

## COMPARATIVE CRANIAL ANATOMY OF TWO NORTH AMERICAN CRETACEOUS PLESIOSAURS

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KENNETH CARPENTER

### INTRODUCTION

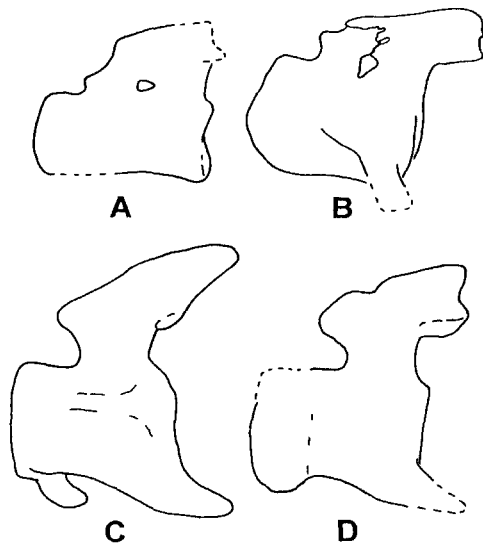
The taxonomy of Western Interior Cretaceous plesiosaurs is in disarray despite the efforts of Williston (1903, 1906, 1908) and Welles (1943, 1952, 1962). The problems are similar to those faced with English Jurassic plesiosaurs, including the inadequacy of type material, differential crushing, and skull-less skeletons. Nevertheless, revision of the English plesiosaurs has, in recent years, outpaced similar work in North America owing to the work of Storrs (Chapter 6), Taylor and Cruickshank (1993), Taylor (1992a), Brown (1981), and Tarlo (1960). Their revision of the plesiosaurs was made possible by the discovery of new specimens, advances in preparation, and new analytical techniques.

Perhaps the most fundamental change in the study of plesiosaurs, however, is philosophical, with the recognition that differences among specimens may not reflect taxonomic differences so much as individual variation, ontogeny, and sexual dimorphism. The significance of ontogenic change in plesiosaurs was best documented by Andrews (1910), who showed that the medial bar formed by the scapula and coracoid splits the coracoid foramen only in adult size. Thus, the presence or absence of this bar should not be used for taxonomic purposes. Even variation or dimorphism may be considerable among plesiosaurs, as briefly noted by Welles (1962) in his study of two specimens of *Aldzadasaurus columbiensis*. However, I differ from Welles in that I recognize the larger, more robust individual as a female because many female reptiles are two thirds to over twice longer than males, with one quarter to 15 times greater mass (Fitch, 1981).

1997. In Callaway, J.M., and Nicholls, E.L. (eds.)  
Ancient Marine Reptiles. Academic Press. p. 191-216.

Other advances in plesiosaur studies have occurred because of new preparation techniques (e.g., Taylor and Cruickshank, 1993; Cruickshank et al., 1991). These techniques were applied in the study of the uncrushed skull of "*Elasmosaurus*" *morgani* from the Cretaceous of North America. To avoid problems associated with differences between matrix and bone, the skull was first acid prepared before being CAT scanned and X-rayed. The skull was then compared with that of the short-necked plesiosaur *Dolichorhynchops osborni*, which also occurs in the marine Cretaceous of North America. The two skulls show similarities that may have evolutionary implications as noted below.

Welles (1949) referred "*E.*" *morgani* to *Elasmosaurus* primarily on the presence of a median pectoral bar, a condition first reported by Cope (1869). A historical account of the discovery of Cope's *Elasmosaurus platyurus* is presented by Almy (1987). Welles (1962) later used this median bar to define the subfamily Elasmosaurinae but, as noted above, this character may be ontogenetic. Indeed, the short and deep atlas-axis in "*E.*" *morgani* contrasts with the long and low one of *E. platyurus* (Figure 1). Welles (1952) noted that Cope's illustration of the pectoral girdles is probably not correct, but I consider the two versions given by Welles (1943, 1949) as unsubstantiated. Unfortunately, the girdles of *Elasmosaurus*



**Figure 1.** Comparison of the atlas-axis complex of A) *Elasmosaurus platyurus*, ANSP 10081; B) *Libonectes morgani*, SMUMP 69120; C) *Thalassomedon hanningtoni*, DMNH 1588; D) *Tuarangisaurus keysi* (after Wiffen and Moislsey, 1986; reversed). Not to scale.

*platyurus* are missing, as first reported by Williston (1906), and recent attempts to relocate them have failed (Arnold Lewis, personal communications). Until the holotype elements are found and their exact morphology is reexamined, I restrict the name, *Elasmosaurus platyurus* to the holotype specimen, ANSP 10081 (not ANSP 18001 as reported by Welles, 1952, 1962). This restriction, and the differences between atlas-axis complexes (Figure 1), leave the holotype "*Elasmosaurus*" *morgani* (SMUSMP 69120) in need of a generic name, for which *Libonectes* is proposed (Appendix 1).

The other plesiosaur, *Dolichorhynchops osborni*, was named by Williston in 1903 based on a nearly complete skeleton from the Smoky Hill Chalk of Kansas. Later, he (Williston, 1906, 1908) concluded that the genus was synonymous with *Trinacromerum* Cragin, 1888. However, differences between the two genera make this synonymy implausible (Carpenter, 1989; in preparation). A revised diagnosis for *Dolichorhynchops osborni* is presented in Appendix 1 based on additional specimens not available to Williston.

Cretaceous plesiosaurs from North America have been divided into three families, Pliosauridae, Polycotyliidae, and Elasmosauridae (Welles, 1962; Williston, 1907, 1908); Brown (1981), however, does not recognize Polycotyliidae. As will be shown elsewhere (Carpenter, in preparation), two families of short-necked plesiosaurs should be recognized in North America, as first noted by Williston (1907, 1908). Here, I elaborate on the skulls of the elasmosaurid *Libonectes morgani* (SMUSMP 69120) and the polycotyliid *Dolichorhynchops osborni* (holotype KUVV 1300, AMNH 5834, FHSM VP404, UCM 35059) as representatives of their two families.

#### Repository Abbreviations

The abbreviations used for the institutions referred to in the text are as follows: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum of Natural History, London; DMNH, Denver Museum of Natural History, Denver; FHSM, Fort Hays Sternberg Museum, Hays, Kansas; HMG, Hunterian Museum, Glasgow University, Glasgow; KUVV, Kansas University, Vertebrate Paleontology, Museum of Natural History, Lawrence; SDSM, South Dakota School of Mines, Rapid City; SMUSMP, Southern Methodist University, Shuler Museum of Paleontology, Dallas; and UCM, University of Colorado Museum, Boulder.

COMPARISON OF *LIBONECTES* AND *DOLICHORHYNCHOPS*

The skull of *Libonectes* is considerably shorter relative to its width than is the case in *Dolichorhynchops*. This difference is due to the proportionally shorter preorbital segment of the skull of *Libonectes* (compare Figure 2A and C and Figure 3A and C). As noted by Williston (1903, 1906), this difference correlates well with neck length and has been used to separate the two families (e.g., Persson, 1963). Comparative measurements of *Libonectes* and *Dolichorhynchops* are given in Table 1 and Figure 4.

The paired premaxillaries form the dorsal rim of the snout, including the anterior and dorsal margins of the external nares of both plesiosaurs (Figures 2C and 3B). They are large, wide bones in *Libonectes*, whereas they are long and slender in *Dolichorhynchops*. *Dolichorhynchops* has six premaxillary teeth and *Libonectes* has five. The first tooth is procumbent and large in both taxa. The rest of the tooth-bearing portion of the premaxilla is proportionally shorter relative to the total length of the premaxilla in *Dolichorhynchops* than in *Libonectes*. The dorsal process separates the frontals to contact the parietals above the orbits in both *Dolichorhynchops* and *Libonectes*. In the primitive elasmosaur *Brancaesaurus*, the frontals are apparently not separated (Wegner, 1914). However, this region is damaged, so the frontal premaxillary and frontal parietal contacts are equivocal. The suture between the orbits of *Libonectes* is unusual in that it is partially open, leaving a groove that extends posteriorly into the anteriormost portion of the parietals. Welles (1949) identified this groove as the pineal foramen, but it does not extend through the premaxilla. In addition, the only expansion in the dorsal part of the braincase that could have housed the pineal is located just in front of the supraoccipital (Figure 5D; see also below). In both *Libonectes* and *Dolichorhynchops*, the pineal foramen is closed dorsally, unlike *Brancaesaurus* Jurassic plesiosaurs (Brown, 1981; Wegner, 1914; Linder, 1913). Its loss is considered synapomorphic for the Upper Cretaceous elasmosaurids and polycotyliids. Ventrally, the premaxillaries in both animals are separated by the vomers, at the anterior end of which is a V-shaped slit here called the vomeronasal fenestra (Figures 2D and 3B), which is discussed further below.

The maxillaries are large bones and extend posterior of the orbits in both taxa. Laterally, the maxilla forms a portion of the external nares rim. The maxilla forms most of the lower rim of the orbit in *Dolichorhynchops* but only a small, anterior portion in *Libonectes*. Within the anterior edge of the orbit, the maxilla projects medially as a small, buttressed wall (Figures 5D and 6B). This wall marks the posterior limits of the nasal chamber formed by the premaxilla dorsally, the maxilla laterally and lateroventrally, and the vomer ventromedially. The lateral surface of the maxilla is pierced by numerous foramina, most likely for blood vessels and

nerves. The maxilla forms part of the rim of the internal nares in *Libonectes*.

The preorbital portion of the maxilla in *Dolichorhynchops* is considerably longer than in *Libonectes*. It holds about 29 teeth, to 14 in *Libonectes*. In both taxa, the teeth are large anteriorly, but become progressively smaller posteriorly. A row of irregular pits containing the tips of replacement teeth occur in a shallow groove medial to the teeth in *Libonectes* (Figure 2D).

The external nares are just anterior to the orbits in both *Libonectes* and *Dolichorhynchops* and are separated from them by the prefrontals (Figures 2C and 3A). In *Brancaesaurus* they are situated as they are in *Libonectes*; however, the external nares are proportionally smaller. The prefrontals are damaged in *Libonectes*, but form a small portion of the anterior edge of the orbits. In *Dolichorhynchops*, the prefrontals form most of the anterior edge.

The lachrymal is absent in both *Dolichorhynchops* and *Libonectes*. The presence of a lachrymal in plesiosaurs is problematical because the area in front of and above the orbits is usually damaged. Nevertheless, it was apparently absent in plesiosauroids, according to Andrews (1910) and Brown (1981), and alleged to be present in the pliosauroids *Peloneustes* and *Liopleurodon* (Taylor and Cruickshank, 1993; Andrews, 1913). Nicholls (personal communications) believes that the presence of the lachrymal in these two pliosauroids needs to be substantiated and questions their homology.

The nasals in plesiosaurs are also problematical because of the damage in front of the orbits. They were identified in "*Plesiosaurus*" *conybeari* by Sollas (1881), but it is more probable that they are prefrontals as in *Libonectes*. The element that Welles (1949) identified as the nasal is here reinterpreted to be the prefrontal. Storrs (1991) unites all plesiosaurs, except *Pistosaurus*, with the loss of this element; I accept it as a synapomorphy for all plesiosaurs above *Pistosaurus*.

The frontals in *Libonectes* and *Dolichorhynchops* are separated by the dorsal process of the premaxillaries (Figures 2C and 3A). Although incomplete in *Libonectes*, the frontals evidently formed the dorsal rim of the orbit. Medially, the frontals extend ventrally on each side of the premaxilla, forming a pair of partial walls inside the orbit (Figure 5D). In life, the cartilaginous internasal and interorbital septum extended from this wall to the top of the palate, as indicated by the scars on the bone surfaces. A gap between the two walls, the olfactory sulcus, probably housed the olfactory (I) nerve.

The frontals in *Dolichorhynchops* have a wing-like process that extends dorsally over the orbit. An oval fenestra, or frontal fenestra, is present in the frontal at its suture with the premaxilla (Figure 6A). The frontals extend posteriorly to contact the parietals. Lateral to this posterior portion of the frontal is a narrow strip of bone that may be a supraorbital. It is present in *Trinacromerum*, but apparently not in elasmosaurs.

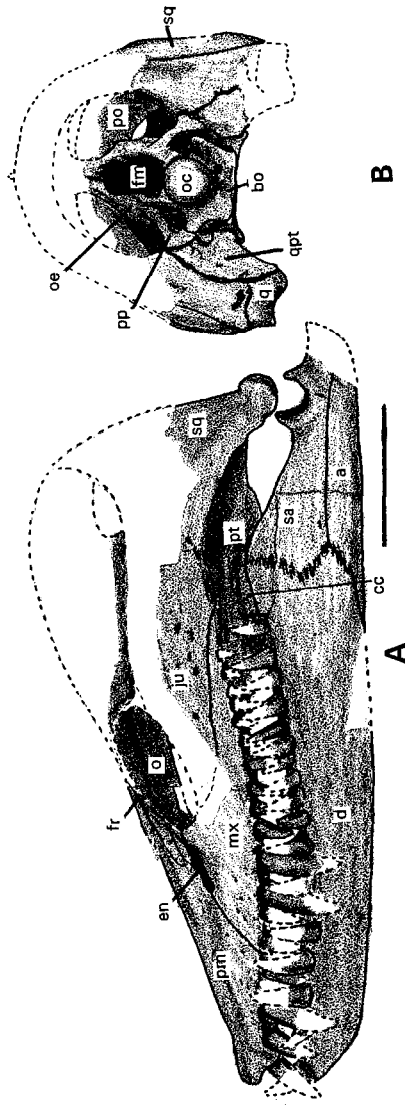


Figure 2. Skull of *Libonectes morgani*, SMUSMP 69120. A) Left lateral view. B) Posterior aspect. Abbreviations in Appendix 2. Scale bar = 10 cm.

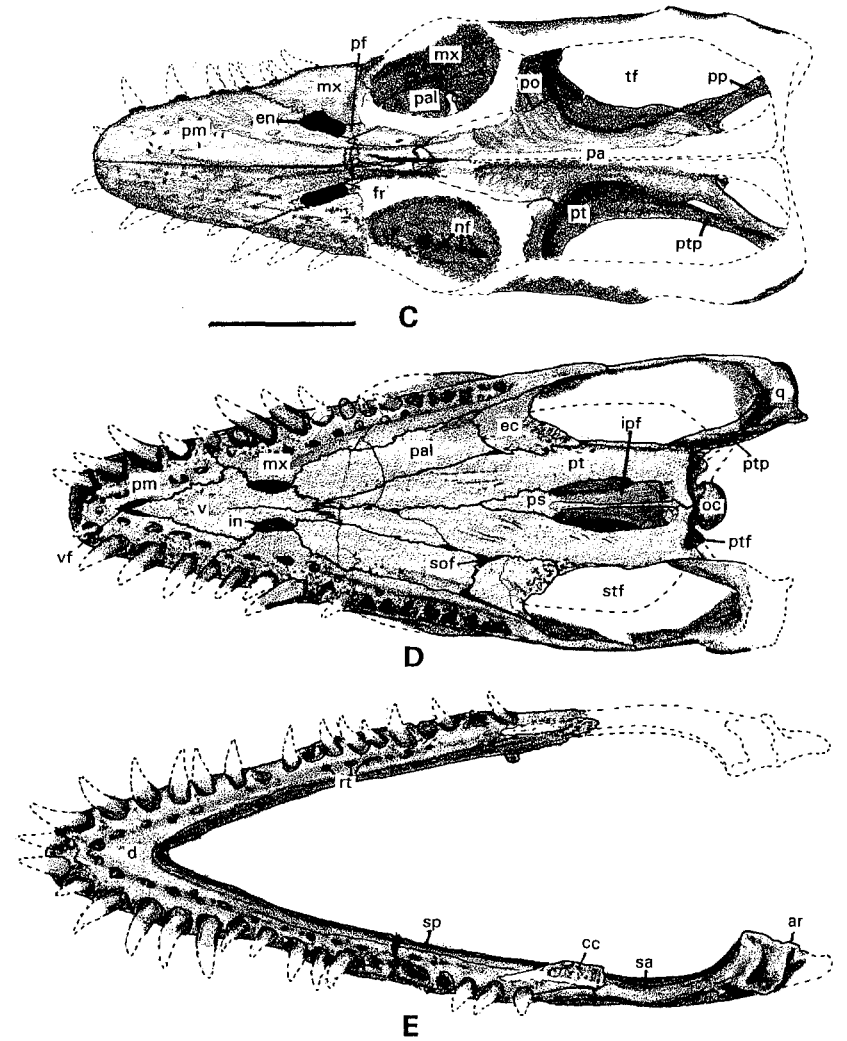
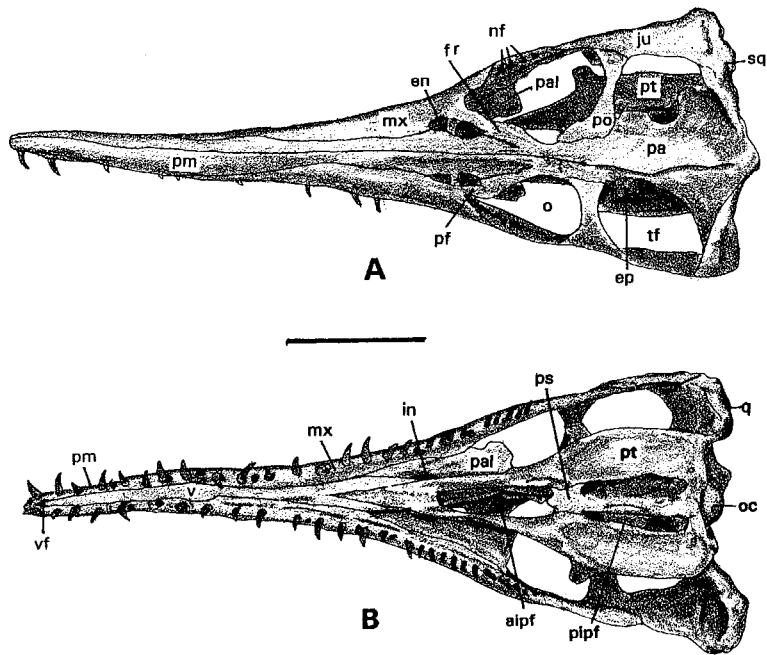


Figure 2 (continued). Skull of *Libonectes morgani*, SMUSMP 69120. C) Dorsal aspect. D) Ventral aspect. E) Dorsal view of mandible. Abbreviations in Appendix 2. Scale bar = 10 cm.

In both *Libonectes* and *Dolichorhynchops*, the postorbital contacts the parietal dorsally and the jugal ventrally (Figures 5B and 6A). In addition, the postorbital contacts the supraorbital in *Dolichorhynchops*. The postorbital forms the rear wall

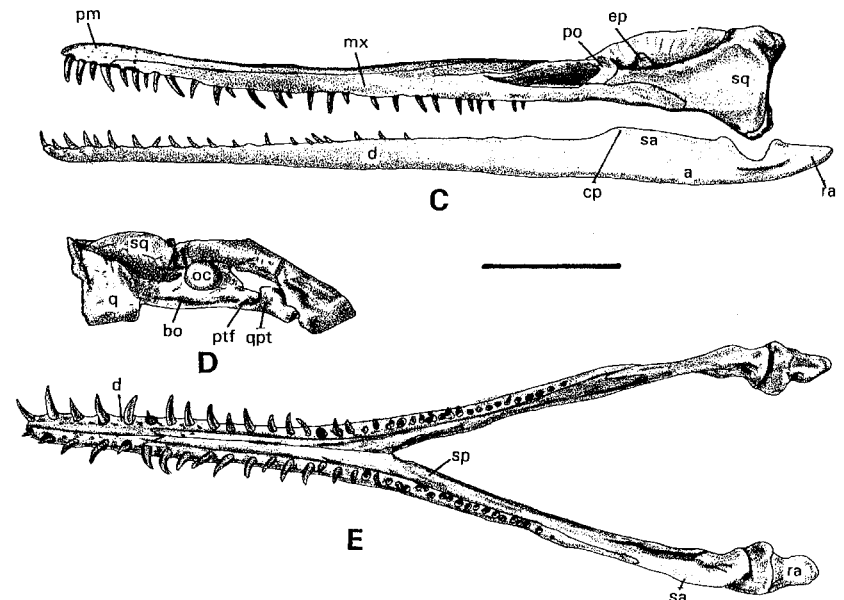


**Figure 3.** Skull of *Dolichorhynchops osborni*, FHSMP VP404. **A)** Dorsal aspect. **B)** Ventral aspect. Abbreviations in Appendix 2. Scale bar = 10 cm.

of the orbit to protect the eyeball from the pseudotemporalis muscle. The thinness of the bone makes them easily damaged, as has happened in *Libonectes* since additional preparation was done.

The jugals are not complete in the holotype of *Libonectes* but they apparently formed most of the lower edge of the orbits as in *Styxosaurus* and *Thalassomedon* (Carpenter, in preparation). In *Dolichorhynchops*, they formed only a small portion of the rear edge (Figure 6A). The jugals in *Libonectes* and *Dolichorhynchops* probably excluded contact between the postorbital and squamosal as in *Styxosaurus* and *Thalassomedon* (Carpenter, in preparation; Figure 6). The sutural contact of the jugal with the squamosal is unknown in *Libonectes*, but in *Styxosaurus* it almost divides the temporal bar obliquely in half (Williston, 1903).

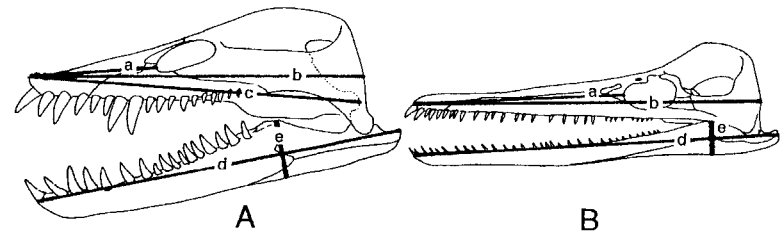
The quadratojugal is not present in either taxon, contrary to Welles (1949). Its presence in other plesiosaurs as advocated by Welles (1943, 1949, 1952, 1962) is unsubstantiated. As early as 1881, the existence of the quadratojugal was questioned by Sollas, but Andrews (1896) suggested that it was fused to the



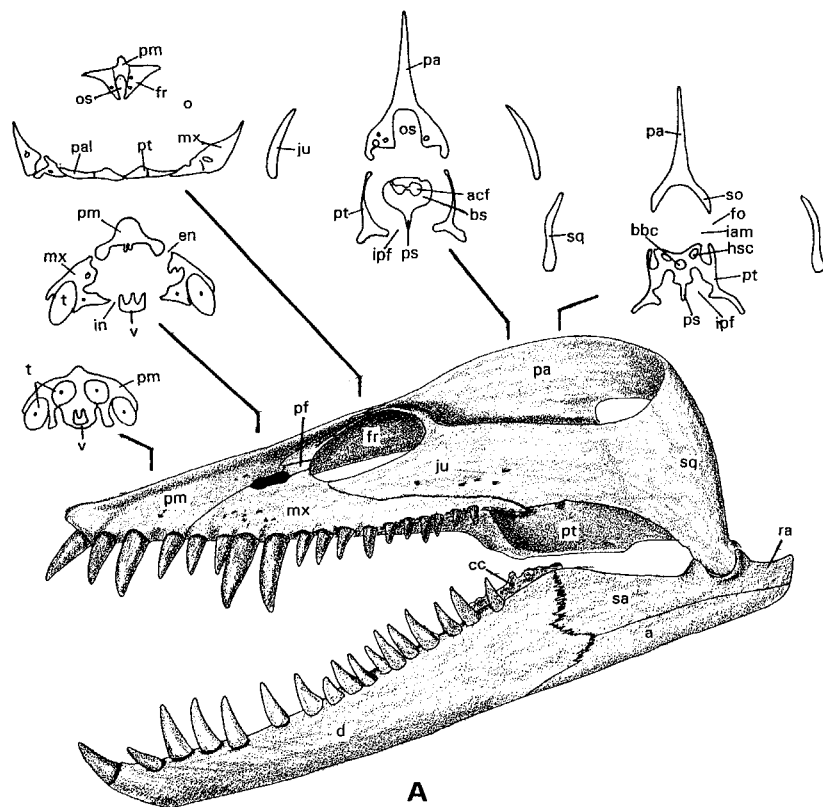
**Figure 3 (continued).** Skull of *Dolichorhynchops osborni*, FHSMP VP404. **C)** Left lateral view. **D)** Posterior aspect. **E)** Dorsal view of mandible. Abbreviations in Appendix 2. Scale bar = 10 cm.

**Table 1.** Cranial comparative measurements (in cm) of *Dolichorhynchops* and *Libonectes* (see Figure 4 for location of measurements).

	a	b	c	d	e
<i>Libonectes</i> (SMUSMP 69120)	18	45.9	46.6	-	7
<i>Dolichorhynchops</i> (FHSMP VP404)	32	51.3	-	56.2	4



**Figure 4.** Locations for measurements in Table 1. **A)** *Libonectes*. **B)** *Dolichorhynchops*.

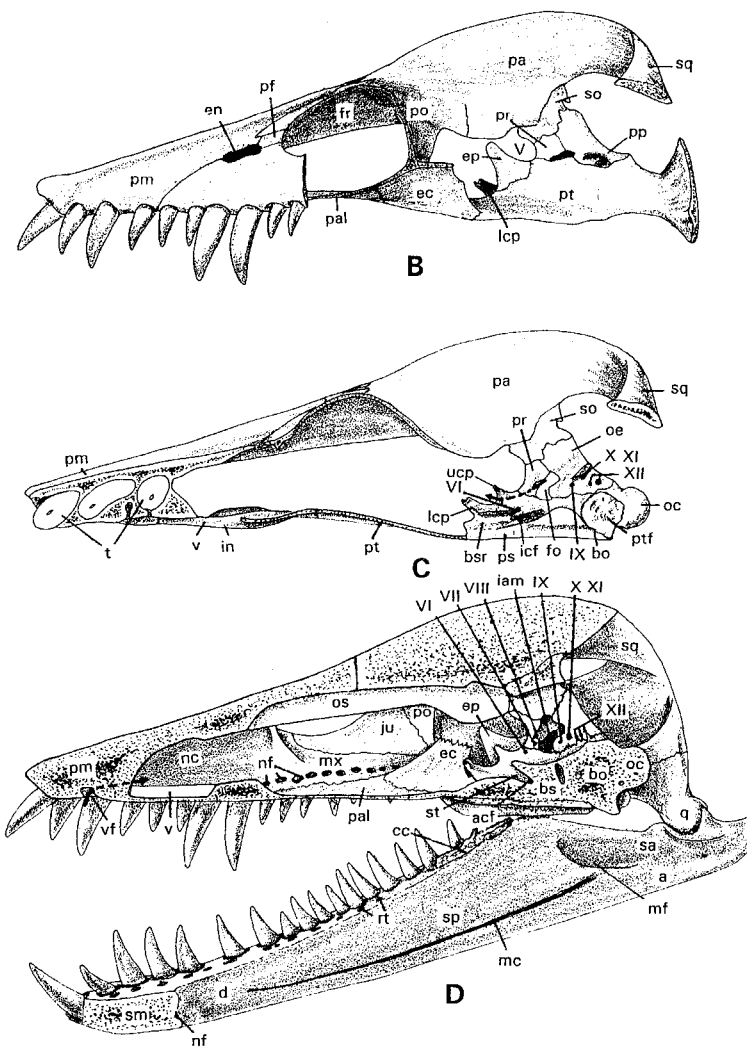


**Figure 5.** Skull of *Libonectes morgani*, SMUMP 69120. **A)** Lateral reconstruction with cross sections from CAT scans. Abbreviations in Appendix 2.

quadrate. More recently, Storrs (1991) considered its loss linked to the elimination of the diapsid lower temporal bar, a character uniting the Sauropterygia. This is the view supported here.

The squamosal is a large element in both *Libonectes* and *Dolichorhynchops* (Figures 5A and 6A), where it forms the posterior wall and part of the lateral wall of the temporal fenestra. The squamosal extends posteriorly beyond the occipital condyle in *Libonectes*; thus, the temporal fenestra is elongated compared to that in *Dolichorhynchops*.

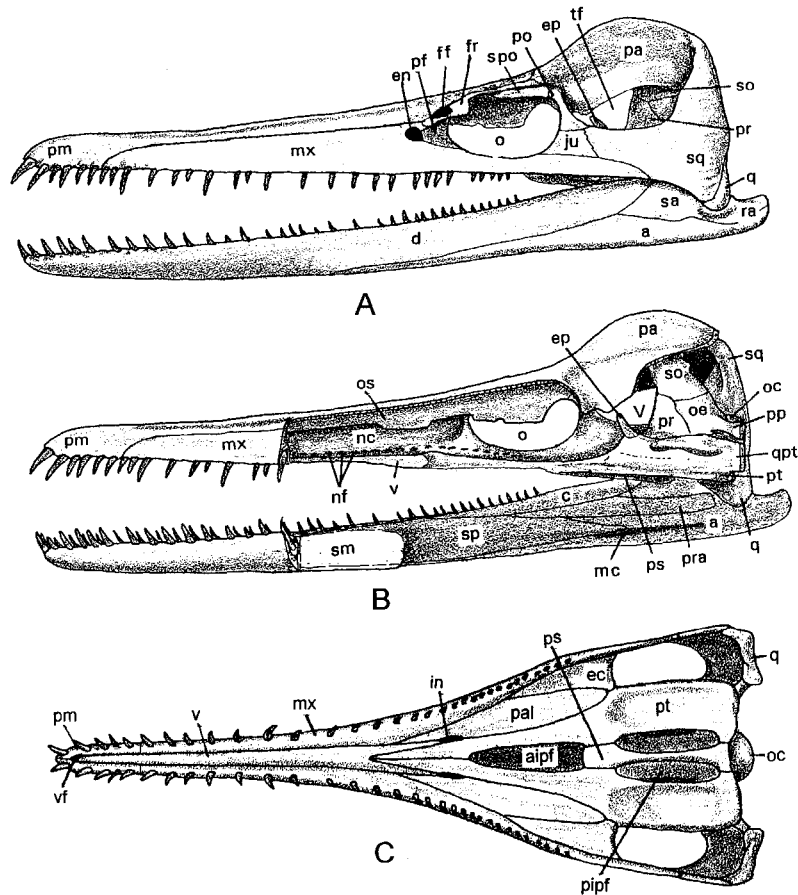
The quadrate of *Libonectes* and *Dolichorhynchops* is short and wide (Figures 2B and 3D). It articulates laterally and dorsally to the squamosal, and medially to the quadrate process of the pterygoid. In *Dolichorhynchops* the points of



**Figure 5 (continued).** Skull of *Libonectes morgani*, SMUMP 69120. **B)** With postorbital section of skull removed. **C)** With side of skull removed exposing braincase. **D)** Sagittal section showing interior of braincase and internal view of right side of skull. Abbreviations in Appendix 2.

articulation with the squamosal and pterygoid processes are shallow fossae, or sockets in the quadrate.

The highest point on the skulls of *Libonectes* and *Dolichorhynchops* is the



**Figure 6.** Composite reconstructed skull of *Dolichorhynchops osborni*. A) Left lateral view. B) With part of skull removed showing braincase. C) Palatal view. Abbreviations in Appendix 2.

parietal crest (Figures 5A and 6A), which rises more sharply relative to the face in *Dolichorhynchops* than in *Libonectes*; the crest is apparently not as tall in *Brancaesaurus*. Laterally, the parietals expand dorsally over the braincase and ventrolaterally down its sides (Figures 5B and 6B). In *Libonectes*, the parietals contact the sides of the supraoccipital, but they are separated a little in *Dolichorhynchops*.

On the palate, the vomers partially separate the left and right premaxillaries and maxillaries in both taxa (Figures 2D and 3B). At the anterior end of the vomer is

the vomeronasal fenestra, which opens dorsally into the nasal chamber. In life, a cartilaginous pocket in the anterior portion of the nasal chamber may have housed the Jacobson or vomeronasal organ. The presence of the vomeronasal organ for underwater olfaction in plesiosaurs was suspected by Cruickshank et al. (1991). The vomeronasal organ is present primitively in many tetrapods, including the most primitive plesiosaur, *Pistosaurus* (Meyer, 1855), but apparently was lost in the earliest plesiosaurs because it is absent in Jurassic plesiosaurs such as *Muraenosaurus*, *Pelonosteus*, *Liopleurodon ferox*, and *P. brachyspondylus* (Taylor and Cruickshank, 1993; Linder, 1913; Andrews, 1910, 1913; also *Plesiosaurus dolichodeirus*, Storrs, personal communications). Its "reappearance" in the advanced elasmosaurs and polycotyliids is believed to be synapomorphic, as is discussed below.

Dorsally on the vomer of *Libonectes*, a thin sheet of bone extends from the premaxilla, dividing the anteriormost portion of the nasal chamber (Figure 5D). In life, this sheet of bone would have separated the two vomeronasal organs. Where the vomer forms the medial edge of the internal nares, three low ridges are present on the dorsal surface. Posteriorly, the vomers contact the palatines and anterior tips of the pterygoids.

The palatines are large, subrectangular sheets of bone in *Libonectes*, but triangular sheets in *Dolichorhynchops* (Figures 2D and 3B). They barely contact the internal nares in *Libonectes*, but form the lateral margins in *Dolichorhynchops*. In *Libonectes* a small fenestra, believed to be the remnant of the suborbital fenestra, is present at the juncture of the palatines, ectopterygoids, and pterygoids. The size of the two fenestra is not the same, indicating that the structure is variable in elasmosaurs. No such fenestra is present in *Dolichorhynchops* (Carpenter, in preparation).

Posterior to the palatines are the ectopterygoids (Figure 2C). These are somewhat C-shaped in *Libonectes*, but triangular in *Dolichorhynchops* (missing in the illustrated specimen, but known from the holotype KUVF 1300 and UCM 35059). In *Libonectes*, a small, triangular scar extends onto the pterygoids adjacent to the subtemporal fenestra, and it may have been formed by pterygoideus muscle. Dorsally, the ectopterygoids brace the postorbital-temporal fenestra bar, transferring stresses generated against the palate upward around the sides of the skull.

Medial to the ectopterygoids, long, slender pterygoids are present in both taxa (Figures 2D and 6B). Posteriorly, the pterygoids are plate-like structures that cover most of the posterior ventral part of the skull. They are partially separated from one another by the interpterygoid fenestra, which in turn is divided by a keel on the parasphenoid. Below the basioccipital, the pterygoids meet one another posterior to the parasphenoid keel. The pterygoids taper anteriorly into two wedges in *Libonectes*. In *Dolichorhynchops*, the pterygoids taper into two slender bars on each

side of the anterior interpterygoid fenestra. Anterior to this fenestra they expand and meet, forming the medial edge of the internal nares.

In *Libonectes*, a vertical process of the pterygoids extends up the sides of the basisphenoid and basiptyergoid, but is separated from them by a gap for the carotid artery and capitis vein. This process possibly prevented the temporalis muscle from impeding blood flow when the jaw closed. Posteriorly in *Dolichorhynchops* and *Libonectes*, this vertical process becomes the pterygoid process, articulating with the quadrate by a peg and socket (shallow fossa). The peg, developed in the pterygoid, is elongated dorsoventrally.

The epiptyergoid in *Libonectes* extends dorsally from the anterior dorsal edge of the vertical pterygoid process (Figure 5B). It is triangular and projects somewhat anteriorly, leaving an ovoid foramen posterodorsally for the trigemial (V) cranial nerve. In *Dolichorhynchops*, the epiptyergoid is a laterally compressed rod of bone that is situated lateral to the sella turcica (Figure 6B).

Anterior to the median keel that divides the interpterygoid fenestra, the parasphenoid expands to form a wedge between the pterygoids in *Libonectes*, and the posterior margin of the anterior interpterygoid fenestra in *Dolichorhynchops* (Figures 2D and 3B). Dorsally, the parasphenoid expands along the sides of the basioccipital and basisphenoid, forming the lower rim of a groove for the internal carotid.

The basioccipital forms the ventroposterior portion of the braincase in both taxa. The occipital condyle is spherical in *Dolichorhynchops*, and somewhat heart shaped in *Libonectes* (i.e., it is wider near the top than at the bottom; compare Figures 2B and 3D). A shallow groove rings the occipital condyle in *Libonectes*, forming a very small neck. The exoccipital-opisthotic in both taxa does not form part of the occipital condyle. This feature is shared with *Plesiosaurus dolichodeirus* (Owen, 1865:Plate 2), "*Plesiosaurus macrocephalus*" (Andrews, 1896), and the cryptoclidids *Muraenosaurus* and *Tricleidus* (Brown, 1981; Andrews, 1910). They do, however, contribute to the condyle in the pliosaurids (Andrews, 1913) and just barely in the cryptoclidid *Cryptoclidus* (Brown, 1981). Ventrally, the basitubera of *Libonectes* and *Dolichorhynchops* have been modified to form a facet to brace the pterygoid plates dorsally. A small anteroposteriorly ovoid fossa is present on the floor of the foramen magnum in *Libonectes*.

The basisphenoid is fused to the anterior of the basioccipital in both taxa. In *Libonectes*, however, fusion is not complete, leaving a cavity seen on the CAT scans (Figure 5A). The basisphenoid in both taxa is pierced laterally by the internal carotid foramen, which opens into the back of the sella turcica housing the pituitary (Figure 5D). The palatine artery and palatine nerve probably continued along the lateral surface of the basisphenoid beneath the pterygoid process.

The sella turcica opens anteroventrally to the dorsal surface of the basicranium.

The abducens (VI) foramen pierces the dorsal surface of the basisphenoid (floor of the braincase). In *Libonectes*, the lower cylindrical process is anterior and lateral to the sella turcica. It projects anterodorsally, ending in a small, grooved process that is aligned with a fenestra for the lateral head vein at the base of the upper cylindrical process. The fenestra opens dorsally in the prootic, just anterior to the fenestra ovalis. Most likely, the lateral head vein was supported by the grooved process of the lower cylindrical process. No such processes are known for *Dolichorhynchops*.

The braincase is a tube open at both ends in both taxa (Figure 7C and 7D). It is composed of the fused exoccipital-opisthotic posteriorly, the prootic anteriorly, and the supraoccipital dorsally (Figures 5C and 7A and B). As noted by Williston (1903), there is no trace of an alisphenoid or orbitosphenoid. The foramen magnum is taller than wide and slightly constricted at the supraoccipital-exoccipital-opisthotic suture (Figures 2B and 6B). The lateral surface of the braincase is pierced by the keyhole-shaped fenestra ovalis in *Libonectes* but this fenestra is partially blocked laterally by the vertical process of the pterygoid (compare Figure 5B and 5C). No stapes was found in *Libonectes* despite the exquisite preservation, including at least one hyoid. It is probable that none was present, in marked contrast to *Brachauchenius* (Williston, 1907) and *Rhomaleosaurus* (Taylor, 1992b). No stapes

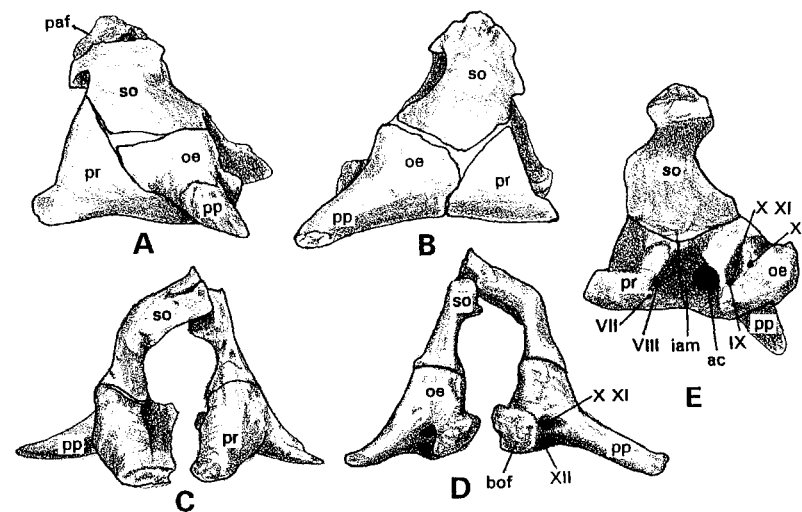


Figure 7. Braincase of *Dolichorhynchops osborni*, FHSM VP404. A) Left lateral view. B) Right lateral view. C) Anterior view. D) Posterior view. E) Medial view of right side. Abbreviations in Appendix 2.



was found in *Libonectes* despite the exquisite preservation, including at least one hyoid. It is probable that none was present, in marked contrast to *Brachauchenius* (Williston, 1907) and *Rhomaleosaurus* (Taylor, 1992b). No stapes is known for any specimen of *Dolichorhynchops* where the fenestra ovalis is closed (Figure 7A and B). Medially, the internal auditory meatus is a chamber or cavity developed primarily in the prootic and exoccipital-opisthotic in both taxa (Figures 5 and 7).

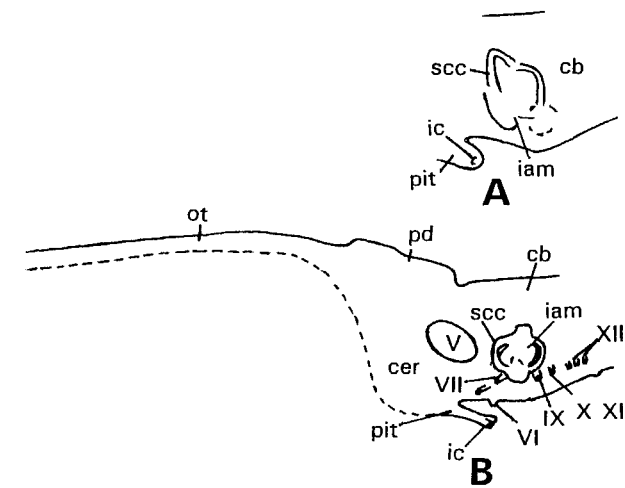
The exoccipital-opisthotic in *Libonectes* and *Dolichorhynchops* is pierced at the base of the paroccipital process by foramina for the vagus (X), accessory (XI), and hypoglossal (XII) nerves. These foramina open into the braincase posterior to the internal auditory meatus. Another foramen, for the glossopharyngeal (IX) nerve, pierces the exoccipital-opisthotic immediately ventral to the anterior edge of the paroccipital process. The posterior semicircular canal is contained mostly within the exoccipital-opisthotic. It opens into the internal auditory meatus in *Libonectes*, and indirectly through the acoustic chamber in *Dolichorhynchops*.

The paroccipital process extends laterally and braces the dorsal part of the quadrate process of the pterygoid in both *Libonectes* and *Dolichorhynchops* (Figure 2B). In life, the internal carotid and lateral head vein passed anteriorly, and the vagus and glossopharyngeal nerves passed posteriorly through the gap between the paroccipital process and the quadrate process of the pterygoid.

The prootic occurs above the sella turcica and anterior to the basisphenoid in *Libonectes* and *Dolichorhynchops*. In lateral view, it is a rectangular element in *Libonectes* (Figure 5D) and a triangular element in *Dolichorhynchops* (Figure 7). A foramen believed to be for the lateral head vein opens just anterior to the fenestra ovalis (see above). Medially, the facial (VII) foramen is present just anterior to the internal auditory meatus (Figure 5D). The anterior semicircular canal occupies the internal part of the prootic. In life, the trigeminal (V) nerve exited from the front of the prootic.

The supraoccipital roofs the braincase (Figures 5C and 7A and B). A short, rough process extends posteriorly over the foramen magnum for the nuchal ligament. Dorsally, the supraoccipital contacts the ventral surface of the parietal. This contact is more extensive in *Libonectes* than in *Dolichorhynchops*.

The only endocranial cast of a plesiosaur described is a partial one of the elasmosaur *Brancaesaurus brancai* (Hopson, 1979, figured by Edinger, 1928; Figure 8A). Owing to the uncrushed state of the *Libonectes morgani* braincase, a latex peel was taken (Figure 8B). The endocast is short and deep, with a slight flexure. The olfactory sulcus is not ossified ventrally, so the maximum thickness of the olfactory tract is unknown. It angles downward posterior to the level of the orbits. Dorsally, an enlargement beneath the parietal may house the remnants of the pineal as well as dura to suspend the brain. The cerebrum is large, although its anterior limit is not known because the front of the prootic is open. The pituitary is small and is



**Figure 8.** Comparison of the endocasts of A) *Brancaesaurus brancai* (from Edinger, 1928) and B) *Libonectes morgani*, SMUMP 69120. Abbreviations in Appendix 2.

slightly taller than wide. The two internal carotids are present at the end of the pituitary cast.

#### SIGNIFICANCE OF THE SIMILARITIES BETWEEN *LIBONECTES* AND *DOLICHORHYNCHOPS*

Although the differences between the elasmosaur *Libonectes* and the polycotyloid *Dolichorhynchops* seem most obvious and important, they are united by several synapomorphies that separate them from their Jurassic ancestors. In the past, phyletic relationships of the plesiosaurs were based primarily on postcranial features because skulls were typically missing or damaged (e.g., Welles, 1962; White, 1940). However, the postcrania are shaped by ecological needs, making their indiscriminate use suspect. For example, enlarged, plate-like pectoral and pelvic girdles have independently developed in aquatic reptiles, such as tangasaurid eosuchians (Currie, 1981). Others, such as the thalattosaurs, tanystrophids, and dolichosaurs (Carroll, 1988), have elongate necks, and still others have reduced metapodials relative to the propodial (e.g., metriorhynchid crocodiles, mosasaurs, and ichthyosaurs; Carroll, 1988). The result is that the postcrania within each group, including plesiosaurs, are conservative throughout their evolution.

The skull is thought to be less affected by ecological parameters, other than the

elongation of the snout that has occurred independently among several reptile groups (e.g., mesosaurs, thalattosaurs, champsosaurs, pleurosaurs, aigialosaurs, mosasaurs, ichthyosaurs, phtyosaurs, and various crocodiles; Carroll, 1988). The utility of cranial features was demonstrated by Russell (1967), who used cranial features in his discussion of mosasaur-aigialosaur relations. Carroll (1988) also used cranial features to link the aquatic pleurosaurs with the sphenodontids.

In *Libonectes* and *Dolichorhynchops*, the synapomorphic cranial features include the presence of a vomeronasal fenestra, expansion of the pterygoids into plates beneath the braincase, and loss of both the pineal foramen and stapes.

An oval opening at the suture between the premaxilla and vomer in *Pistosaurus* is probably the vomeronasal fenestra (Meyer, 1855:Plate 21, Figure 3). It is apparently absent in Jurassic plesiosaurs, although this region of the palate is not documented in all taxa. The vomeronasal fenestra apparently reappeared in the Lower Cretaceous elasmosaurid *Brancasaurus* (Wegner, 1914:Figure 1). This reappearance may be due to uncovering of the vomeronasal organ in one lineage of plesiosaurs that gave rise to elasmosaurids and polycotyliids.

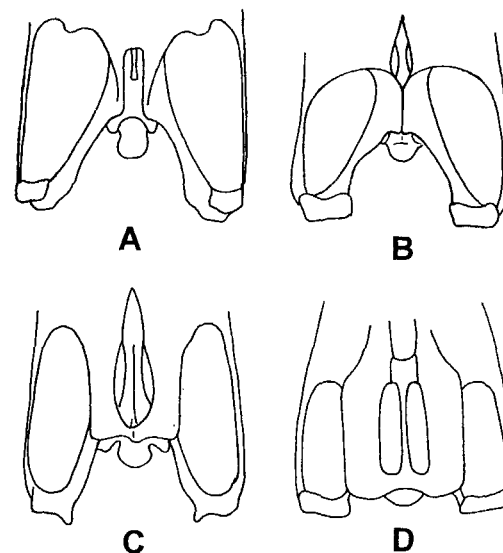
The expansion of the pterygoids beneath the braincase has apparently occurred independently twice and these may be designated as types A and B. The type A pterygoids are folded under to meet on the midline below the basicranium. An incipient version is seen in *Pistosaurus* (Figure 9A); it is seen in the pliosaurs *Liopleurodon* (Figure 9B), *Peloneustes*, *Pliosaurus*, *Simolestes*, and *Brachauchenius* (Andrews, 1913; Linder, 1913; Williston, 1903). The type B pterygoids form a horizontal plate beneath the basicranium (Figure 9C and D) occurring in all elasmosaurids (e.g., *Libonectes*) and polycotyliids (e.g., *Dolichorhynchops*). Its presence in the pliosaur *Rhomaleosaurus* (White, 1940) and the plesiosauroid *Plesiosaurus hawkinsii* (Owen, 1865) suggests a possible closer relationship than previously recognized. Incipient type B pterygoids are seen in *Plesiosaurus dolichodeirus* and *Plesiosaurus macrocephalus* (Andrews, 1896).

Another feature uniting *Libonectes* and *Dolichorhynchops* is the closure of the pineal foramen. The presence of this foramen is considered plesiomorphic for reptiles, including sauropterygians, so its absence is a synapomorphy for elasmosaurids and polycotyliids.

The stapes are apparently absent in both *Libonectes* and *Dolichorhynchops* (Storrs, personal communication, is skeptical), which, if true, may be a synapomorphy. Certainly, the presence of one is plesiomorphic for vertebrates.

## CONCLUSIONS

Traditionally, the short-necked polycotyliids were thought to have descended



**Figure 9.** Comparison of the two pterygoid types. **A)** Incipient type A, *Pistosaurus* (after Meyer, 1855). **B)** Type A, *Liopleurodon* (after Andrews, 1913). **C)** Type B, *Libonectes*. **D)** Type B, *Dolichorhynchops*.

from a short-necked pliosauroid, while the elasmosaurids were thought to have descended from a long-necked cryptoclidid (Figure 10; Welles, 1943:Figure 37). While it is true that there are differences that separate *Libonectes* and *Dolichorhynchops*, there are a few synapomorphies in the skull which may indicate a closer relationship than hitherto realized. On the basis of these synapomorphies, I venture as a hypothesis that *Libonectes* and *Dolichorhynchops* share a common ancestor, and that both are more closely related to the plesiosauroids than either is to the pliosauroids. Williston (1906:226, 1907:485) independently reached a similar conclusion, stating that the short neck was not a primitive character and that it had been acquired independently in more than one phylum. This conclusion is in marked contrast to the more traditional approach (e.g., Brown, 1981) which places *Dolichorhynchops* with the pliosauroids and *Libonectes* with the elasmosaurids.

One major objection to this hypothesis is that it requires a reduction in the number of cervical vertebrae independent from that in pliosauroids. Brown (1981) estimated that the primitive number of cervicals in plesiosauroids is 28-32, whereas *Dolichorhynchops* has 19. However, considering that *Pistosaurus* probably had about 24 cervicals (Sues, 1991), Brown's estimation may be too high. In addition,

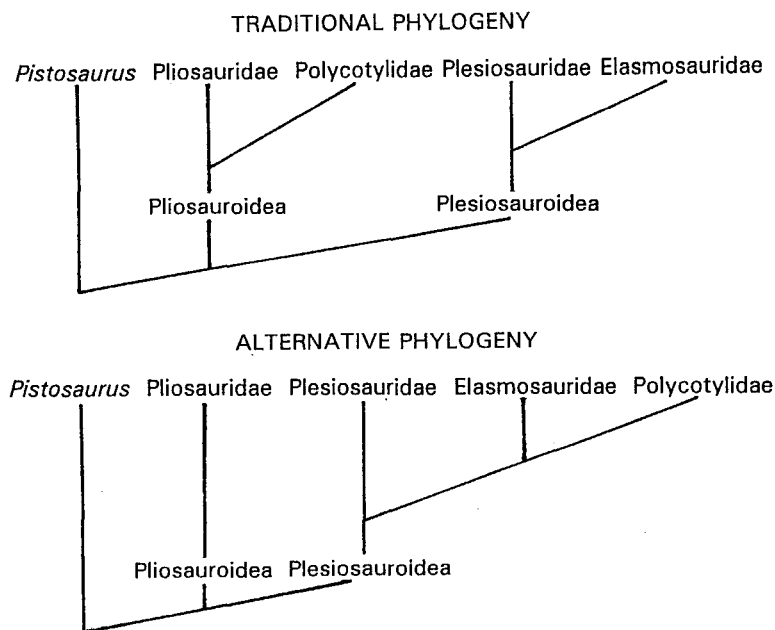


Figure 10. Contrasting phylogenetic schemes (see text for details).

*Polycotylus* has 26 cervicals (Williston, 1906), about the same as the primitive elasmosaurid *Tricleidus* (Brown, 1981). A reduction in the number of cervical vertebrae independent of the pliosaurs, therefore, is not unreasonable, and if true, then it is unlikely that Bakker's (1993) scheme of deriving *Libonectes* and *Dolichorhynchops* from an Upper Jurassic pliosaur is possible. Bakker based his conclusion on the sharing of a specialized palate (i.e., covering of the basicranium by the pterygoids) by Cretaceous pliosaurids, elasmosaurids, and the Jurassic *Pliosaurus*. However, as shown above, this condition in *Libonectes* and *Dolichorhynchops* is more similar to that in Jurassic plesiosaurids than in Jurassic pliosaurids.

### SUMMARY

The skulls of "*Elasmosaurus*" *morgani* and *Dolichorhynchops osborni* are compared as representatives of the Cretaceous plesiosaur families Elasmosauridae and Polycotylidae, respectively. Cranial features and the atlas-axis complex appear to be more stable evolutionarily than postcranial features. Thus, similarities indicate

that the short-necked Cretaceous polycotylids are the sister-group to long-necked elasmosaurids. This implies that the short-necked polycotylids of the Cretaceous are not descended from the short-necked pliosaurs of the Jurassic. The short neck has appeared independently at least twice in the Plesiosauria and the term *pliosaur* to refer to any short-necked plesiosaur should be abandoned to avoid any phyletic implications. Differences between "*Elasmosaurus morgani*" and *Elasmosaurus platyurus* demonstrate that the two species belong to different genera and a new name is proposed for "*E.*" *morgani*.

### ACKNOWLEDGMENTS

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#### APPENDIX 1

Diagnosis of *Libonectes morgani* and *Dolichorhynchops osborni*:

Class REPTILIA  
Subclass SAUROPTERYGIA Owen, 1860  
Order PLESIOSAURIA Blainville, 1835  
Superfamily PLESIOSAUROIDEA  
Family ELASMOSAURIDAE

Genus *LIBONECTES* n. g.

**Etymology:** *Libonectes* for "southwest diver," Greek masculine gender from *libo* "southwest wind" + *nektes* "swimmer," alluding to the American Southwest, where the holotype was found.

**Diagnosis:** Cretaceous elasmosaurid with 62 (?) cervical vertebrae as in *Thalassomedon* and *Styxosaurus*, compared to 37 in *Brancaesaurus*, 46 in *Morenosaurus*, 56 in *Alzadasaurus*, 57 in *Aphrosaurus*, 60 in *Hydrotherosaurus*, 63 (?) in *Hydralmosaurus*, and 74 in *Elasmosaurus (sensu stricto)*. Preorbital length/skull length (of limited taxonomic utility) 38.6, whereas ratio is 42.3 in *Alzadasaurus*, 39.1 in *Thalassomedon*, 38.6-41.6 in *Styxosaurus*, and 34.3 in *Tuarangisaurus*. Atlas-axis centrum short and deep like in *Tuarangisaurus* (Figure 1), whereas it is long and low in *Elasmosaurus platyurus*; neural spine low, with postzygapophyses of axis extending well beyond posterior face of centrum, whereas neural spine tall and postzygapophyses of axis do not extend beyond centrum in *Thalassomedon hanningtoni*; *Tuarangisaurus* atlas-axis intermediate between *Libonectes* and *Thalassomedon* in shape and size of neural spine.

*LIBONECTES MORGANI* (Welles, 1949)

*Elasmosaurus morgani* Welles, 1949

**Holotype:** SMUSMP 69120: skull, most of the cervicals, gastralia, and gastroliths. The pectoral girdle and forelimb were apparently discarded long ago

(Storrs, 1991).

**Type locality:** Britton Formation (Turonian), Eagle Ford Group, near Cedar Hill, Dallas County, Texas.

**Diagnosis:** As for the genus.

Family POLYCOTYLIDAE

*DOLICHORHYNCHOPS OSBORNI* Williston, 1903

*Dolichorhynchops osborni* Williston, 1903

*Trinacromerum osborni* Williston, 1908

*Trinacromerum osborni* Russell, 1935

*Trinacromerum osborni* Riggs, 1944

*Dolichorhynchops osborni* Persson, 1963

*Dolichorhynchops osborni* Kuhn, 1964

*Dolichorhynchops osborni* Thurmond, 1968

*Dolichorhynchops osborni* Hampe, 1992

**Holotype:** KUVF 1300 nearly complete skeleton (Williston, 1903).

**Type locality:** *Hesperornis* biozone, Smoky Hill Chalk Member, Niobrara Formation, Logan County, Kansas.

**Referred specimens:** FHSM VP404, a nearly complete skeleton from the Smoky Hill Chalk, near Russell Springs, Logan County, Kansas. MCZ 1064, partial skeleton and skull of a young individual from the Smoky Hill Chalk, in Logan County, Kansas. UCM 35059, a partial skeleton and skull from the Sharon Springs Member of the Pierre Shale, Mule Creek drainage, Niobrara County, Wyoming. AMNH 5834, skull from the Sharon Springs Member of the Pierre Shale, Mule Creek drainage, Niobrara County, Wyoming. UNSM 50133, skull from the Sharon Springs Member of the Pierre Shale, Hat Creek drainage, Fall River County, South Dakota. KUVF 40001, skull from the Sharon Springs Member of the Pierre Shale, Hat Creek drainage, Fall River County, South Dakota.

**Diagnosis:** More derived than *Trinacromerum* in having vertical suspensorium, supratemporal fenestra as wide as long, shorter pterygoids, interpterygoid fenestra, parasphenoid, jugals, horizontal process of the squamosal, and parietals; teeth covered with finer striae and more slender than in *Trinacromerum* and *Polycotylus*; 19 cervicals, 26 in *Polycotylus* and 20 in *Trinacromerum*; anterior chevrons borne almost exclusively on single caudal, shared equally by adjacent caudals in *Trinacromerum*.

## APPENDIX 2

Anatomical Abbreviations: **a** = angular, **acf** = anterior carotid foramen, **ac** = acoustic chamber, **aipf** = anterior interpterygoid fenestra, **ar** = articular, **bbc** = basioccipital-basisphenoid cavity, **bo** = basioccipital, **bof** = basioccipital facet of opisthotic-exoccipital, **bs** = basisphenoid, **bsr** = basisphenoid rostrum, **c** = coronoid, **cb** = cerebellum, **cc** = coronoid cartilage (ossified), **cer** = cerebrum, **cp** = coronoid process, **d** = dentary, **ec** = ectopterygoid, **en** = external nares, **ep** = epipterygoid, **ff** = frontal fenestra (supraorbital fenestra), **fm** = foramen magnum, **fo** = fenestra ovalis, **fr** = frontal, **hsc** = horizontal semi-circular canal, **iam** = internal auditory meatus, **ic** = internal carotid, **icf** = internal carotid foramen, **in** = internal nares, **ipf** = interpterygoid fenestra, **ju** = jugal, **lcp** = lower cylindrical process, **mc** = Meckelian canal, **mf** = mandible fossa, **mx** = maxilla, **nc** = nasal chamber, **nf** = nutrient foramen, **o** = orbit, **oc** = occipital condyle, **oe** = opisthotic-exoccipital, **os** = olfactory sulcus, **ot** = olfactory tract, **pa** = parietal, **paf** = parietal facet of supraoccipital, **pal** = palatine, **pd** = pineal and dura, **pf** = prefrontal, **pipf** = posterior interpterygoid fenestra, **pit** = pituitary, **pm** = premaxilla, **po** = postorbital, **pp** = paroccipital process, **pr** = prootic, **pra** = prearticular, **ps** = parasphenoid, **pt** = pterygoid, **ptf** = pterygoid facet of basioccipital, **ptp** = pterygoid process, **q** = quadrate, **qpt** = quadrate ramus of pterygoid, **ra** = retroarticular, **rt** = replacement tooth, **sa** = surangular, **scc** = semicircular canal, **sm** = symphysis, **so** = supraoccipital, **sof** = suborbital fenestra, **sp** = splenial, **spo** = supraorbital, **sq** = squamosal, **st** = sella turcica, **stf** = subtemporal fenestra, **t** = tooth (in cross section), **tf** = temporal fenestra, **ucp** = upper cylindrical process, **v** = vomer, **vf** = vomeronasal fenestra, **V** = trigeminal foramen, **VI** = abducens foramen, **VII** = facial foramen, **VIII** = acoustic foramen, **IX** = glossopharyngeal foramen, **X** = vagus foramen, **XI** = accessory foramen, **XII** = hypoglossal foramen.