

TRINACROMERUM BONNERI, NEW SPECIES,
LAST AND FASTEST PLIOSAUR
OF THE WESTERN INTERIOR SEAWAY

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Abstract.— The Pierre Shale represents the final days of the Western Interior Seaway before its regression at the end of the Mesozoic, and records the last of the marine reptiles that dominated the seas much as their contemporary dinosaur counterparts dominated the land. *Trinacromerum bonneri*, n. sp., is the first pliosaur (short-necked plesiosaur) to be described from this formation in the northern Great Plains; as such it represents the final radiation of polycotyloid pliosaurs in North America. Pliosaurs have long been regarded as particularly high-speed swimmers, but *T. bonneri* carried this trend to an extreme. Development of the longest wingfins known in pliosaurs maximized its velocity. Unique limb and vertebral structures resisted pressures of the surrounding water that were generated by its own swimming velocity. Such adaptations include tongue-and-groove articular surfaces between critical limb elements and highly interlocking cervical vertebrae.

Plesiosaurs were large marine reptiles of the epicontinental seaways that flooded much of Europe and North America during the Mesozoic. Although contemporaries of dinosaurs, they were both systematically and ecologically very different. Secondarily aquatic and derived from primitive terrestrial diapsids (Storrs 1993:66), plesiosaurs are sauropterygians, all of which generally display a strong evolutionary trend toward an aquatic niche. Specifically, sauropterygians tend to develop long oar-shaped limbs through hyperphalangy. These modified limbs have been referred to variously as paddles, oars, fins, flippers, and wings, and it is unlikely that any one of these terms will gain dominance since each bears disputed functional implications. This paper introduces and uses the term "wingfin" for plesiosaur limbs in an attempt to standardize terminology.

Within the plesiosaurs, members of the pliosaur subtaxon have always been regarded as particularly high-speed swimmers (Williston 1906; Tarlo 1960; Welles 1962; Robinson 1975; 1977; Nicholls & Russell 1991; Bakker 1993). This paper describes and names a new species that exhibits several adaptations for high-velocity subaqueous swimming, including enormous wingfins, unique tongue-and-groove wingfin articular surfaces, and interlocking cervical vertebrae.

Sauropterygians are a monophyletic clade with synapomorphies that

include: "single temporal fenestra (homologous to the upper opening of diapsids), no supratemporal, postparietal, tabular, or lacrimal, retracted nares, a large retroarticular process on the mandible, no trunk vertebral intercentra, three or more sacral vertebrae, no sternum, a divided scapulo-lacoracoid, pectoral and thyroid fenestration, and ... a scapula that lies superficially to the clavicle" (Storrs 1993:66-67). Welles divided pleisosaurs into two infraorders: the long-necked Plesiosauroidea and the Pliosauroidae, the latter defined as short-necked, with large heads, long ischia, and "pendulous propodials" (Welles 1943). While some workers (e.g. White 1940), have argued against the use of neck length as a character of infra-ordinal significance, the dichotomy apparently reflects a basic difference in locomotory adaptations (see Storrs 1993, for review).

Generally, the pliosauroids were highly maneuverable animals, capable of changing direction skillfully in pursuit of large prey, whereas plesiosauroids swam steadily and with more endurance, utilizing mobility of the neck to graze upon numerous small prey objects en route (Robinson 1975; 1977). In the absence of a definitive taxonomic revision, however, Storrs (1993) warns that "the traditional Plesiosauroidea . . . and Pliosauroidae . . . may or may not be valid monophyletic groups."

Within the Pliosauroidae, Welles (1943) originally recognized two families: the Jurassic Pliosauridae and the primarily Cretaceous Polycotylidae, but in an extensive 1962 revision he changed the family name Polycotylidae to Dolichorhynchopidae and relegated 16 of the 19 existing species names as *nomina vana*. Although not recognized by the International Code of Zoological Nomenclature, the term *nomen vanum* is commonly used (Thurmond 1968; Chorn & Whetstone 1978), but Welles (1943) used the designation improperly to remove two of the three existing generic names that were based on *nomen vanum* species, as well as one of the two existing family names that was, in turn, based upon a *nomen vanum* genus. Considerable confusion regarding the availability of "Polycotylid" generic names and the proper family name for the taxon ensued. Although a definitive taxonomic revision is beyond the scope of this work, it is important to review, evaluate, and stabilize nomenclature itself in this case.

Thurmond (1968) re-referred one group of seven polycotylid species names based on centra, which Welles (1943) considered indeterminate material, to *nomen oblitum* Status. This term, however, refers to a senior synonym that has remained unused for a period of 50 years (ICZN: Article 23), and none of these seven names is a senior synonym.

The appropriate term for a species based on indeterminate material is nomen dubium, defined as "a descriptive term meaning name of un-known or doubtful application" (ICZN: Appendices). Nomina dubia are still available names, and remain so unless placed on the official index of rejected names published by the Commission (Mayr 1969). Six other "nomen vanum" species, *Polycotylus dolichopus*, *Polycotylus ichthyospondylus*, *Polycotylus latipinnis*, *Polycotylus tenuis*, *Trinacro-merum anonymum*, and *Trinacromerum latimanus*, are not referable to nomen dubium Status because each is based on well-described material that is simply not diagnostic at the present time, given the lack of clearly defined genus and species taxonomic characteristics. However, when Welles (1943) removed *Polycotylus latipinnis* as the type species of the genus *Polycotylus*, he also removed the generic name *Polycotylus*. Welles also rejected the genus name *Trinacromerum* because he referred its type species, *T. bentonianum* to nomen vanum Status as well, but for a different reason: although based on valid material, the specimen had been described inadequately (by Cragin in 1888) and then lost (after a 1908 redescription by Williston), which precluded the possibility of validating the name by a new description (Welles 1962:59).

Only three species and one genus survived Welles' revision: *Dolichorhynchops osborni*, *Trinacromerum kirki* and *Trinacromerum willistoni*. Since Williston had previously synonymized *Trinacromerum* and *Dolichorhynchops* (1903; 1908), Welles referred *Trinacromerum kirki* and *Trinacromerum willistoni* to *Dolichorhynchops*. He then changed the family name to Dolichorhynchopidae, since *Dolichorhynchops* had now become the type genus of the family. Welles realized that the change in family name was not consistent with the Code some time before 1968, and communicated to John Thurmond that he had prepared his 1962 revision under the 1926 Code, which allowed such a change of family name in the event of a change in the name of the type genus. Thurmond therefore resurrected the Family Polycotylidae in 1968, the type genus of which remained *Dolichoryhynchops* because of Williston's synonymy and Welles' improper designation of *Trinacromerum* as nomen vanum. Then, in 1976, the type and paratype specimens of *Trinacromerum bentonianum* Cragin were relocated by the author, through efforts of Marianne Stoller of the Department of Anthropology at Colorado College in Colorado Springs, and Nicholas Hotton of the U.S. National Museum (as briefly reported in Storrs 1981). Both specimens are located at the Smithsonian and catalogued as USNM 10945 and USNM 10946. Each bears an old Colorado College label and notes indicating

that they were the specimens from which Cragin had described *T. bentonianum* (Hotton, pers. comm.).

Since the genus *Trinacromerum* (Cragin 1888) is older than *Dolichorhynchops* (Williston 1902) the synonymy of Williston (1903; 1908) places *Dolichorhynchops* in *Trinacromerum*. Storrs (1981:44) considers the vertebral characters of *Polycotylus latipinnus* to be diagnostic, and therefore recognizes the genus as a valid taxon that "has long been misunderstood and . . . synonymized". If *P. latipinnus* material is diagnostic, and if *Polycotylus* is synonymous with *Trinacromerum*, then *Polycotylus* would be the senior synonym since Cope established the genus in 1869, which antedates the 1888 establishment of *Trinacromerum*. However, Storrs uses the same vertebral characters that validate *Polycotylus* to distinguish it from *Trinacromerum*, meaning that if the genus is valid it is also not synonymous with *Trinacromerum*.

Nomenclature is therefore stabilized at present as follows:

Family Polycotylidae Williston 1908

Genus *Polycotylus* Cope 1869 (type genus)

Polycotylus latipinnis Cope 1869 (type species)

Polycotylus dolichopus Williston 1906

Polycotylus ichthyospondylus Seeley 1869

Polycotylus tenuis Hector 1874

nomina dubia:

Polycotylus balticus Bogolubov 1911

Polycotylus brevispondylus Bogolubov 1911

Polycotylus donicus Pravoslavev 1915

Polycotylus ichthyospondylus Bogolubov 1911

Polycotylus orientalis Bogolubov 1911

Polycotylus ultimus Bogolubov 1911

Genus *Trinacromerum* Cragin 1888

Trinacromerum bentonianum Cragin 1888 (type species)

Trinacromerum anonymum Williston 1903

Trinacromerum (Ceraunosaurus) brownorum Thurmond 1968

Trinacromerum kirki Russell 1935

Trinacromerum latimanus Williston 1903

Trinacromerum (Dolichorhynchops) osborni Williston 1902

nomen dubium:

Trinacromerum ichthyospondylus Pravoslavev 1915

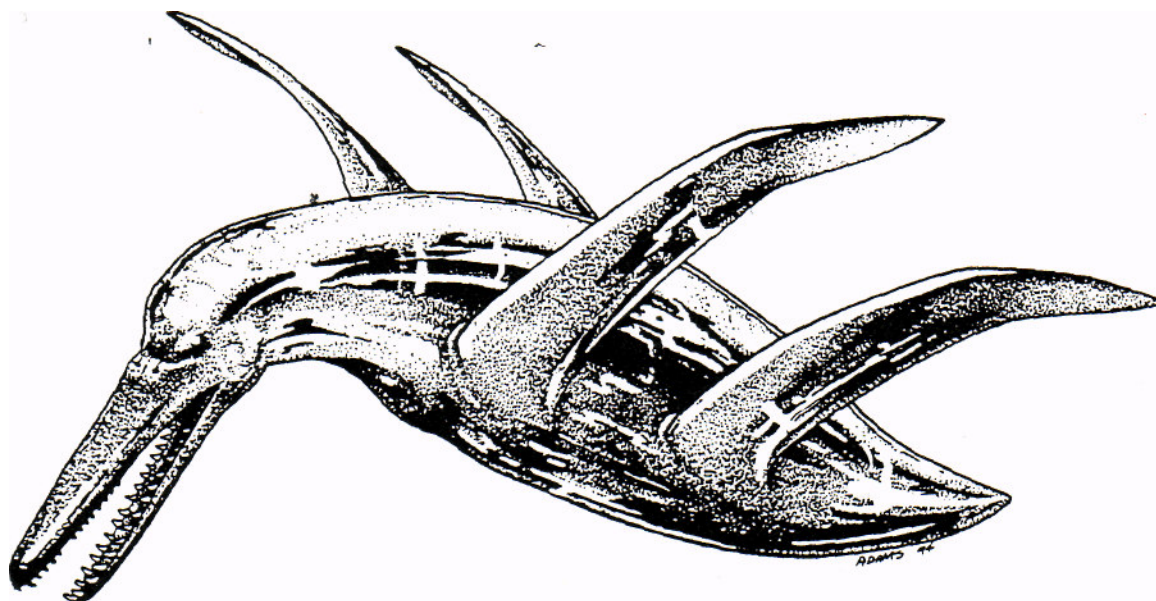


Figure 1. Reconstruction of *Trinacromerum bonneri* in a pose of subaqueous flight. Front and rear limbs move synchronously (Robinson 1975; 1977; Nicholls & Russell 1991; Storrs 1993; Nicholls and Russell have suggested that the limbs may not have been capable of moving dorsally to the degree illustrated.) Estimated length of approximately 3.5 m.

Museum abbreviations: KUMNH = University of Kansas Museum of Natural History, Lawrence, Kansas; TAMU = Texas A&M University, College Station, Texas; USNM = United States National Museum, Washington D.C.

SYSTEMATIC PALEONTOLOGY
 Order Sauropterygia Owen 1860
 Suborder Plesiosauria de Blainville 1835
 Family Polycotylidae Williston 1908
Trinacromerum bonneri, new species
 (Figures 1-8 and 10-14)

Disposition of types.—Holotype (KUMNH 40002), complete skeleton minus skull (Figs. 2-6 and 10-14); Paratype (KUMNH 40001), skull, lower jaws, first three cervical vertebrae (articulated), pubes and ischia, left humerus and femur, vertebrae and ribs (Figs. 2, 5-8 and 14).

Type locality.— Johnson Ranch, 3 mi NE of Redbird, Niobrara County, Wyoming; 1 mi E of the ranch house, about 10 ft above the Ardmore Bentonite.

Paratype locality.— Wallace Ranch, Section 16, T35N, R57W, Fall River County, South Dakota, 10 ft below the Ardmore Bentonite; approximately 4 mi from type locality.

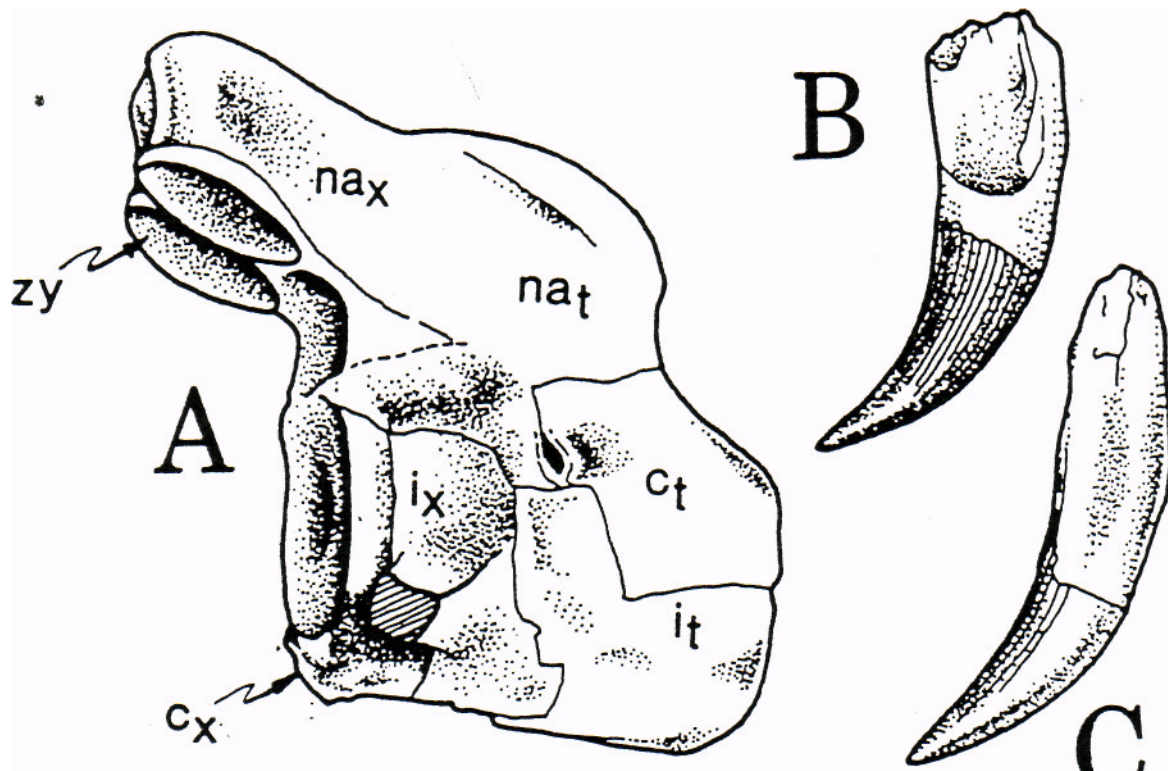


Figure 2. A. Atlas-axis of *Trinacromerum bonneri*, KUMNH 40002. Abbreviations: = axial neural arch, naj = atlas neural arch, zy = zygapophyses, cx = axial centrum, q = atlas centrum, ix = axial intercentrum, i = atlas intercentrum. B and C. Maxillary teeth of *T. bonneri*, KUMNH 40001, labial (B) and lingual (C) views. Scale = 5 cm.

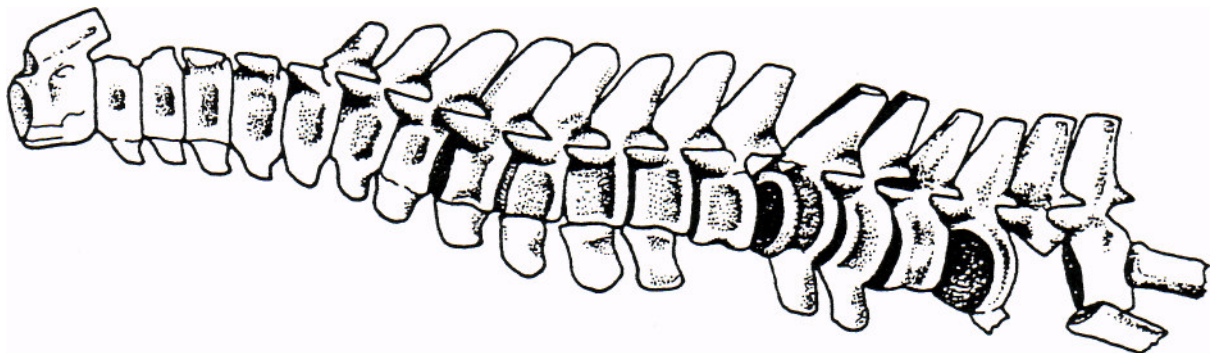


Figure 3. Cervical vertebrae of *Trinacromerum bonneri*, KUMNH 40002, preserved in articulation. Note size and orientation of zygapophyses in middle region of the neck. Scale = 5 cm.

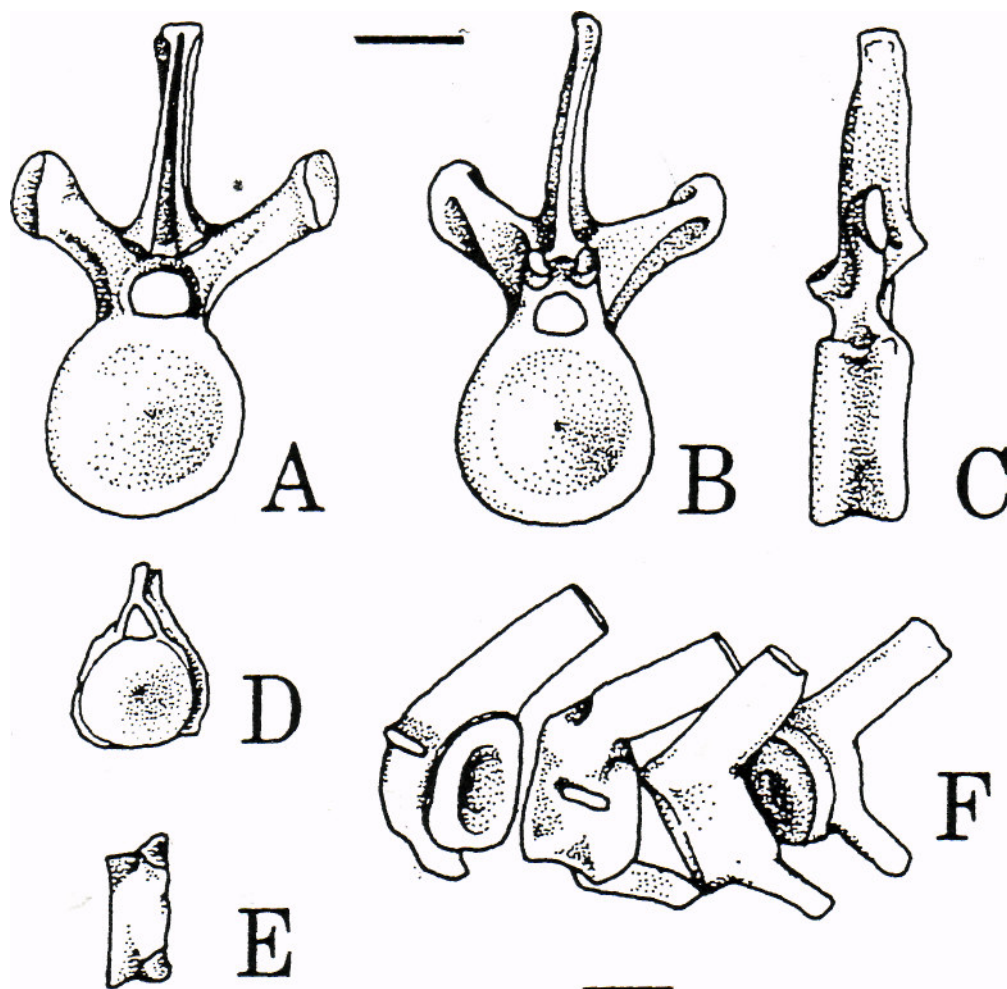


Figure 4. Vertebrae of *Trinacromerum bonneri*, KUMNH 40002. A. 20th dorsal, posterior view. B. Same, anterior view. C. Same, left lateral view. D. 15th caudal, anterior view. E. Same, ventral view. F. Caudal vertebrae 8-11, in situ. Scale = 5 cm.

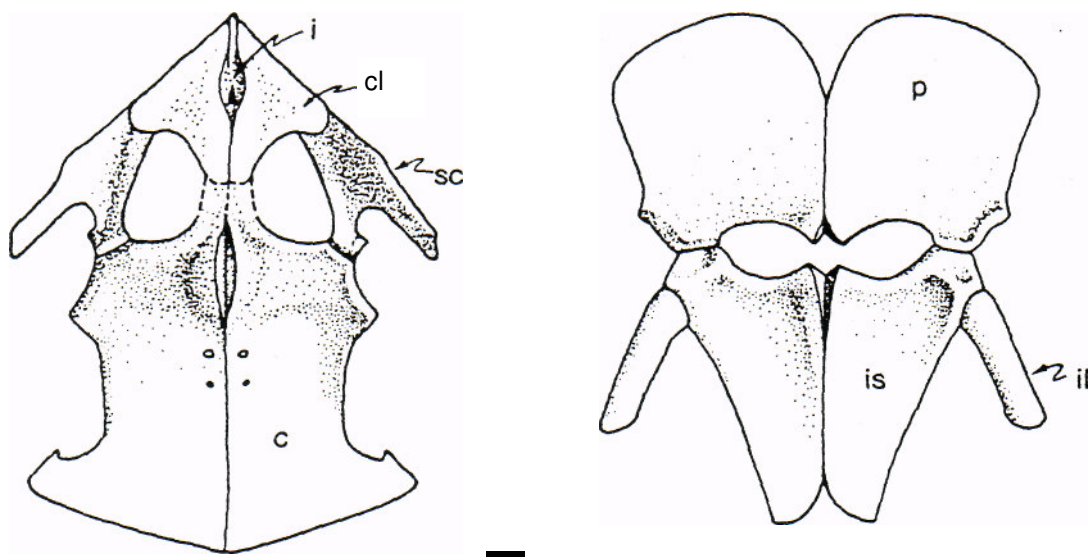


Figure 5. Reconstructed girdles of *Trinacromerum bonneri*, KUMNH 40002 and 40001, dorsal view. A. Reconstructed pectum. Abbreviations: cl = clavicle, i = interclavicle, c = coracoid, sc = scapula. B. Reconstructed pelvis. Abbreviations: p = pubis, is = ischium, il = ilium. Scale = 5 cm.

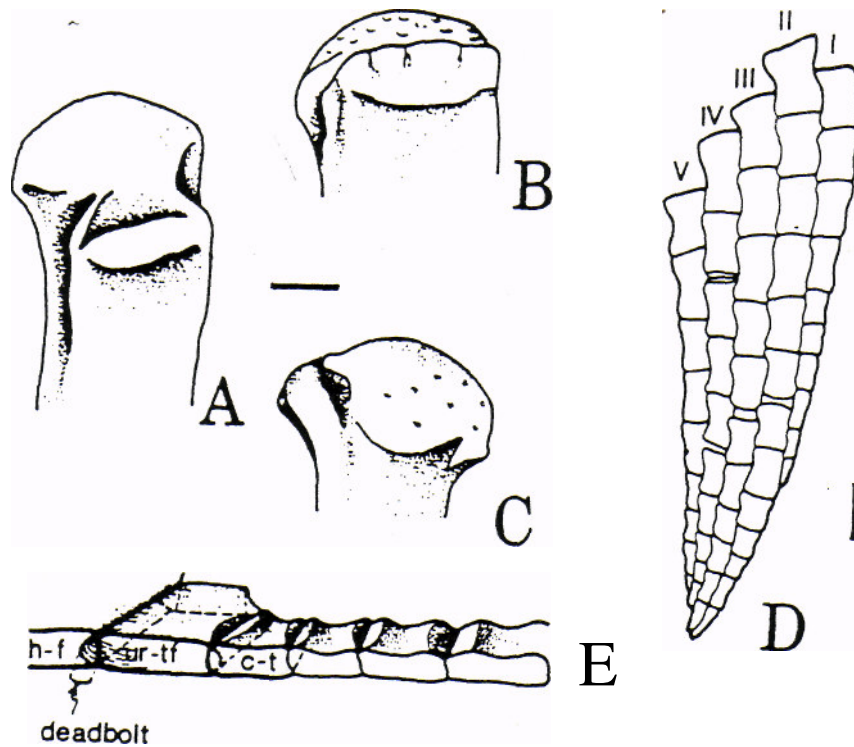


Figure 6. A - C. Proximal ends of humeri of *Trinacromerum bonneri*. A. Ventral view, KUMNH 40002. B. Ventral view, KUMNH 40001. C. Lateral view, KUMNH 40002. D. Detail of phalangeal arrangement of distal portion of left rear wingfin. I, II, III, IV, and V denote digit numbers. E. Longitudinal section through anterior and proximal portion of front or rear wingfin of *T. bonneri*. Abbreviations: h-f = humerus or femur, propodial; ru-tf = radius/ulna or tibia/fibula, first row of epipodials; c-t = first carpal or tarsal, second row of epipodials. Tongue and groove articular surfaces occur between h-f and ru-tf and between ru-tf and c-t. Scale = 5 cm.

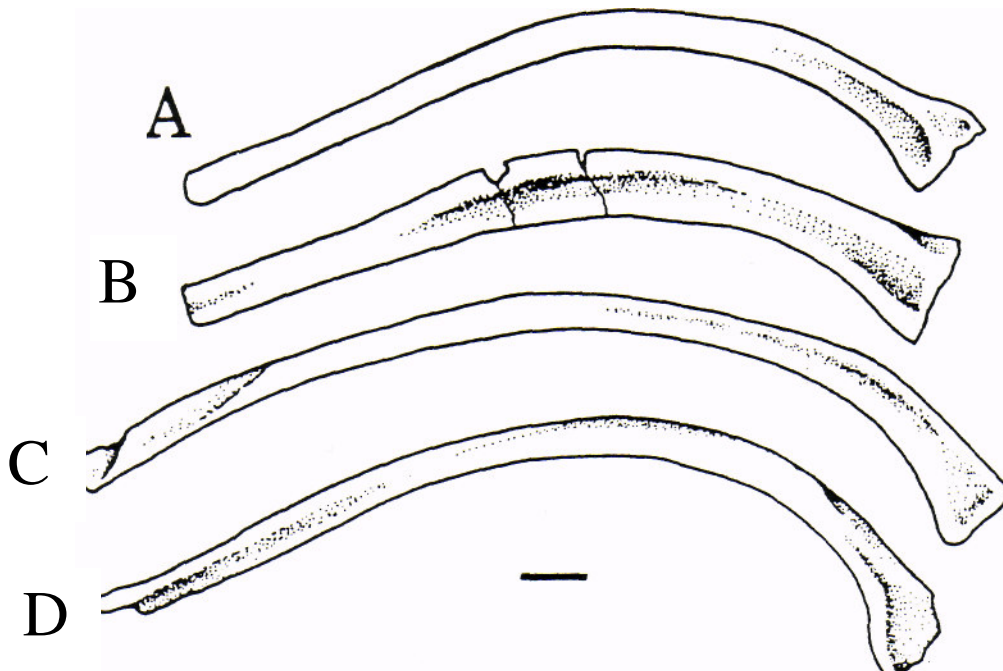


Figure 7. Dorsal ribs of *Trinacromerum bonneri*, KUMNH 40001. A and B. Anterior dorsals. C and D. Posterior dorsals. Scale = 5 cm.

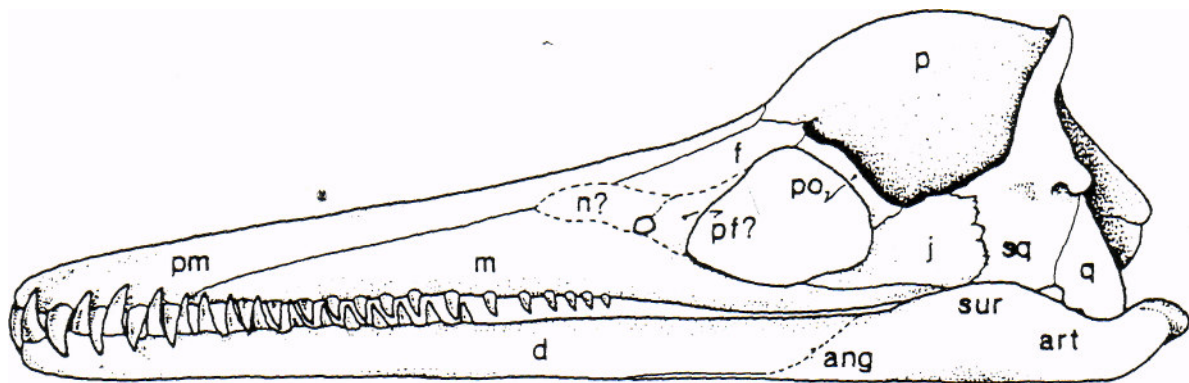


Figure 8. Reconstructed skull and lower jaw of *Trinacromerum bonneri*, KUMNH 40001. Abbreviations: pm = premaxilla, m = maxilla, f = frontal, n = nasal, pf = prefrontal, po = postorbital, p = parietal, sq = squamosal, j = jugal, q = quadrate, d = dentary, ang = angular, sur = surangular, art = articular. Scale = 5 cm.

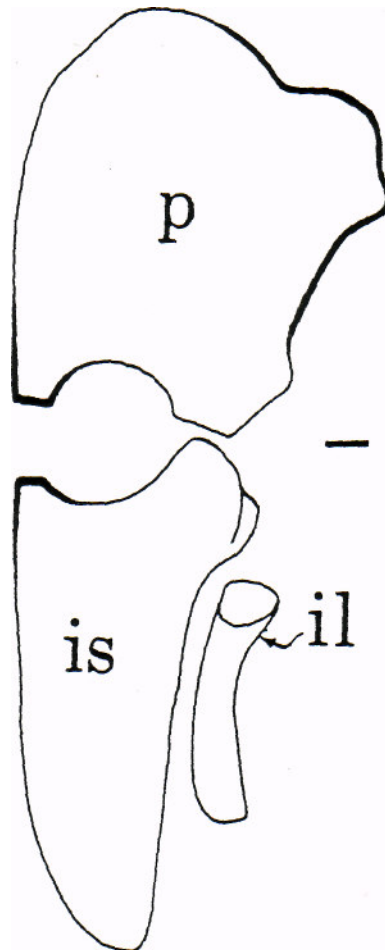


Figure 9. Right pubis, ischium, and ilium of *Trinacromerum kirki* pelvis, dorsal view. The truncated pubis and ischium medial articular region and the unique anterolateral pubic border are drawn with heavy lines for emphasis. Compare to Figure 5B. Medial to left. Drawn from photograph in Russell 1935.

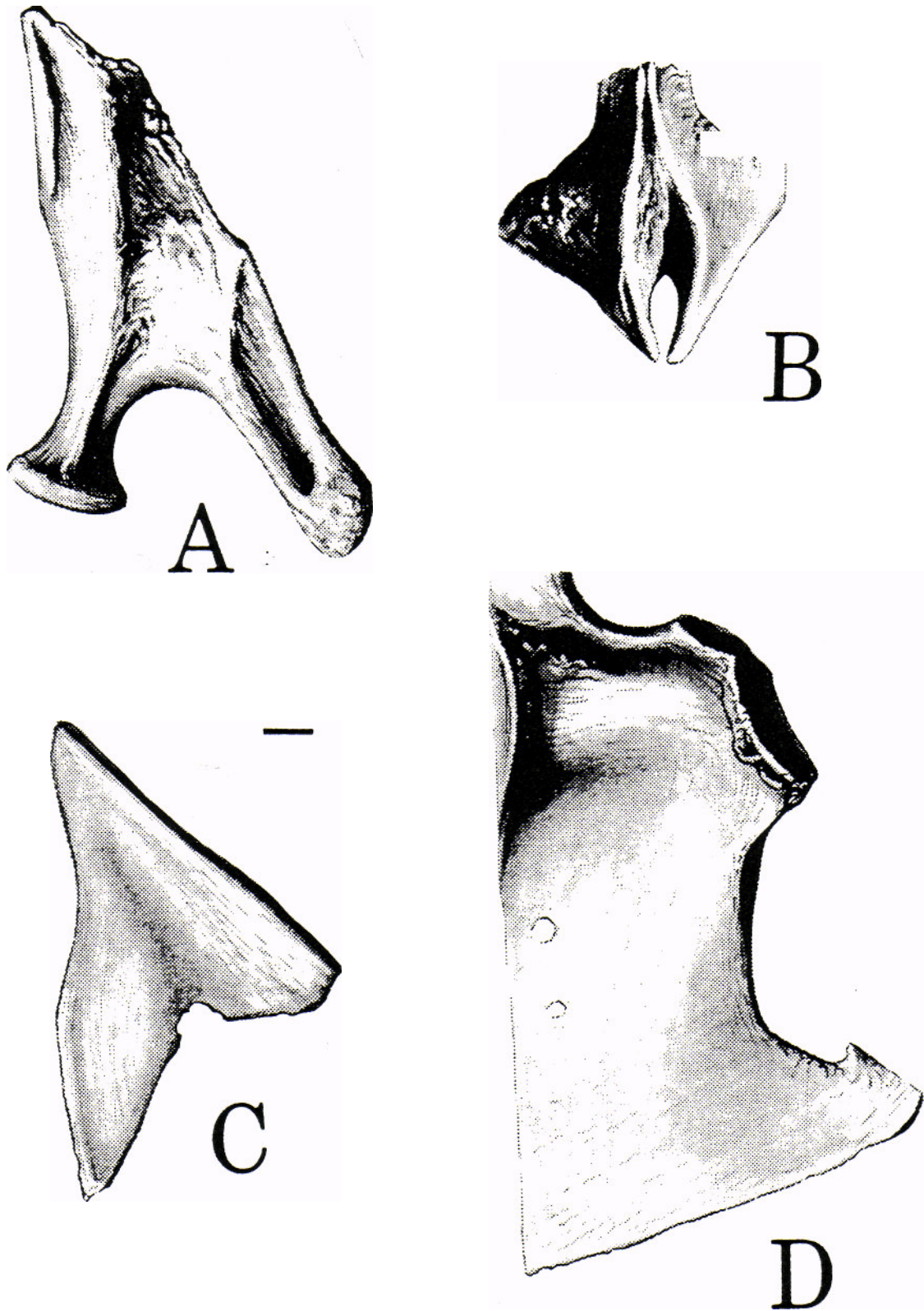


Figure 10. Pectrum elements of *Trinacromerum bonneri*, KUMNH 40002. A. Left scapula, ventral view. B. Interclavicle, ventral view. C. Left clavicle, ventral view. D. Right coracoid, dorsal view. Scale = 5 cm.

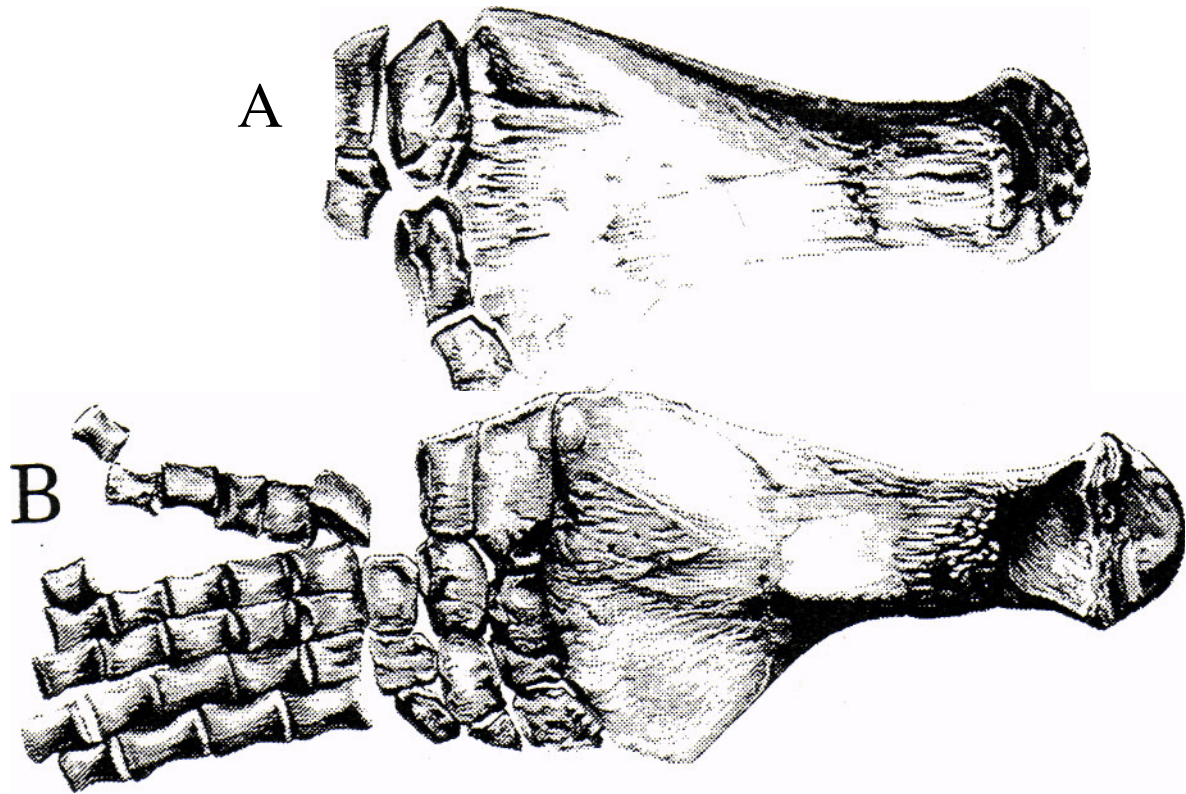


Figure 11. Humeri and associated epipodials of *T. bonneri*, KUMNH 40002. A. Left humerus and epipodials, dorsal view. B. Right humerus and epipodials, ventral view. Scale = 5 cm.

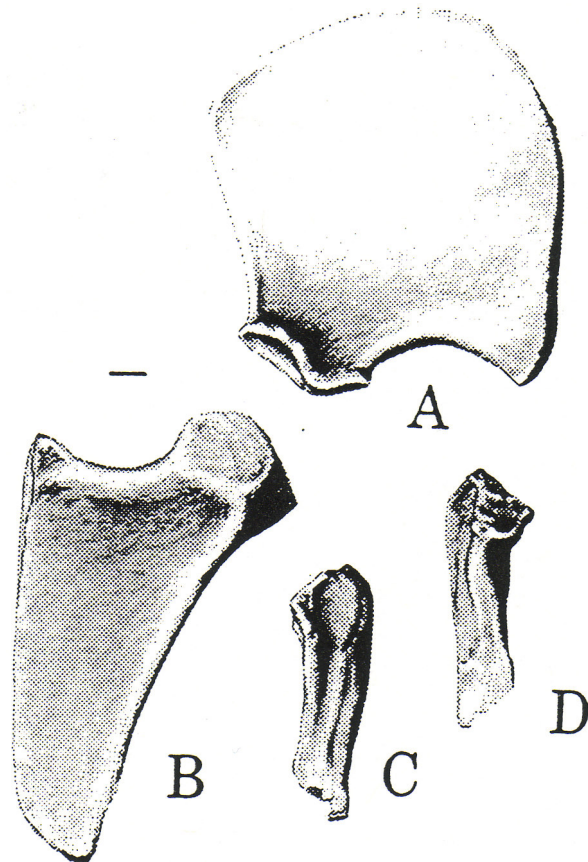


Figure 12. Pelvis elements of *T. bonneri*, KUMNH 40002. A. Right pubis, dorsal views. B. Left ischium, dorsal view. C. Right ilium, anterior view. D. Same, posterior view. Scale = 5 cm.

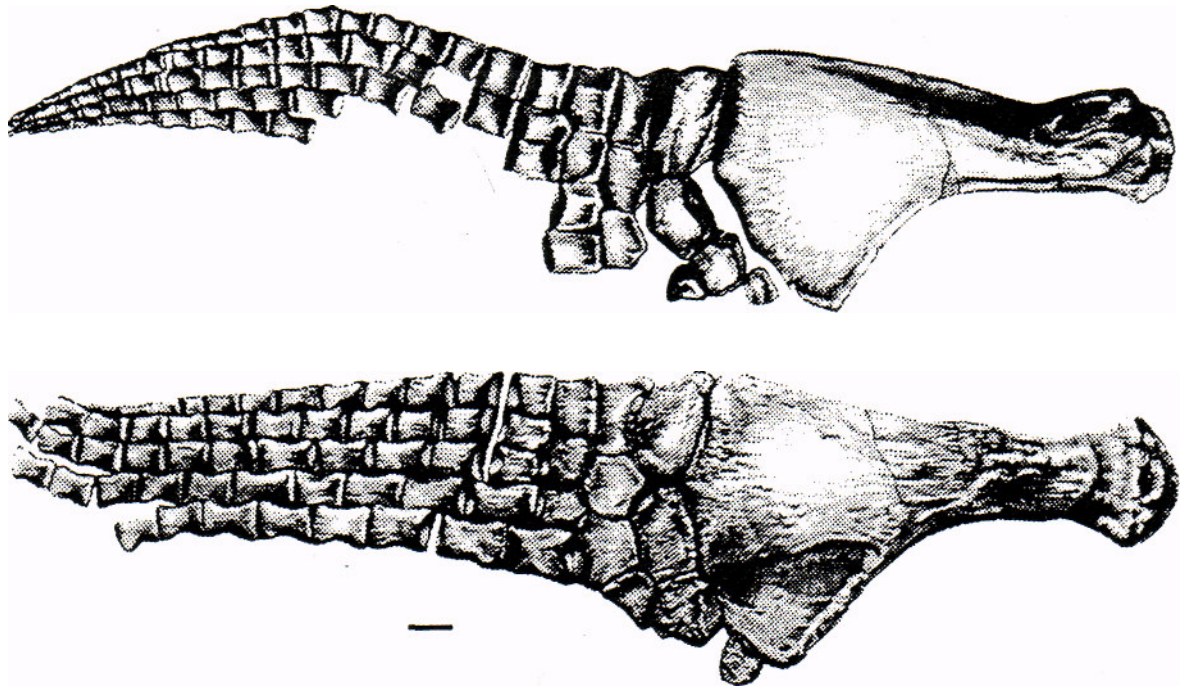


Figure 13. Femora and associated epipodials of *T. bonneri*, KUMNH 40002. A. Left femur and wingfin, dorsal view. B. Right femur and wingfm, ventral view. Scale = 5 cm.

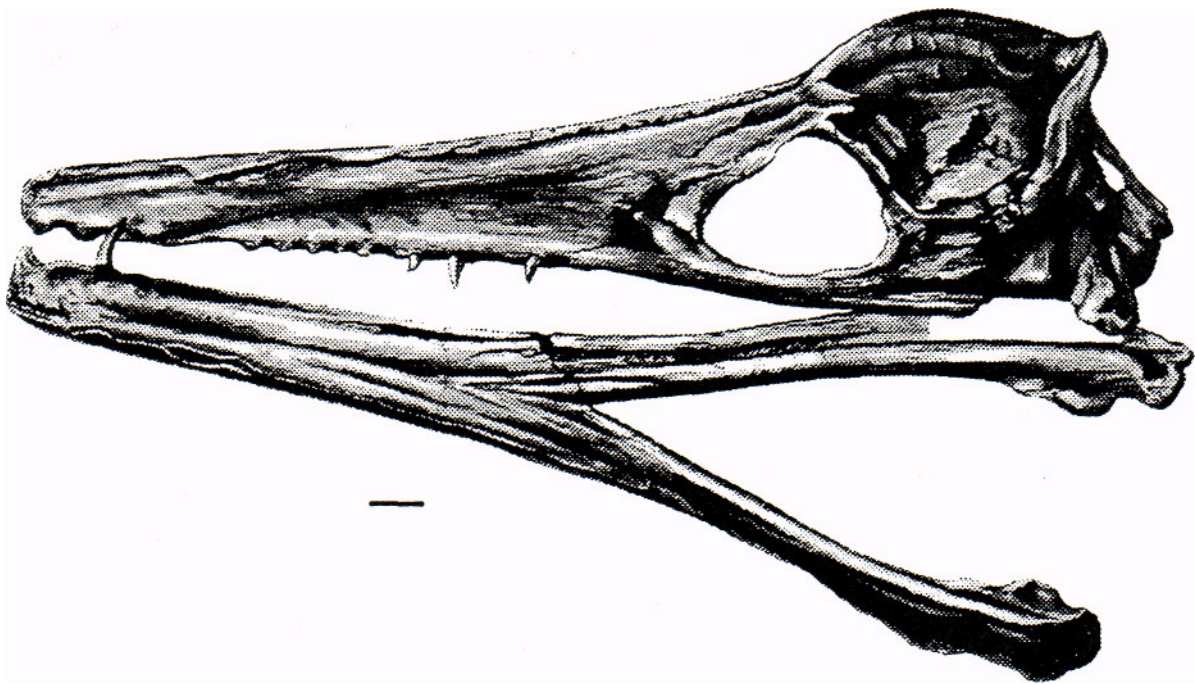


Figure 14. Skull and lower jaws of *Trinacromerum bonneri*, KUMNH 40001. Scale = 5 cm.

Type horizon.—Sharon Springs Member of Pierre Shale.

Age.—Campanian.

Referred specimens.—TAMU 3001, Taylor Marl of McLennan County, Texas, referred to *Trinacromerum* cf. *T. kirki* (Storrs 1981), in Texas Memorial Museum, Austin, Texas; fragmentary materials collected in 1966 at the South Dakota Wallace Ranch locality: USNM 50144 (adult) and USNM 55810 (juvenile), and proximal end of juvenile humerus at University of Nebraska.

Diagnosis.—Wingfins equal in length to dorsal spinal column; "tongue-and-groove" propodial-epipodial articulation; cervical vertebrae closely interlocked by zygapophysis-neural spine embrasures. Nineteen cervical vertebrae (including atlas and axis). Twenty-eight dorsal vertebrae (3 pectoral and 3 sacral); sacral vertebrae not fused, contra "many species of polycotylids" (Bonner 1964); dorsal vertebrae with very small paired nutrient foramina neither set in depressions nor separated by keel, contra *T. osborni* (Williston 1908). Nineteen caudal vertebrae, most with unexpectedly long neural spines. Humerus:femur ratio >1, unlike almost all other pliosaurs (Storrs 1993). Pubis and ischium borders meet at angle caused by tapering curves at sutural ends of both bones, as in description of TAMU 3001; pubis-ischium symphysis is not truncated as it is in *T. osborni*, *T. kirki*, *T. willistoni* and *reconstruction* of TAMU 3001 (Storrs 1981; Russell 1935). Prominent short spur on anterior edge of posterior coracoid process. Pubis margin smooth rather than emarginated as in *T. kirki* (Figs. 5B and 9).

Etymology.—The name proposed for the new species is in honor of Orville Bonner, preparator at the University of Kansas. Mr. Bonner has devoted most of his life to the collection, preparation, and study of the rich faunas of the Niobrara Chalk and Pierre Shale. His considerable preparation skills and wide knowledge of Great Plains paleontology have proven invaluable to graduate students at the University of Kansas for many years.

Remarks.—The skeleton KUMNH 40002 has been designated as holotype and the skull KUMNH 40001 as paratype because only postcranial characters have heretofore been used in pliosaur systematics. Measurements of *Trinacromerum bonneri* are given in Table 1.

Table 1. Measurements of *Trinacromerum bonneri*.

Skull (KUMNH 40001)			
Total length, snout to posterior edge of quadrate		93.5 cm	
Height (dorsoventral, along squamosal-quadrate)		29.5 cm	
Lower jaws (KUMNH 40001)			
Length (anteroposterior)		98.3 cm	
Symphysis length			
Total width, both madibles in articulation at snout		5.2 cm	
at posteriormost point of symphysis		10.7cm	
Interclavicle (KUMNH 40002)			
Length		21.6 cm	
Width		20.8 cm	
Greatest width of foramen		2.1 cm	
Length of foramen		6.0 cm	
Clavicle (KUMNH 40002, right)			
Total length		36.9 cm	
Length of external margin		27.0 cm	
Scapula (KUMNH 40002, left)			
Length, shortest part of anterior edge to end of dorsal process		39.5 cm	
Length, anterior edge to articulation with glenoid		34.4 cm	
Coracoid (KUMNH 40002, right)			
Length (to top of suture)		71.5cm	
Greatest width at glenoid		33.5 cm	
	<u>40002R</u>	<u>4002L</u>	<u>4001</u>
Humerus			
Length	52.6 cm	54.5 cm	57.8 cm
Diameter at head (anteroposteriorly)	13.0cm	14.5 cm	12.4 cm
Diameter at distal end	32.0 cm	32.5 cm	36.0 cm
Pubis			
Width, side-to-side as articulated	43.4 cm	44.0 cm	43.6 cm
Anteroposterior extent	43.0 cm	43.0 cm	44.4 cm
Width of neck	17.0 cm	16.4 cm	17.3 cm
Length of symphysis	38.0 cm*	40.2 cm	35.0 cm
Ischium			
Length, to bar	46.2 cm	46.1 cm	
Width, anterior end	28.2 cm	28.1 cm	
Ilium			
Length	28.5 cm	26.7 cm +	29.6 cm
Diameter of shaft at middle	6.3 cm	7.5 cm	6.0 cm
Diameter of base, largest	9.3 cm	9.0 cm	10.0 cm
Femur			
Length	51.5cm	53.0 cm	52.0 cm
Diameter at capitulum (greatest)	14.8 cm	12.5 cm*	12.0cm*
Diameter at distal end (greatest)	30.0 cm	28.0 cm	-

* indicates measurement is an estimate

● indicates measurement is too short due to breakage of measured area

- indicates portion measured is absent

FUNCTIONAL IMPLICATIONS

Wingfins of *Trinacromerum bonneri* are much longer relative to body size than those of any other polycotyloid. Index of thorax length to hind wingfin length for *T. bonneri* is 1.03 (thorax length = 148 cm; wingfin length = 144 cm), compared to indices of 1.50 in the *T. kirki* type specimen and 1.65 in the Fort Hayes *T. osborni* specimen. *T. bonneri* wingfin elongation occurred within the epipodial regions (radius/ulna and tibia/fibula, plus first and second supernumeraries), rather than via lengthening of humerus or femur. The femur of the complete hind wingfin of *T. bonneri* comprises only 35.7% of the total wingfin length, whereas it averages 41.2% of the wingfin in *T. kirki* and *T. osborni*. (*Trinacromerum kirki* type = 41.5%; *T. osborni* type = 41.2%; Ft. Hayes *T. osborni* = 41.3%). A unique "tongue-and-groove" articulation between propodials and epipodials, however, effectively increased the functional length of the propodial, since very little (if any) movement could have occurred at this type of joint. If tibia and fibula lengths are added to femur length in *T. bonneri*, the resulting length of the "functional propodial" accounts for 40% of total wingfin length, remarkably close to the 41% values for other members of the genus.

Tongue-and-groove articulation characterizes both fore and hind wingfins of *T. bonneri*, differing only in depth of the articular surfaces (Fig. 6). Elements of the first (most proximal) row of epipodials articulate at four distinct facets on the propodial, and elements of the second epipodial row articulate against the propodials just proximal to them. The articular facets are long, slender, concave "grooves", into each of which fits a projecting epipodial "tongue" (analogous to a tongue-and-groove carpentry joint). The epipodial tongue is bounded by a small but distinct rim that marks the distal extent of the propodial over it when the two are articulated. The longest and deepest of these tongue and groove facets are on the leading edges of the wingfins. Those of the fore wingfin are better developed than those of the hind (2 cm deep on humero-radius facet), and the more proximal facets are deeper and more well-developed than are those between the first and second epipodial rows. Generally tight fitting of epipodials and phalanges throughout the wingfins amplifies the overall effect.

Torsion and bending of the wingfin surface caused by resistant water pressure during the attack stroke phase of propulsion is a critical factor in plesiosaur mechanical adaptations (Robinson 1975; 1977; Nicholls & Russell 1991). While hyperphalangy increased wingfin length and therefore wing loading (which increased swimming efficiency and speed),

the fact that so much of the wingfin was composed of a pavement of numerous small elements laid essentially side-by-side made the wingfin more subject to torsion and bending along the numerous joint surfaces. Previous studies have noted offset joint rows and slight lapping of phalangeal articulations as adaptations that reduced torsion and bending of the wingfin in the epipodial region of earlier pliosaurs (Robinson 1975; 1977). The tongue-and-groove articular system seen in *T. bonneri* further increased wingfin strength and rigidity along the longitudinal axis and minimized torsion of the wingfin surface as a whole, which permitted the development of longer wingfins with more wingloading area and greater propulsive power. Water pressure resistance was highest during the attack stroke at the leading edge of the wingfin, which corresponds to the location of the deepest tongue-and-groove facets. Torsion resistance was further enhanced by the perpendicular orientation of the anteriormost (radius or tibia) articular facets to the long axis of the articulating propodial. The tongue-and-groove facet rim that projects distally beyond the articulation surfaces also projects past the angles between the facets, further reducing the possibility of torsion and bending at these joints.

The neck region of *T. bonneri*, particularly size, shape, and facet orientation of the cervical zygapophyses mid-neck, also displays remarkable adaptations to resist torsion and bending caused by water resistance (Fig. 3). Each zygapophysis is extraordinarily robust, broader and thicker in the area of articulation than in the area of origin on the centrum, and each bears a very large, flat, horizontal articular surface (as opposed to inclined articulating surfaces on dorsal vertebrae). Each pair of posterior zygapophyses tightly embraces the anterior edge of the neural spine of the vertebra to which it articulates. Horizontal zygapophyseal articular facets are commonly reconstructed as facilitating lateral (side-side) movement (Romer 1956), but the tight embrasure between neural spines and zygapophyses precludes lateral motion between individual cervical vertebrae. The broad horizontal zygapophyseal facets may instead be interpreted as adaptations to resist dorso-ventral bending (by reducing vertically oriented stresses at the joints, since stress = force per unit area), while the neural spine embrasures would have resisted lateral bending between individual cervicals. Taken together, these vertebral modifications would have resisted torsion and bending of the neck by water resistance. Smaller and less robust zygapophyses near the head and body ends of the neck presumably facilitated the mobility requirements at these major points. This agrees with Storrs' reconstruction of *Trinacromerum* neck flexi-

bility based on the fact that intervertebral cartilage in the TAMU 3001 specimen (now referred to *T. bonneri*) thins posteriad (Storrs 1981). It also agrees with the general perception of pliosaurs as extremely manuevable swimmers, since high-speed directional changes would produce the type of water resistance forces the neck is designed to reduce and resist.

PHYLOGENETIC IMPLICATIONS

Some postcranial characters commonly considered diagnostic in pliosaurs, specifically hindlimb:forelimb ratios and pelvis morphology, should not be heavily weighted. The proposal that hindlimbs are larger than forelimbs in pliosaurs (and the opposite in long-necked plesiosaurs, or elasmosaurs) fails when applied to *T. bonneri*, in which the humerus is longer than the femur. Humerus:femur values for the Trinacro-merwn osborni type and Fort Hayes specimens and the type of *T. kirki* are 0.90, 0.98 and 0.96, respectively, while the value for *T. bonneri* is 1.06. Humerus length exceeds femoral in *Trinacromerum* sp., MDM P80.06.14 as well (figured in Nicholls & Russell 1991). As can be seen, humerus:femur ratios are not even distributed very far to either side of 1.00 in polycotylics, although statistical significance is impossible to evaluate due to small sample size.

Pelvic element morphology, such as pubis-ischium midline symphysis shape, may also prove to be nondiagnostic in pliosaurs, but for different reasons. Ventral placement and plate-like morphology of the pelvic elements, together with the possibility of live-bearing, makes sexual dimorphism a likely source of variation in this region.

Many workers believe that the use of postcranial characters in pliosaur systematics is generally problematic. Despite numerous revision attempts (Williston 1903; 1906; 1907; 1908; Welles 1943; 1962; Riggs 1944; Tarlo 1958; Persson 1963; Sues 1987; Storrs 1993; Bakker 1993), the state of chaos lamented by Williston nearly 100 years ago persists: "There are few orders of reptiles so long and so widely known ... of which our knowledge is more unsatisfactory . . . Very few figures or adequate descriptions have been published of our numerous and diverse types. Not only are the specific characters of the descriptions almost wholly undecipherable, but the generic characters even can be satisfactorily made out in but few ..." (Williston 1903:3). A data base of cranial characters might help resolve problems of pliosaur phylogeny, but there is "little reliable information on the cra-

nial structure . . . and many characters (such as the presence or absence of nasal and quadratojugal) have yet to be confirmed on better preserved and (or) prepared skull material" of plesiosaurs (Sues 1987:129). The lack of data reflects, in part, real ambiguities in the bones. Nasal and prefrontal sutures, for example, are essentially obliterated by heavily rugose striations anterior and dorsal to the external nares in polycotylids (including *T. bonneri*). This region, as well as similar areas on the maxilla below the nares, may indicate the presence of strong muscles that closed the nostril and kept it watertight during submerged high-speed swimming.

It is commonly argued that postcrania display primarily functional or gradual characters that are unsuitable for constructing hypotheses of phylogenetic relationships, and that cranial characters provide more reliable indicators of common ancestry (for example see Bakker 1993). The possibility that at least some plesiosaur cranial characters may also reflect adaptations to swimming and diving suggests the more probable non-dualistic nature of character distribution, with morphology of any particular character being determined by a combination "of function, phylogeny, and developmental constraint, regardless of whether the element is cranial or postcranial. Because of the rich interplay of function and phylogeny in plesiosaur morphology, future revisions of plesiosaurs may therefore contribute not only to our understanding of the taxon itself, but to our understanding of the interface between functional and phylogenetic processes in evolution.

CONCLUSIONS

Trinacromerum bonneri, a member of the final radiation of polycotylid plesiosaurs in the North American Western Interior Seaway, displays a unique set of structural adaptations for high-speed swimming. The wingfins are the longest known in polycotylid plesiosaurs, each being approximately the same length as the thorax. This lengthening was accomplished via elongation of the epipodial region relative to the propodium, which effectively increased wingloading and therefore swimming velocity. Development of tongue-and-groove articulation within the first two rows of epipodials reduced and resisted the increased torsion and bending of the wingfin hydrofoil otherwise caused by the increase in its surface area. The cervical vertebrae also show adaptations to high-speed swimming. A combination of massive zygapophyseal and neural spine embasures on all but the most anterior and posterior cervicals resisted hydraulic forces generated by swimming and high-

speed directional changes.

The "truncated" and "normal" pubis-ischium contacts of the medial symphysis region in *T. kirki* and *T. bonneri*, respectively, and the differences between the shapes of their anterolateral pubic borders, may be sexually dimorphic rather than phylogenetically significant. The significance of this variation cannot be evaluated in the absence of a database of cranial characters in the taxon, however. Compilation of such a database may have been hindered by the very types of high-speed swimming adaptations that have drawn the search for apomorphies to pliosaur postcrania. However, this problematic interplay of function and phylogeny in pliosaur morphology may eventually contribute to our understanding of the interface between functional and phylogenetic processes in evolution.

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