow between suborbital fenestrae (also in crocodylids).

REFERRED SPECIMENS: No additional specimens can be referred to this species with certainty. Some isolated teeth from near the type locality (Buffetaut and Ford, 1979) may belong to this taxon (see below), but an identification cannot be made with certainty.

DESCRIPTION OF THE HOLOTYPE

Preservation

The holotype (figs. 2–9) is generally well preserved but the bone is fragmented. Although most surfaces are smooth, in many places they have been fragmented and appear grainy. Most sutures are very clear, but some are difficult to distinguish from the many cracks in the bone. The braincase is nearly undistorted, but other parts of the skull have been affected by diagenetic compression. In particular, the rostrum has been compressed vertically and the right side of the skull has been dislocated dorsally.

Comparison of the specimen with the plates in Owen (1874) indicates that it has received minor damage subsequent to 1874. Glue-filled cracks demonstrate that the skull was at one time separated into large pieces, and the missing fragments may have been lost at this time. (The glue was removed and the skull pieces reglued during the recent preparation.) Dorsal to the foramen magnum, the medialmost part of the exoccipital is missing. A fragment is also missing from the left ectopterygoid between the suborbital fenestra and the enlarged dental alveoli.

General Shape

The skull table is nearly as long as it is wide, in contrast to the typical eusuchian condition where the skull table is significantly wider than long. The anterior corners of the skull table are rounded, as in *Bernissartia fagesii* (Norell and Clark, 1990), and the lateral edges are straight and parallel. The occipital (posterior) edge is gently sigmoidal due to the postoccipital processes of the supraoccipital.

Immediately anterior to the orbits, the rostrum is constricted, and the anterior part of the preserved portion of the maxilla is much narrower than the posterior part. This is reminiscent of the rostrum of the extant eusuchian *Gavialis* and the extinct primitive neosuchian *Pholidosaurus*, suggesting that it may have been elongate and tubular as in these taxa (as implied by Kålin, 1955: fig. 14). Several features of the skull, however, indicate that the rostrum was not elongate:

(1) Taxa that have an elongate rostrum typically have well-developed tubera on the basioccipital for the attachment of axial musculature (Langston, 1973). Tubera are entirely absent from the basioccipital of *Hylaeochampsia vectiana*, and the area of the basioccipital on which these muscles attached shows virtually no muscle scars.

(2) *Gavialis* and *Pholidosaurus* both have very broad skull tables with large, circular supratemporal fenestrae. The supratemporal fenestrae of *Hylaeochampsia vectiana* are smaller and longitudinally elongate, rather than circular, and the skull table is relatively narrow.

(3) Enlarged posterior teeth similar to those that occupied the posterior alveolus in *Hy-*

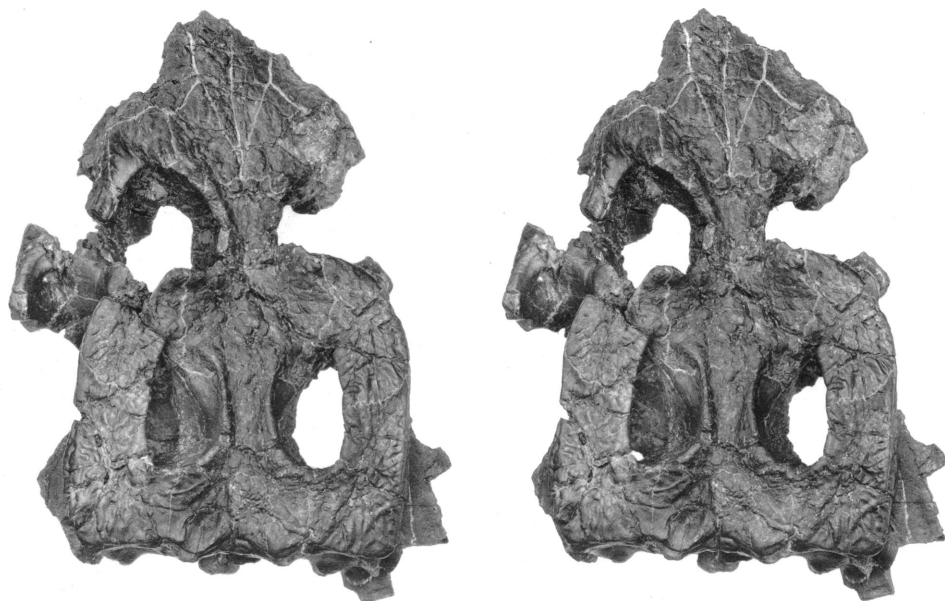


Fig. 2. Stereo pairs of the holotype of *Hylaeochampsa vectiana* Owen, 1874, in dorsal view.

laeochampsa vectiana are present in several taxa of neosuchians (e.g., primitive alligatorids and *Bernissartia*), and none have an elongate rostrum. Some thalattosuchians, such as *Machimosaurus hugii* (see Krebs, 1967), have bulbous teeth and a moderately long rostrum, but the dentition is homodont and the anterior teeth are not smaller than the posterior teeth.

(4) Longirostrine crocodylomorphs generally have elongate prefrontals and lacrimals, whereas those of *Hylaeochampsa vectiana* are distinctly short.

The rostrum of *Hylaeochampsa vectiana* therefore appears to have been both narrow and short, an unusual morphology among Crocodylomorpha. In other Crocodylomorpha with enlarged posterior crushing teeth, the posterior ends of the upper two tooth rows are broadly separated and nearly parallel. In *Hylaeochampsa vectiana*, however, the upper tooth rows converge below the constriction and, by extrapolation, were closely situated on the narrow rostrum anterior to the constriction.

Openings of the Skull

Both orbits are preserved, but their margins are damaged. Each orbit is nearly circular, though the lacrimal has a small indentation in its posterior margin. The orbit as preserved faces dorsolaterally but appears to have been oriented slightly more laterally before being vertically compressed. The maxilla and jugal form a broadly expanded region beneath the orbit, but unlike a similar expansion in *Gavialis*, that of *Hylaeochampsa vectiana* is concave rather than convex dorsally.

Each supratemporal fenestra is moderately large compared with that of other Eusuchia. It is elliptical with a parasagittal long axis. The medial edge of each fenestra is laterally concave and has an everted rim. Posteriorly the squamosal and parietal extend slightly over the fenestra and are continuous ventrally with the quadrate. Consequently, there is no shelf beneath the temporo-orbital foramen and the posterior wall of the supratemporal fenestra is smooth.

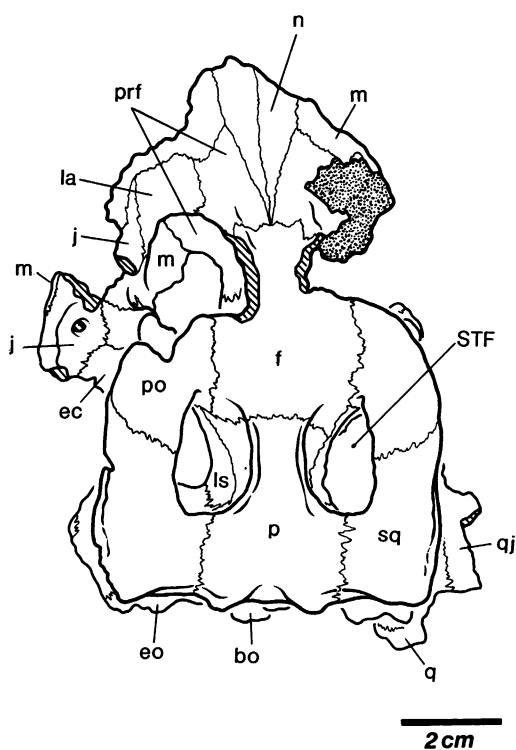


Fig. 3. Schematic drawing of the holotype of *Hylaeochampsia vectiana* Owen, 1874, in dorsal view corresponding to figure 2.

Most of the jugal is not preserved, and thus the shape of the lateral temporal fenestra is not entirely evident. It appears similar in shape to that of other Eusuchia and somewhat elongate, most like that of *Gavialis*.

The suborbital fenestra is very narrow due to the great breadth of the ectopterygoid and posterior maxillary teeth. It extends from directly beneath the anterior end of the orbit posteriorly to end nearly opposite the anterior end of the supratemporal fenestra. Its posterior end tapers strongly, but anteriorly the dorsal process of the palatine that meets the prefrontal forms a gently concave anterior border to the fenestra. The fenestra is about one-third as wide as it is long.

The small, circular choana lies entirely within the pterygoids. It is similar in size to that of some species of *Crocodylus* (e.g., *C. porosus*). There is no evidence for a median septum, and choanal labia are absent. The choana opens ventrally, rather than postero-ventrally as in many Eusuchia.

The posttemporal fenestrae are virtually closed, but this may be an artifact of dorso-ventral crushing. The postoccipital process of the supraoccipital forms a horizontal shelf beneath the fenestra, and this shelf extends posteriorly beyond the posterior edge of the parietal.

Bones of the Skull

The posteriormost part of each maxilla is preserved. It is highly modified to enclose the enlarged alveoli for the posteriormost teeth. The maxilla is nearly vertical anterior to the orbit, though this orientation has been diminished by compression. It contacts the nasal dorsally and the prefrontal and lacrimal posteriorly. It underlies the jugal beneath the orbit and contacts the ectopterygoid posteriorly on the palate. The maxilla forms the anteriormost preserved part of the secondary palate and contacts the palatine posteriorly.

The nasal tapers posteriorly and terminates opposite the anterior margin of the orbit. It apparently meets the frontal, but, as in some Eusuchia, the prefrontals have overgrown the frontal and meet dorsally posterior to the nasals along the midline.

The prefrontal is large with an upturned orbital edge continuous with the supraciliary rim of the frontal. The prefrontal tapers anteriorly and meets the nasal medially, the lacrimal laterally, the maxilla anterolaterally, and the frontal posteriorly. An extremely broad prefrontal pillar descends to meet the palatine directly dorsomedial to the enlarged posterior dental alveolus, but the two pillars do not appear to meet on the midline. The pillar forms a nearly complete anterior wall to the orbit, pierced only by a lateral opening ventral to the lacrimal.

The lacrimal is broad and short. The medial portion is more horizontally oriented than the lateral portion, and the change in attitude is marked by a slight indentation at the anterior angle of the orbit. The dorsal surface of the lacrimal anterior to this indentation is unsculpted and slightly depressed. The lacrimal is separated from the nasal by the prefrontal and rests ventrally on the jugal. The anterior contact with the maxilla is sigmoidal anteriorly. The lacrimal foramen is similar in size and position to that of other Eusuchia.

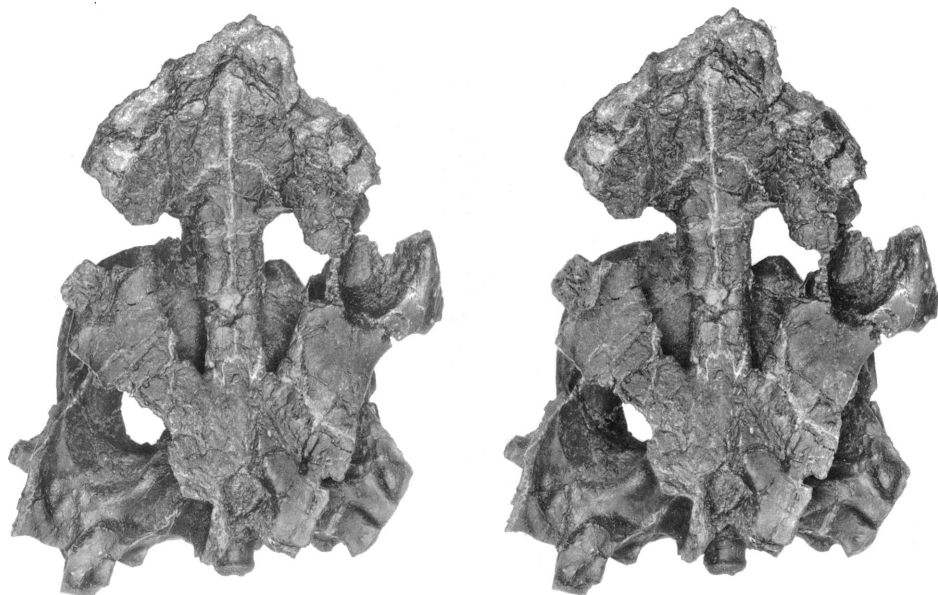


Fig. 4. Stereo pairs of the holotype of *Hylaeochampsia vectiana* Owen, 1874, in ventral view.

No antorbital fenestra is present between the lacrimal and maxilla.

The jugal is represented only by the anterior portion of the left element. It forms the ventrolateral portion of the massive postorbital bar and the ventral rim of the orbit. The postorbital bar is not inset from the jugal anteriorly, but it is distinctly inset posteriorly. Two foramina pierce the postorbital bar, one on the posterior surface of the jugal at the base of the bar, the other on the anterior surface of the bar at the contact between the jugal and postorbital. A thin process of the jugal extends anteriorly ventral to the lacrimal. The jugal turns upward immediately posterior to the postorbital bar and is twisted so that further posteriorly the medial surface becomes dorsomedially directed. This twisting suggests that the missing portion of the lower temporal bar was strongly arched dorsally. The jugal apparently forms a portion of the alveolar roof of the posterior maxillary teeth.

The quadrate is unusually short, extending a brief distance posteriorly beyond the occiput. Medially, the quadrate contacts the exoccipital and with it and the squamosal en-

closes the cranioquadrate passage. Anterior to the cranioquadrate canal, the quadrate forms a large dorsally projecting process. This process forms the anterior border of a passage leading medially into the canal. A small opening on the anterodorsal surface of the quadrate, just anterior to the otic notch, may be the siphonial opening. The small foramen aerum occurs at the contact between the quadrate and the exoccipital posterior to the cranioquadrate passage on the dorsal surface of the quadrate. Ventrally, the quadrate bears a large boss in a position corresponding to the middle of muscle scar "A" of Iordansky (1964). The oval boss parallels the long axis of the skull near the contact with the quadratojugal. Only a small part of the medial surface of the mandibular articulation is preserved. This surface is very flat and does not form a condyle, and is thus similar to the articulation surface of *Gavialis*. The quadrate contacts the pterygoid ventromedially, and the posterior edge of the quadrate forms a flat surface confluent with the occiput. Most contacts with bones of the braincase wall are not well displayed.

The incompletely preserved quadratojugal

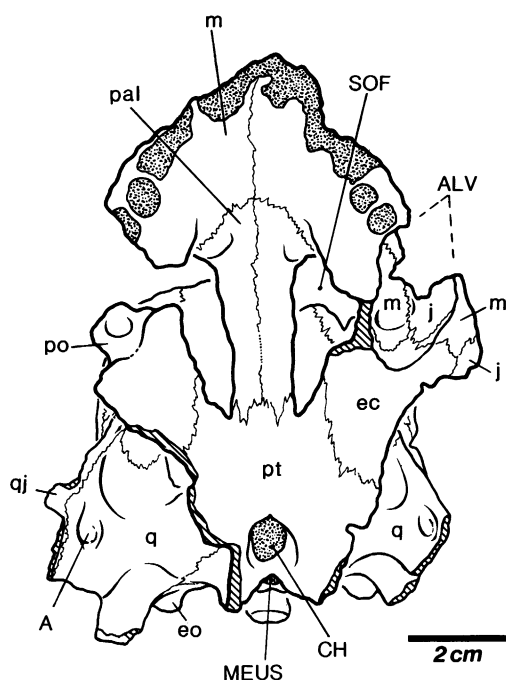


Fig. 5. Schematic drawing of the holotype of *Hylaeochampsia vectiana* Owen, 1874, in ventral view corresponding to figure 4.

is very broad ventrally but tapers dorsally to its contact with the postorbital and squamosal, isolating the quadrate from the infratemporal fenestra. The contact with the postorbital and squamosal is very strong, unlike the poorly developed contact in those extant crocodylians where these bones meet (e.g., alligatorids). The dorsal surface of the quadratojugal is broader than the ventral surface because its medial edge overlaps the lateral edge of the quadrate.

The postorbital is a large bone forming the rounded anterolateral corner of the skull table and most of the postorbital bar. The dorsal surface is flat with a gently convex anterolateral edge. Posteriorly, the postorbital extends midway along the length of the supratemporal fenestra. It contacts the quadratojugal posteroventrally, but a distinct postorbital process (as occurs, for example, in *Caiman*) descending to meet the quadratojugal is lacking. The postorbital meets the frontal medially along a parasagittal contact, and it contacts a tiny part of the parietal at the anterior border of the supratemporal fe-

nestra. The ventrally directed postorbital process contacts the ectopterygoid and jugal in the postorbital bar, which is massive and transversely compressed. The bar is inset from the skull table, and the dorsal part of the postorbital overhangs it. A short, prominent spine on the anterior edge of the dorsal part of the bar is comparable to that in *Gavialis gangeticus*.

The dorsal surface of the undivided frontal is transversely concave, forming raised supraciliary ridges dorsal to the orbits. The lateral edges of the frontal are not preserved, so the height of these ridges is undetermined. The frontal was, however, much narrower than in *Gavialis*. The frontal meets the parietal posteriorly between the anterior ends of the supratemporal fenestrae, the frontal forming the anterior $\frac{1}{4}$ of the medial border of each fenestra. The anterior contact between the frontal and the prefrontals is transverse. Cristae cranii are but weakly developed on the ventral surface of the frontal, being low and rounded rather than sharply ridged.

The undivided parietal plate forms the posterior boundary of the skull table but does not extend onto the occipital surface. Its posterior edge is indented on the midline and again laterally above the posttemporal fenestra. The suture between the parietal and the supraoccipital is indistinct, but a postparietal (dermosupraoccipital) is not apparent. Posterolaterally, the parietal meets the squamosals in a broad contact. The lateral edge bordering the supratemporal fenestra (the interfenestral bar) is concave, forming an everted rim around the fenestra. The parietal forms the vertical posteromedial wall of the supratemporal fenestra and borders the foramen for the temporo-orbital artery.

The squamosal forms the posterolateral corner of the skull table. Its dorsal surface is flat except where it forms the upturned posterior edge of the supratemporal fenestra. A slender process extends anteriorly lateral to the postorbital, reaching to a point above the postorbital bar. The groove on the lateral surface for attachment of the external ear musculature is poorly developed. The occipital portion of the squamosal is posteriorly convex, and the posterolateral process roofing the cranioquadrate passage is extremely short.



Fig. 6. Stereo pairs of the holotype of *Hylaeochampsia vectiana* Owen, 1874, in lateral views.

The squamosal is broad lateral to the supratemporal fenestra in comparison with that of other Eusuchia.

The supraoccipital, in posterior view, is much wider than tall. The ventral edge is broadly angular, not sharply triangular as in most other Eusuchia. Dorsolaterally, a postoccipital process protrudes from beneath each posttemporal fenestra. The dorsal surface of this process is nearly horizontal, rather than facing dorsolaterally as in most Eusuchia. The occipital surface is depressed along the midline, and there is no hint of a median nuchal crest dorsal to the foramen magnum. The bone is exposed dorsally as a smooth shelf posterior and slightly ventral to the posterior edge of the skull table. The dorsal surface of the supraoccipital is exposed on the left side beneath the parietal, where the parietal is broken, exposing the passage leading into the transverse canal. The supraoccipital apparently does not form a dorsal roof to the transverse canal.

The exoccipitals form most of the occipital surface. The two bones meet above the foramen magnum, where they form a nearly horizontal shelf with which the proatlas pre-

sumably articulated. The paroccipital process is unusually complex, bearing a large protuberance on its occipital surface medial to the entrance to the cranioquadrate canal. A broad ventrolateral projection of the exoccipital forms the ventral surface of the cranioquadrate canal. This ventrolateral process is much smaller than in primitive Mesoeucrocodylia, e.g., thalattosuchians, but is slightly larger than in all other Eusuchia. The most dorsolateral part of the paroccipital process curves dorsolaterally along its contact with the squamosal. The dorsal edge of the process is concave. Two hypoglossal foramina are present, the more posteromedial one being slightly the larger of the two. The foramen vagi is poorly preserved but lies immediately lateral to the hypoglossal foramina. The posterior carotid foramen enters the cranium at the base of the exoccipital, which is damaged near the occipital condyle, but apparently formed a small part of the condyle.

The basioccipital forms most of the small occipital condyle. The occipital condyle is slightly excavated at its center. A small midline ridge descends from the condyle, and basal tubera are absent. The ventralmost part

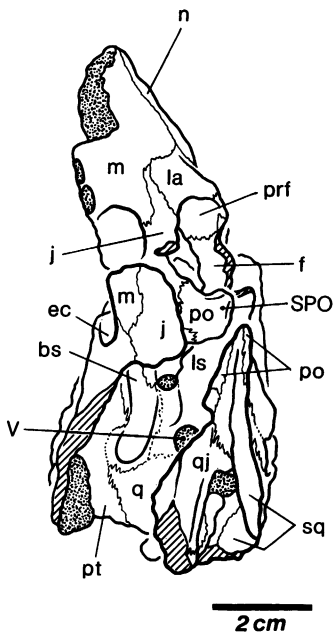


Fig. 7. Schematic drawing of the holotype of *Hylaeochampsia vectiana* Owen, 1874. Left lateral view corresponding to figure 6.

of the basioccipital is slightly concave where it roofs the entrance to the median eustachian opening. The basioccipital is covered laterally by the basisphenoid and pterygoid and is not exposed on the lateral wall of the braincase.

The position of the lateral eustachian openings is unclear. A depression in the ventrolateral edge of the basioccipital on the left side may lead to an opening, but a similar depression is lacking on the right side. Another possibility is a posterior opening between the exoccipital dorsomedially and the quadrate and the pterygoid ventrolaterally, immediately lateral to the carotid foramen, but this would be an unusually dorsal position for the eustachian opening.

Very little of the basisphenoid is exposed. Its entire ventral surface is covered by the pterygoid, but a slender portion is exposed on the occiput between the pterygoid and basioccipital. The basisphenoid rostrum is exposed anteriorly on the midline between the posterior ends of the orbits, but it is very poorly preserved.

The laterosphenoid forms the anterolateral

wall of the braincase. Most of the laterosphenoid is poorly preserved and most of its features and contacts are indistinct, but it appears to meet the quadrate posteriorly and the pterygoid ventrally. The paired bones meet broadly on the midline anteriorly. Each capitate process contacts the postorbital anterodorsally, where it lies within a fossa on the ventral surface of that bone. The cotylar crest is low and rounded and its ventralmost part is robust. The laterosphenoid forms the anterior edge of the trigeminal opening, and no trigeminal bridge is apparent. A small foramen, probably vascular, exits anteroventrally close to the middle of the anterior edge of the bone.

The prootic is not visible on the lateral braincase wall. The opisthotic is fused to the exoccipital on the occiput, and its otic portion is not exposed.

The palatines are very narrow with parallel sides. Posteriorly, the palatine contacts the pterygoid anterior to the end of the suborbital fenestra. It does not extend posterolaterally behind the fenestra and thus does not meet the ectopterygoid. Anteriorly, the palatine extends only a short distance beyond the suborbital fenestra. Its anterior contact with the maxilla is gently rounded in ventral view. The ventral surface of the palatine is slightly convex transversely, and its ventrolateral edge is gently rounded.

The ectopterygoid is extremely robust and forms the posterior margin of the enlarged dental alveoli. It contacts the postorbital dorsally and forms the ventromedial part of the postorbital bar. It extends anteriorly to meet the maxilla, but the contact between these two bones medial to the posteriormost dental alveoli is not preserved. The ectopterygoid forms the lateral edge of the incompletely preserved pterygoid flange medially but does not extend to the posterior end of the flange. The ectopterygoid does not extend posterior to the postorbital bar, and thus lacks the posterior jugal process present in many Eusuchia.

The pterygoid plate has a broad, flat ventral surface facing somewhat anteriorly. The paired bones appear to be fused posterior to the choana and, unlike in other Eusuchia, also appear to be fused anteriorly. The pterygoid extends dorsally to meet the quadrate,



Fig. 8. Stereo pairs of the holotype of *Hylaeochampsia vectiana* Owen, 1874, in occipital view.

and its posterior edge expands to form a flat surface confluent with the occiput. The pterygoid wings posterodorsal to the choana are large and robust. A midline notch lies between the wings posterior to the choana. The pterygoid is not depressed below the braincase as in alligatorids (Norell, 1989), so that the choana and median eustachian opening are at the same level. Anterior to the choana the pterygoid is flat, lacking a depression as occurs in some Eusuchia (e.g., *Osteolaemus tetraspis*). The pterygoid extends anteriorly to overlie the palatine dorsally, and it appears to contact the prefrontal pillar. The pterygoid flanges are incompletely preserved. A bulla is lacking on the dorsal surface of the pterygoid.

Dentition

Teeth are absent from the specimen, but alveoli for the posteriormost maxillary teeth are preserved. These comprise two distinct alveoli on each side anteriorly and a single large alveolus posteriorly. The large alveolus may have housed a single, large tooth, but more likely it housed several broad teeth. Although there are no septa within the alveolus indicating the presence of multiple teeth, it is not unusual in taxa with large posterior teeth for the septa between the most posterior teeth to be absent. The anterior alveoli lie entirely within the maxilla and are positioned opposite the anterior end of the palatine. Both are nearly circular in cross section. They are similar in size and shape to the maxillary alveoli of crocodylids, though the more posterior of the two is slightly larger than the other. The large posterior alveolus is formed

mainly by the maxilla, but the posterior and posterolateral edges are formed by the ectopterygoid, and the jugal forms a small part of the roof.

The posteriormost dentition undoubtedly comprised low, broad, crushing teeth. Because of their posterior position in the jaw and the correspondingly short distance between the upper and lower jaw at this point (even with the jaws maximally depressed), there is little doubt that these teeth were low-crowned. Judging from other Eusuchia in which the posterior teeth are extremely broad (e.g., the primitive alligatorid *Allognathosuchus*), the teeth within the large alveolus were undoubtedly bulbous, the morphotype that Buffetaut and Ford (1979) termed "tribodont." Comparisons of alveolar measurement in several Eusuchia are presented in figure 10.

Bulbous teeth of a kind that might be expected in *Hylaeochampsia vectiana* have been reported from the Wealden Formation near the type locality (Buffetaut and Ford, 1979). These teeth were identified as belonging to *Bernissartia* sp. indet., a genus otherwise known only from the Wealden of Belgium and the correlative Cerrada Roya locality in Spain (Buscalioni and Sanz, 1990). They are indeed similar to teeth of *Bernissartia fagesii*, but until the posterior teeth of *Hylaeochampsia vectiana* become known the possibility that some or all of these teeth are from this species cannot be ruled out. One tooth in particular (Buffetaut and Ford, 1979: fig. 2) is broader than any known teeth of *Bernissartia*. All of these teeth are smaller than those indicated by the alveoli on the *Hylaeochampsia vec-*

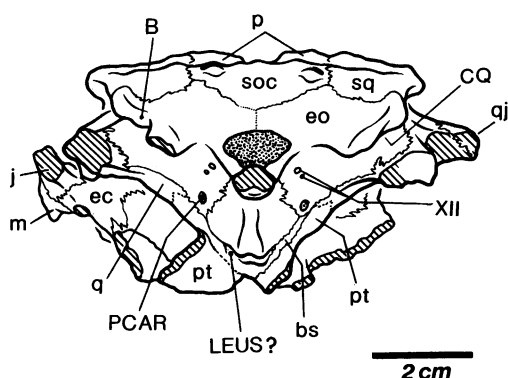


Fig. 9. Schematic drawing of the holotype of *Hylaeochampsa vectiana* Owen, 1874, in occipital view corresponding to figure 8.

tiana holotype, but they could be from smaller individuals.

DISCUSSION

Specializations of *Hylaeochampsa vectiana*

Our new interpretation of the palate of *Hylaeochampsa vectiana* reveals it to be less aberrant than was previously thought, but this species nevertheless possesses a large number of unusual features. Several of these features appear to be related to the enlarged posterior teeth, their presumed role in crushing prey, and the consequent high levels of stress the skull had to absorb during this process.

Enlarged posterior maxillary teeth are present in several advanced neosuchians, but the great breadth of the posteriormost alveoli of *Hylaeochampsa vectiana* is unmatched. The correspondingly large size of the ectopterygoid, which surrounds the alveoli and undoubtedly serves to reinforce the palate, is also unique among Crocodylomorpha. The unusually great extent of the prefrontal pillar may be related to the posterior crushing teeth. The pillar undoubtedly reinforces the rostrum against vertical compression and torsion, and its position directly dorsomedial to the enlarged teeth suggests that it resisted the forces incurred when prey were crushed between these teeth. The apparent fusion of the pterygoids anterior to the choana, if real, may also be related to reinforcing the palate.

The large process on the ventral surface of the quadrate in the position of tendon scar "A" may also be related to the enlarged posterior crushing teeth. Although nearly all Crocodylomorpha of which we are aware lack this process, a similar process is present on the quadrate of *Brachychampsa montana* (UCMP 133901), a primitive alligatorid with enlarged posterior crushing teeth. The A tendon is the origin for the middle part of the M. adductor posterior, which descends to insert on the floor of the mandibular adductor fossa of the mandible (Busbey, 1989). A clear functional interpretation for the large process on the quadrate of *Hylaeochampsa vectiana* is not obvious, however.

Other unique or unusual features of *Hylaeochampsa vectiana* include:

(1) The prominent boss on the dorsolateral part of the paroccipital process. In large specimens of some alligatorids, such as *Paleosuchus trigonatus* (USNM RA 300660) and *Alligator mississippiensis* (USNM RA 209862), this edge of the paroccipital process is turned posteriorly. In no specimen that we observed, however, is this boss so strongly developed as in *Hylaeochampsa vectiana*.

(2) The unusually long skull table, that, unlike those in other Eusuchia, is nearly as long as it is wide. A long skull table is present in thalattosuchians and dyrosaurs but is highly modified by extremely large supratemporal fenestrae.

(3) The unusually narrow supratemporal fossa and fenestra, and their nearly flat posterior wall. The supratemporal fossa and fenestra exhibit great variation in size and shape among Crocodylomorpha, but long, narrow fenestra and fossa are typically present only in juveniles where they are oriented obliquely, rather than parasagittally.

(4) The relatively extensive, flat occipital surface on the quadrate and pterygoid. In other Crocodylomorpha the pterygoid and quadrate thin posteriorly and have little or no exposure on the occiput.

(5) The twisted subtemporal portion of the jugal. We are unaware of other Crocodylomorpha with this feature.

(6) The unusually short distal portion of the quadrate. Primitive crocodyliforms, such as protosuchids, have short quadrates, but this condition is unusual among neosuchians.

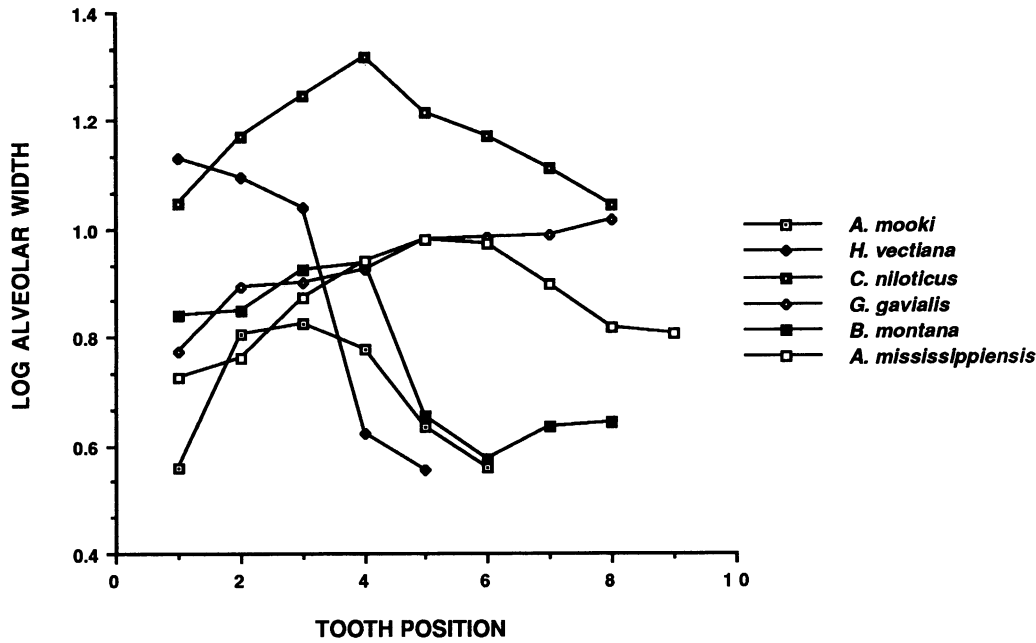


Fig. 10. Alveolar width in log-transformed mm (vertical axis) at sequential posterior tooth loci (horizontal axis) in *Hylaeochampsia vectiana* and several representative Eusuchia. The confluent alveoli of *Hylaeochampsia vectiana* are inferred to represent three loci. *Allognathosuchus mooki* (AMNH DVP 6780); *Alligator mississippiensis* (AMNH DVP 1106); *Brachychampsia montana* (AMNH DVP 5032); *Crocodylus niloticus* (AMNH DH 24714); *Gavialis gangeticus* (AMNH DH 15176); *Hylaeochampsia vectiana* (BMNH R 177).

(7) The apparently short yet constricted rostrum. This is unusual among Crocodylomorpha but, curiously, a similar rostrum is present in another neosuchian from the

Wealden of the Isle of Wight, the supposed goniopholidid *Vectisuchus leptognathus* Buffetaut and Hutt (1980). Among neosuchians with enlarged posterior teeth, *Hylaeochampsia vectiana* alone has a constricted rostrum.

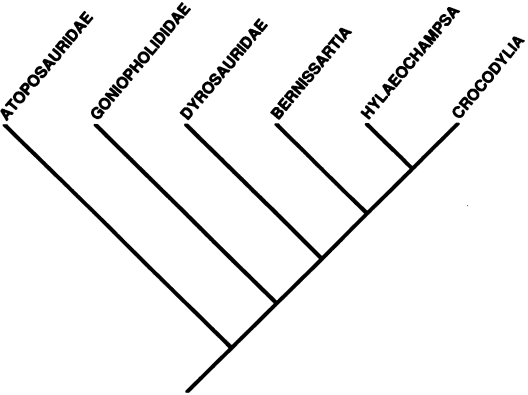


Fig. 11. Cladogram of relationships among advanced Neosuchia, from Norell and Clark (1990, fig. 3) with *Hylaeochampsia vectiana* added as discussed in the text.

Phylogenetic Relationships

Elsewhere we have presented phylogenetic analyses of Crocodylomorpha (Clark, in Benton and Clark, 1988) and advanced Neosuchia (Norell and Clark, 1990). The synapomorphy schemes resulting from those analyses are an appropriate starting point from which to begin to understand the phylogenetic relationships of *Hylaeochampsia vectiana*. Our phylogenetic analysis of advanced neosuchians involved 16 characters and 6 taxa, including the extant Crocodylia (treated as a single terminal taxon), *Leidyosuchus formidabilis*, *Bernissartia fagesii*, Dyrosauridae, Goniopholididae, and Atoposauridae. The analysis resulted in a single most parsimonious cladogram (fig. 11).

Hylaeochampsia vectiana can be scored for 4 of the 16 characters used in that analysis—(1) the choana is within the pterygoids, (2) an antorbital fenestra is absent, (3) the postorbital bar is inset from the dorsal part of the postorbital, and (4) the basisphenoid is not exposed ventrally between the pterygoid and basioccipital. Interpolating *Hylaeochampsia vectiana* into this scheme requires no homoplasy and places it within the Eusuchia: characters 2 and 4 indicate that it is more closely related to extant crocodylians than are atoposaurs, character 3 places it within the clade comprising *Bernissartia* and Eusuchia, and character 1 places it within Eusuchia. No features indicate that *Hylaeochampsia vectiana* is more closely related to any non-eusuchian clade than to the Eusuchia.

In addition to these four characters, a fifth character may also indicate that *Hylaeochampsia vectiana* is a member of the clade comprising *Bernissartia* and Eusuchia. Enlarged posterior teeth are present in *Bernissartia*, alligatorids primitively, the primitive crocodylid *Osteolaemus tetraspis*, and *Hylaeochampsia vectiana*. If three primitive Eusuchia without expanded posterior teeth but whose relationships are poorly understood—*Stomatosuchus inermis*, *Dolichochampsia minima*, and *Leidyosuchus formidabilis*—are not considered, then it is most parsimonious for this to be a synapomorphy of *Bernissartia* and Eusuchia. However, if they are considered then it is equally parsimonious either for *Bernissartia* and *Hylaeochampsia vectiana* to form a clade or for *Hylaeochampsia vectiana* to be more closely related to extant Crocodylia than it is to *Bernissartia*.

Three characters that were not considered in our previous analysis suggest that *Hylaeochampsia vectiana* lies outside of the crown group of extant Crocodylia. A crown group comprises the living members of a group and the descendants of their closest common ancestor (see de Queiroz and Gauthier, 1990). None of these characters, however, is unambiguous.

In our earlier analysis we did not consider the position of the frontoparietal suture relative to the supratemporal fenestra because it appears to be correlated with the size of the fenestra, which varies continuously among taxa of Crocodylomorpha. The relationships

between the frontal, postorbital, and parietal irrespective of the fenestra may not be correlated with the size of the fenestra, however. The frontal either extends posterolaterally between the postorbital and parietal, or else the postorbital contacts the parietal posterolateral to the frontal. The condition in *Hylaeochampsia vectiana* is somewhat intermediate, in that there is a small contact between the parietal and postorbital, but this contact is much more restricted than in forms (such as extant Crocodylia) with a broad contact.

The rounded anterolateral corner of its postorbital may also indicate that *Hylaeochampsia vectiana* lies outside the crocodylian crown group. The postorbital of *Bernissartia* has a similarly rounded corner, whereas in most extant Crocodylia the postorbital is squared off. The conditions in several outgroups are, however, unclear. In dyrosaurs the postorbital has a peculiar anterior process and is thus autapomorphic, but in some goniopholidids (Mook, 1942) and atoposaurs (Clark, 1986) the postorbital is squared off. Furthermore, in some extant crocodylians (e.g., *Crocodylus rhombifer*) the postorbital is somewhat rounded, and the character states are thus not discrete.

The firm suture between the quadratojugal and the postorbital and squamosal may also indicate a more primitive position for *Hylaeochampsia vectiana* within the Eusuchia. Primitively in crocodyliiforms the quadratojugal has a broad contact with the postorbital and squamosal (Clark, in Benton and Clark, 1988), and this feature is retained in primitive Metasuchia (e.g., *Araripesuchus*). This contrasts with the condition in extant Crocodylia, where the quadratojugal either (1) does not reach the postorbital, (2) briefly contacts a descending process of the postorbital (alligatorids), or (3) is inserted between the squamosal and postorbital. As in other Neosuchia, but unlike *Araripesuchus* and more primitive crocodyliiforms, the quadratojugal of *Hylaeochampsia vectiana* tapers dorsally, but its dorsal contact is much firmer than in extant Crocodylia. The condition in other primitive Eusuchia and eusuchian outgroups is poorly known, however, and a short descending process of the postorbital may be present in *Bernissartia* (Norell and Clark, 1990).

The larger size of the ventrolateral part of the exoccipital of *Hylaeochampsa vectiana* relative to other Eusuchia is reminiscent of the large size of this structure primitively in crocodyliforms (Clark, in Benton and Clark, 1988). It is not, however, as large as in non-metasuchian crocodyliforms. This part of the exoccipital is poorly known in goniopholidids, but the exoccipitals of dyrosaurids and *Bernissartia* (Buscalioni and Sanz, 1990) are similar to those of Eusuchia. This may indicate a more primitive position for *Hylaeochampsa vectiana* than is proposed here, but the four characters outlined above argue otherwise.

Several authors have suggested that *Hylaeochampsa vectiana* evolved a eusuchian-type palate independent of Eusuchia. An explicit treatment of this hypothesis, one that provides synapomorphies either of some other primitive Neosuchia with Eusuchia or of *Hylaeochampsa vectiana* with a noneusuchian clade, has not, however, been presented. Buffetaut (1975: 17) has given the most detailed exposition of this idea, and he presented two reasons for considering this species to be "le produit d'une évolution parallèle." First, he considered it to possess "caractères aberrants," specifically the enigmatic opening in the palate. Second, he considered the choana to be too far back in comparison with that of Late Cretaceous Eusuchia, which thus appear to be more plesiomorphic than *Hylaeochampsa vectiana*.

As outlined above, *Hylaeochampsa vectiana* is indeed aberrant in several respects, although our reinterpretation of the palatal opening makes it much less aberrant than was previously thought. Such autapomorphic specializations, however, offer no evidence regarding the relationships of *Hylaeochampsa vectiana* other than to indicate that it was not a direct ancestor of later Eusuchia.

The choana of *Hylaeochampsa vectiana* is indeed further posterior than the choanae of some Late Cretaceous Eusuchia, but the present evidence suggests that in at least one of these it is a secondary condition. The choanae of the taxa cited by Buffetaut—the alligatorid *Albertochampsa* and the primitive eusuchian *Leidyosuchus*—are further anterior than in *Hylaeochampsa vectiana*. Those of *Albertochampsa* and a related primitive al-

ligatorid, *Brachychampsa*, however, are unusually large, and their anterior extent is at least partly related to this overall expansion. Furthermore, the choanae of other Late Cretaceous Eusuchia—*Thoracosaurus neocesariensis* (USNM VP 72) and *Dolichochampsa minima* (Gasparini and Buffetaut, 1980)—are not as far anterior as in either *Leidyosuchus* or the primitive alligatorids. Finally, the choanae of gavialids are very far posterior, and there is some evidence suggesting that this family is the sister taxon to the remaining extant Eusuchia (Norell, 1989); at the least, this demonstrates that the evolution of choanal position within Eusuchia has not been simple.

Norell (1989) noted that among extant crocodylians only *Tomistoma schlegelii* and *Crocodylus* lack a posterior process of the ectopterygoid, and that the process is present on the ectopterygoids of *Bernissartia fagesii* and goniopholidids. He therefore concluded that the lack of a process is a derived character allying *T. schlegelii* with *Crocodylus*. The absence of this process in *Hylaeochampsa vectiana* does not invalidate this inference, but it does indicate that the evolution of this character was not so simple as previously supposed and that attention should be paid to the state of this character in other primitive Eusuchia.

Crushing teeth confined to the posterior end of the tooth row are known only among Eusuchia and their closest relatives, and the discovery that *Hylaeochampsa vectiana* possesses them strongly suggests that such teeth were present primitively in Eusuchia. Bulbous posterior teeth, termed tribodont by Buffetaut and Ford (1979), are present in *Bernissartia fagesii* and *Hylaeochampsa vectiana* as well as in primitive alligatorids and crocodylids. Many primitive alligatorids have such teeth, and they are present in a primitive taxon in this clade, *Brachychampsa montana* (UCMP 133901). Among crocodylids, tribodont teeth are present in the most primitive extant form, *Osteolaemus tetraspis* (Buffetaut and Ford, 1979), and in the primitive Eocene crocodylid "*Crocodylus*" *affinis* (Norell and Storrs, 1989).

In addition to the participation of the pterygoid in the secondary palate, two other features of the palate of Eusuchia stand out in

comparison with the palates of many "mesosuchians." First, the tooth row extends further posteriorly in the oral cavity in Eusuchia. In many primitive Mesoeucrocodylia the posterior end of the tooth row lies anterior to the orbit, and often the tooth row does not extend posteriorly to the end of the maxilla. Second, the ectopterygoid, which buttresses the pterygoid flanges, is much larger in Eusuchia than in many primitive Mesoeucrocodylia.

The relationships hypothesized above indicate that the evolutionary appearance of both of these features preceded the evolutionary appearance of pterygoid participation in the secondary palate. Dyrosaurids and *Bernissartia fagesii* both possess these two features, whereas the primitive conditions are present in goniopholidids and atoposaurids. The posterior movement of the tooth row strongly suggests that the evolutionary appearance of the eusuchian palate was preceded by a posterior shift in the posteriormost position within the mouth at which prey were processed between the closing jaws. This is self-evident if the posterior teeth were being used in prey capture and manipulation. Considering that the ectopterygoid braces the pterygoid flanges and the palate, its increased size is also consistent with this idea, suggesting that larger forces were (and in extant Eusuchia are) experienced by the posterior part of the palate.

The implications of the events preceding the appearance of the eusuchian palate regarding its adaptive significance are unclear. Two hypotheses for the function of the secondary palate in crocodylians (and mammals) have been posited. The first relates to the extension of the internal narial passage, which is separated from the oral cavity by the secondary palate. The separation of the narial passage from the oral cavity allows animals to breathe while prey is captured, and to open the mouth under water. In crocodylians this separation is accomplished by the urohyal valve at the posterior end of the mouth, comprising a fold of tissue descending from the palate anterior to the choana to meet a similar fold on the dorsum of the tongue. Although the function of this system has been alluded to often, we know of no detailed studies of this topic. The second hy-

pothesis (Langston, 1973; Thomason and Russell, 1986) suggests that the secondary palate functions primarily as a reinforcement against torsional forces met by the rostrum during prey capture.

Without detailed studies of the function of these structures in living crocodylians, and without an adequate understanding of their possible functions in the closest relatives of Eusuchia with mesosuchian-type palates, little can be inferred regarding the transition to the eusuchian condition. For example, it is critical to understand the position of the urohyal valve in *Bernissartia* and dyrosaurids, its relationship to maximum gape, and whether the maximum gape in these forms was comparable to that of Eusuchia. Until these can be ascertained it will not be possible to address which of the two hypotheses better explains the lengthening of the secondary palate during the transition to Eusuchia.

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