LIFE RESTORATION OF *CHAMPSOSAURUS* HUNTING.

Painting by Jerome Connolly in The Science Museum of Minnesota.

THE LEPIDOSAURIAN REPTILE
CHAMPSOSAURUS IN NORTH AMERICA

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INTRODUCTION

Remains of the moderate-sized eosuchian reptile, *Champsosaurus,* are common in many late Cretaceous and early Tertiary deposits of western North America and in the Tertiary of Europe; yet, they are poorly represented in major museum collections and, by and large, not identified to specific level. The prime limiting factor responsible for the latter situation is the incompleteness of materials and the extreme morphological uniformity that runs throughout the group.

During the course of several seasons, the writer made extensive collections of fossil vertebrates in western North America. A sizable quantity of champsosaurian material was included in these collections. Confusion in trying to work out the taxonomy of this material provided the incentive for the initiation of the present study.

Handicaps encountered by most workers have been due chiefly to inadequate samples resulting in much synonymy. It was felt, however, that if enough material was analyzed, specific taxonomy could be improved upon. As comparisons were made, characters that are considered significant in delineating species were found. Many are subtle in expression, yet are consistent in their occurrence. Due to the lack of skulls, most distinctions rest on postcranial features. Age and individual variations have definite trends as well that have been helpful in the present overall study. Age variations, however, are much easier to determine than the latter, which must be regarded as only suggestive.

Most informative of this group is a very large form from the late Paleocene that is herein referred to as the new species, *Champsosaurus gigas.* In being very abundant and fairly complete, it presents much interesting morphological evidence—some new and some in a better light; hence, the discussions of general morphology and functional morphology draw heavily from it.

The present study treats *Champsosaurus,* the long-snouted North American form. Only brief reference is made to other champsosaurids. In addition to the rather large sample of *Champsosaurus* now in The Science Museum of Minnesota, materials from seven other institutions were examined. Certain other materials, namely, those in the Royal Ontario Museum, were not examined but are referred to in the present work.

In the present work, the term "Clarkforkian" is used rather than Tiffanian (Wood, 1967) to designate the late Paleocene span from Olive to the Eocene boundary. Figure 1 is a correlation chart for North American champsosaurs.

INTRODUCTION
ACKNOWLEDGMENTS

ABBREVIATIONS

The following list refers to the abbreviations for the institutions cited in the present work:

AMNH	American Museum of Natural History
FMNH	Field Museum of Natural History
USNM	United States National Museum
NMNS	National Museum of Natural Sciences, Ottawa
PU	Museum of Princeton University
ROM	Royal Ontario Museum, Toronto
SDSM	South Dakota School of Mines and Technology
SMM	Science Museum of Minnesota
SMNH	Saskatchewan Museum of Natural History, Regina

SPECIES OF CHAMPSOSAURS

In 1876, E. D. Cope erected the suborder Choristodera referring to the "noncoossifications" of certain reptiles as distinctive. Noncoossifications of the sacral vertebrae with one another and the neural arches with the centra, and the absence of the chordal perforation of the centra were his major diagnostic criteria. To this taxon he assigned his newly founded "rhynchocephalian" *Champsosaurus*. Allocation of this genus to the rhynchocephalia was later amended by Romer (1945) on grounds that the typical rhynchocephalian beak is wanting. The subordinal status of *Champsosaurus* remains.

In recent communication to the writer, Dr. Donald Baird has pointed out an interesting first account of champsosaur remains. In 1873, 3 years prior to Cope's description, Joseph Leidy described and figured a single sacral vertebra for which he proposed the name *Nothosaurus occiduus*. This specimen is that of a champsosaurid, but further determination is doubtful.

It is debatable whether to use *Nothosaurus* as a senior synonym or not. However, it is my contention that *Nothosaurus* is no longer a valid term and is, therefore, declared a *nomen vanum* (ref. p. 11).

Aside from a few exceptionally fine skeletons that are descriptive of the "valid" species, collections mostly comprise assortments of vertebrae, heavy limb extremities, and rib fragments. The characteristic spool-shaped vertebral centra, which are the most abundant remnants of skeletons and readily identified as belonging to champsosaur, have often been regarded as diagnostic on the specific taxonomic level and are the basis for new names. This has been found not to be the case by Brown (1905), Russell (1956), and the present study. Consequently, a number of species have been placed in synonymy.

Cope's original description (1876) of *Champsosaurus* included four species based on vertebrae largely from the Judith River beds (late Cretaceous) of Montana. In later publications (1881 and 1882), he described three additional species, again on vertebrae, bringing the total number to seven. These latter three are from the Puerco (lower Paleocene) of New Mexico. In reviewing the osteology of the genus, Brown (1905) considered only four of Cope's types acceptable because of insufficient and eroded remains. Those accepted by Brown (ibid.) are: the type species, *C. annectens, C. profundus, C. australis,* and *C. saponensis*. Three are considered invalid: *C. brevicollis, C. vaccinsulensis,* and *C. puercensis*. In his account, Brown (ibid.) describes two additional new species. These are *C. laramiensis* and *C. ambulator* from the Hell Creek beds of Montana. Both of these descriptions are based on nearly complete skeletons.

In his description of *C. albertensis*, Parks (1927) states that *C. albertensis* is very close to and may be identical with *C. annectens*. In a subsequent report, Parks (1933) states concerning the occurrence of this genus in the Belly River sediments of

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Alberta, Canada: "On the basis of scattered vertebrae alone, eight to ten species might be differentiated with reasonable assurance." He recognized *C. natator, C. inflatus, C. cf. profundus, C. cf. australis,* and *C. inelegans* from the Belly River beds. In addition, he acknowledges *C. saponensis* of Cope and *C. laramiensis* and *C. ambulator* of Brown as valid. Russell (1956) believes that not only are those species rejected by Brown invalid but *C. annectens, C. australis, C. inflatus,* and *C. inelegans* as well. The uncertainty of identifications relying on vertebrae of the various portions of the column are grounds for the exceptions taken.

In attempting to evaluate the present large number of vertebrae available both as complete columns and as individual bones, it was extremely difficult and most often impossible to delineate species. Many juvenile bones and a few nearly complete skeletons are included in the sample as well, but specific morphological distinctions based on vertebrae are not made easier because of it. Differences between young and old specimens are a matter of degree and proportion. It is for this reason that the juvenile specimens are considered such rather than merely as smaller species.

All species considered valid in the present work show other morphological differences and are stratigraphically separated from one another except for *C. laramiensis* and *C. ambulator,* (Fig. 1). These, however, are readily separated morphologically when sufficient materials are available.

Russell's conclusions of validity of species are concurred with generally. The following species are recognized in the present work:

Order CHORISTODERA
Family CHAMPSOSAURIDAE
Genus CHAMPSOSAURUS
Champsosaurus natator Parks, 1933

? Champsosaurus annectens Cope, 1876.

? Champsosaurus profundus Cope, 1876.

? Champsosaurus brevicollis Cope, 1876.

Champsosaurus natator Parks, 1933, p. 122.

Champsosaurus inflatus Parks, 1933, p. 131.

Champsosaurus inelegans Parks, 1933, p. 135.

TYPE. ROM 5737 ct.

HORIZON AND LOCALITY. Belly River formation, Upper Cretaceous, Red Deer River, Alberta, Canada.

REFERRED SPECIMENS. ROM 5738 ct., 5739; SMM P68.55.1.

DISCUSSION. The type from the Oldman formation of Alberta, Canada is well documented by essentially complete skeletal materials including the skull (Parks, 1933; Russell, 1956; Fox, 1968). Other described species from the Oldman and equivalent Judith River beds are based on very incomplete materials.

Cope described four species in 1876 from the Judith River beds of Montana. Three of these seem best included under *C. natator* as senior synonyms because no differences that are considered significant can be found. However, this allocation is made provisionally as their inclusion here is mostly because of stratigraphic agreement.

The species are *C. annectens*, the type species of *Champsosaurus*, which was founded on a single centrum of indeterminable specific affinities; and *C. profundus*, defined on vertebral measurements that differ slightly from *C. natator* (Parks 1933). The unreliability of this argument for distinction has been substantiated; and *C. brevicollis*, which is indeterminable because of weathering effects, is probably part of the same population as well.

In 1933, Parks described *C. inflatus* from the Belly River formation distinguishing it from *C. natator* by its ilium, which has a forward extension of the blade, and a partial sacrum in which the neural spines are unusually short.

		ALBERTA	SASKATCHEWAN	MONTANA	DAKOTAS	WYOMING	COLORADO	NEW MEXICO
EOC.					Golden Valley	Willwood		
PALEOCENE	"CLARKFORKIAN"		Ravenscrag	Bear Creek / Olive	Sentinel Butte		Plateau Valley	
	TIFFANIAN			Circle	Tongue River			
	TORREJONIAN			Lebo				
	PUERCAN			Tullock	Cannonball			Puerco
U. CRETACEOUS			Frenchman	Hell Creek	Hell Creek	Lance	Arapahoe / Laramie	McDermott
		Edmonton	Whitemud / Eastend	Lennep	Fox Hills	Lewis	Fox Hills	Kirtland / Fruitland
		Bearpaw	Bearpaw	Bearpaw	Pierre		Pierre	Lewis
		Belly River		Judith River / Claggett / Eagle				

Fig. 1. Correlation chart of champsosaur-bearing strata in North America. Occurrence indicated by stippling. The names "Circle" and "Olive" refer to local faunas containing champsosaurs.

The ilium is smaller, lighter, and very likely of a younger specimen than that to which it is compared by Parks (ibid., Plate IV, Figs. 2 and 3). In figure 54 of the present work, a series of ilia are compared to illustrate age variations. Note the shape of the blade in younger forms.

From Parks' description and figures of the sacral vertebrae of *C. inflatus*, it would appear that they differ from *C. natator* only in the neural spines. These, however, look to be abnormal in his figures (ibid., Plate II, Figs. 10, 11, and Plate III, Fig. 10), lacking definite dorsal terminations and the height that would make them consistent with those of the dorsal series. For example, the vertebra in figure 3 (Parks ibid., Plate II) is one of the last few dorsals. The height of the neural spine is much greater than that of the first sacral of *C. inflatus*, which has probably been reduced by weathering or disease.

In further description, Parks (ibid.) misinterpreted the third cervical vertebra, which he designated as the type of *C. inelegans*, as a more posterior element. As a consequence, in his comparison with his type of *C. natator* in which the third cervical vertebra is missing, he found dissimilarity. Russell (1956, part VII, Figs. 6, 7, and 8) shows the third cervical of *C. natator*. It does not differ significantly from that of *C. inelegans*; therefore, this species and that discussed above are both herein regarded as junior synonyms of *C. natator*.

Champsosaurus albertensis Parks, 1927

Champsosaurus albertensis Parks, 1927, p. 10.

TYPE. ROM.
HORIZON AND LOCALITY. Edmonton formation, Red Deer River, Alberta, Canada.

DIAGNOSIS. Relatively large species with shortened epipodials.

DISCUSSION. This species is known only from the Edmonton. Its lower limbs are significantly shorter than those of *C. natator*, which has elongated epipodials. It is also substantially shorter in lower limbs than other species. Neither cervical nor anterior dorsal ribs are noted as having uncinate processes as is the case of *C. natator* and *C. laramiensis* also from the Cretaceous.

Champsosaurus laramiensis Brown, 1905

? *Champsosaurus australis* Cope, 1881, p. 670.

? *Champsosaurus puercensis* Cope, 1882, p. 195.

? *Champsosaurus saponensis* Cope, 1882, p. 196.

Champsosaurus laramiensis Brown, 1905, p. 8.

TYPE. AMNH 982.
HORIZON AND LOCALITY. Hell Creek beds, Tullock formation, Garfield County, Montana.

REFERRED SPECIMENS. AMNH 981; SMM P62.10.1, P63.13.1, P63.14.1, P64.10.1, P65.3.1, P65.9.1, P68.55.1, P68.68.1, P69.10.1, P69.13.1, P69.14.1.

DISCUSSION. The type specimen is a nearly complete skeleton. As far as can be determined, it is the sole representative of the genus in the Hell Creek formation. Its range includes the Frenchman formation of Saskatchewan and is perhaps wider. It extends into the Tullock (Paleocene) formation in northeastern Montana and evidently to the Puerco of New Mexico.

It is clearly distinct from *C. ambulator*, also of the Tullock; viz., having a less spatula-shaped termination of the snout and fewer palatal teeth. In the postcranial skeleton, the girdles are of lighter construction and the limbs somewhat longer. The humerus of *C. laramiensis* shows less twisting of the shaft; the ento- and ecto-tuberosities are higher and more confluent with the proximal head. The delto-pectoral ridge is only moderately developed, and the distal end is less massive with an ectepi-

condylar groove like all other species except *C. ambulator*. The femur has the trochanter located higher on the shaft than in *C. ambulator*.

None of Brown's specimens of *C. laramiensis* show the incising of certain dorsal ribs that are present in larger specimens of this species; nor is development of uncinate processes on the cervical and dorsal ribs indicated—features that it has in common with *C. natator* and *C. gigas*.

Cope described *C. australis* upon eleven vertebral centra, four of which he figured (1884, Plate XXIIIb, Figs. 1-4). These are juvenile elements and may represent more than a single individual. Their characteristically greater width as compared to length and height that Cope used as distinguishing features is attributed to immaturity and is typical of all extremely young forms.

C. saponensis is also included here because its size and form of the six cervicals and dorsals that are preserved agree closely with those of *C. laramiensis,* especially the pronounced ventral carina more typically *C. laramiensis* than *C. ambulator*.

Cope's figures of his type of *C. puercensis* (1884, part XXIII, Figs. 5, 6, and 10) are probably of posterior dorsal vertebrae of an adult animal. Narrowing of the base of the anterior face is a striking feature that occurs to various degrees in *C. laramiensis*. It seems to be more of an individual variation than one of age. Size and form, such as, development of the facets on both atlas and axis, also indicate adult development like that seen in *C. laramiensis* as well as other species (Figs. 7, 8, and 9, ibid.).

Because of stratigraphic occurrence of the above and general agreement with *C. laramiensis*, these forms seem most appropriately inserted here as senior synonyms; however, this is done provisionally. Under this arrangement, the geographic range of *C. laramiensis* is extended even further. *C. ambulator,* as far as the record indicates, comprised a more limited population with a much smaller geographic and geologic range.

Champsosaurus ambulator Brown, 1905

Champsosaurus ambulator Brown, 1905, p. 22.

TYPE. AMNH 983.

REFERRED SPECIMEN. SMM P63.14.1.

HORIZON AND LOCALITY. Hell Creek beds, Tullock formation, Garfield County, Montana.

DIAGNOSIS. A relatively short-limbed species with heavy girdles.

DISCUSSION. This species occurs only in the Tullock formation where it is associated with *C. laramiensis*. Differences between it and the latter are noted in the preceding discussion. Following are a number of salient morphological features that distinguish this species: prominent infraglenoid process on the coracoid, strong deltoid ridge and radial condyle on the humerus, ectepicondylar groove closed distally on the humerus, low position of trochanter on the femur, and very elongate inner border on the pubis.

Champsosaurus vaccinsulensis Cope, 1876
nomen vanum

Champsosaurus vaccinsulensis Cope, 1876.

TYPE. In AMNH.

HORIZON AND LOCALITY. Judith River beds, Montana.

DISCUSSION. The type specimen is a weathered vertebral centrum and belongs to a different order, as Brown (1905) has indicated.

Nothosaurus occiduus Leidy, 1873
nomen vanum

Nothosaurus occiduus Leidy, 1873, p. 287, figures 11-13, pl. XV

Nothosaurops occiduus Leidy, 1873, figures 11-13, pl. XV

TYPE. Not located.

HORIZON AND LOCALITY. Moreau River, upper Missouri River.

DISCUSSION. This species is based on a single sacral vertebral centrum of some champsosaurid of uncertain stratigraphic and geographic position. It was collected by Professor Hayden on the Moreau River, a tributary of the upper Missouri. Unfortunately, no reliable stratigraphic level can be stated for this specimen as the Moreau flows through a variety of sedimentary deposits of different ages. *Nothosaurus* is herein considered a *nomen vanum* because of the above and lack of general use.

In the description of plate XV (Leidy, 1873), the name *Nothosaurops occiduus* appears. This is interpreted as a typographical error and is included as a junior synonym being that *Nothosaurus occiduus,* as it appears in the title, is the correct spelling.

Champsosaurus gigas, new species

TYPE. SMM P71.2.1. A nearly complete skeleton with a partial skull and lower jaw of young adult animal.

HORIZON AND LOCALITY. Sentinel Butte formation, Ft. Union Gp., late Paleocene, NE¼SW¼ sec. 28, T. 141 N., R. 104 W., Golden Valley County, North Dakota.

REFERRED SPECIMENS. SMM P60.2004, postcranial skeleton lacking portions of limbs and girdles and the feet; PU 16239, complete skull, somewhat distorted with partial lower jaw; PU 16240, complete skull, somewhat distorted; SDSM 53508, postcranial skeleton lacking most of the anterior half; USNM 20521, partial postcranial skeleton; FMNH PR93 and P26132, partial skulls and skeletons.

DIAGNOSIS. A very large species having unusually long hind limbs and a pronounced development of rib incising. The geographic range of this form is quite large.

DISCUSSION. The occurrence of a large champsosaur in the late Paleocene of western North America has been of interest for some time (Langston 1958). Its size identifies it in the latest Paleocene ("Clarkforkian") Tiffanian deposits where it is found in prodigious numbers. A possible ancestor, *C. laramiensis,* is abundant in Puercan strata; but neither it nor any of the other abundantly represented early Paleocene champsosaurs shows a tendency toward gigantism. Because of the extreme conservativeness exhibited throughout this group, particular attention has been given to subtlety of morphological detail. During the course of many comparisons upon an admixture of juvenile and adult specimens, some relationships were brought out that are considered significant. This, in addition to its stratigraphic position and its size, has resulted in recognition of a new species herein described as *Champsosaurus gigas.*

SKULL

Of the eight specimens used in the present study, two have complete skulls (Figs. 2, 3, 4, and 5). Both are of similar size, and judged to be adults. They are generally well preserved but crushed as well as otherwise distorted. There is displacement of elements especially in the posterior regions. PU 16239 has essentially one half of the lower jaw associated with it. Teeth are present in both specimens. The skull and jaws of the type SMM P71.2.1 are preserved in part but badly fragmented and of use mainly in a determination of sutural paths.
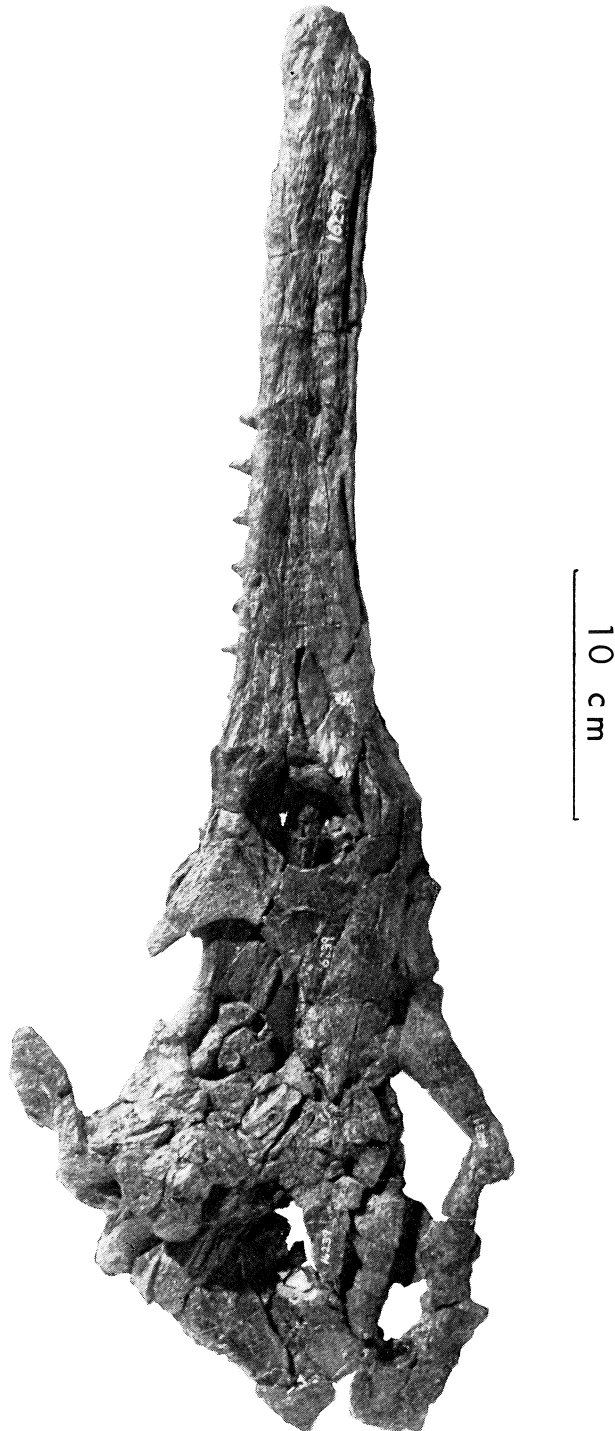
Fig. 2. Skull of *Champsosaurus gigas*, PU 16239. Dorsal view.
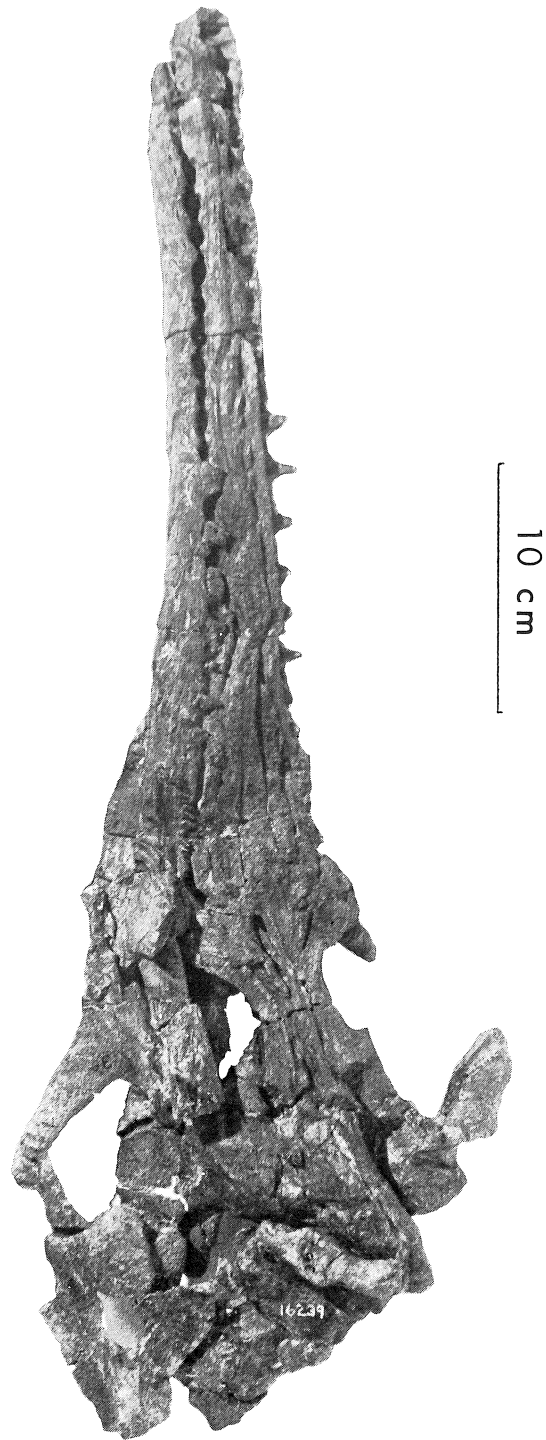
Fig. 3.   Skull of *Champsosaurus gigas,* PU 16239. Ventral view.
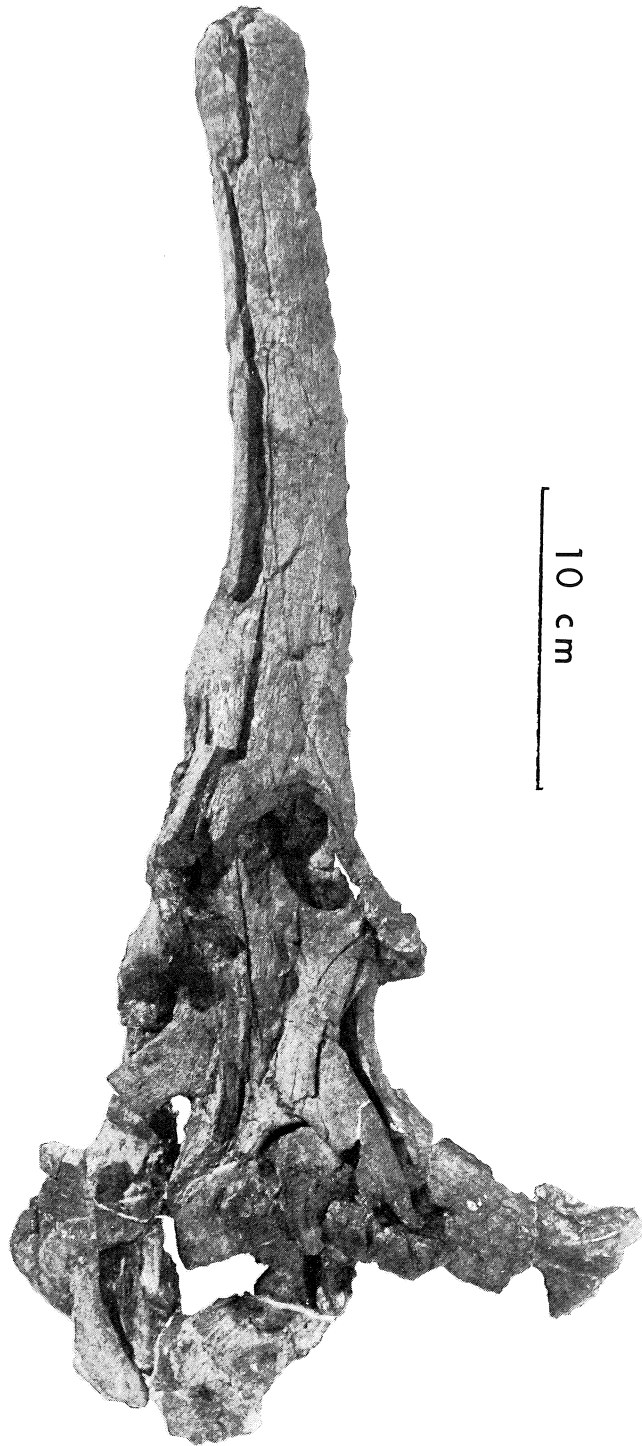
Fig. 4. Skull of *Champsosaurus* gigas, PU 16240. Dorsal view.

10 cm
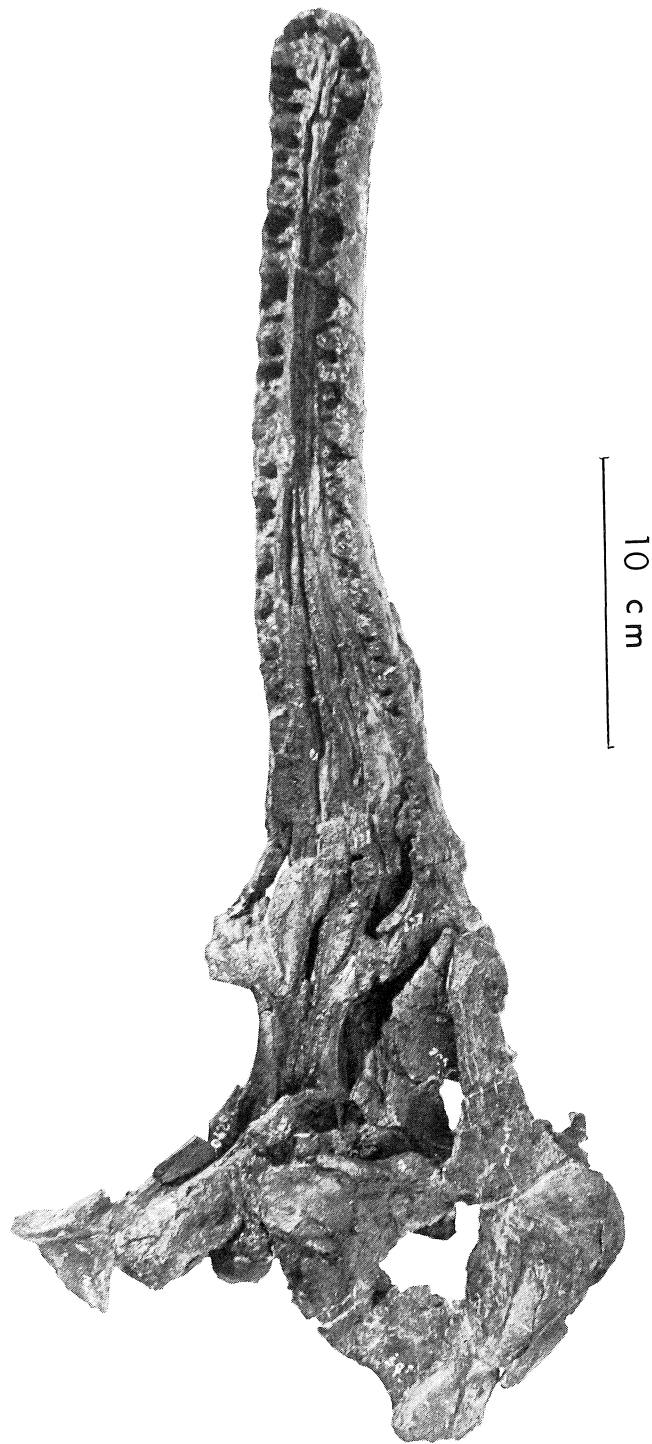
Fig. 5. Skull of *Champsosaurus* gigas, PU 16240. Ventral View.

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PREMAXILLAE

The premaxillae are short and form the bluntly rounded, somewhat bulbous tip of the snout. The sutures defining these elements are not entirely clear in either PU 16239 or PU 16240, probably due to age; and they are not preserved in the type. Laterally, the maxillo-premaxillary suture begins at about the level of the seventh tooth and meanders dorsally toward midline. In dorsal aspect, the premaxillae narrow slightly as they approach the maxillae. Just anterior to the maxillo-premaxillary junction, there is a deep lateral groove, probably vascular, that emerges from a small lateral foramen near the suture and arches forward toward the oral margin. It is a marked feature on both PU 16239 and PU 16240.

Anteriorly, these elements nearly enclose the fused external nares. The anteriormost projection of the nasals interrupts them dorsally on midline. This area is somewhat crushed in the present skulls, and separation has taken place along the sutures. Medially, they are separated for their entire length by the narrow nasals. The external nares open forward with the floor of the narial chamber extending a bit further forward than the upper rim of the opening.

Ventrally, the maxillo-premaxillary sutures apparently follow much the same course as they do dorsally. Centrally, these bones have a direct connection. There is a small shallow pit present on the midline near the anterior end. This does not penetrate to the interior surface as it does in some forms. There are provisions for seven teeth in each premaxilla—the third and fourth being the largest in the entire skull.

MAXILLAE

The maxillae of *C. gigas* are long elements comprising the greater part of the snout. They contact the premaxillae at a slight posterior constriction of the latter and extend rearward until they unite with the prefrontals and lachrymals medially and the jugals intertonguing laterally. They are separated for their length medially by the nasals and the tapering prefrontals. Above the oral margin, a series of pits that are in line with that noted in the premaxillae characterize this bone.

Ventrally, the maxillae continue below the orbits, being separated from them by the overlying jugals. Posteriorly, on their inner surfaces they border the palatine opening and adjoin the palatines, vomers, and finally the thin, neomorphic ossification called internarial by Russell (1956) and ethmoid by Brown (1905). Teeth are present along the oral borders of these elements. In PU 16240, there are from 25-27 teeth present in each element. The teeth in the hinder one third are appreciably smaller—a condition consistent with other species.

NASALS

As in other forms, the nasals are coossified medially. Their length is about two thirds that of the snout, extending from the narial rim rearward along midline and forming a wedge as they do in *C. laramiensis* between the anterior points of the paired prefrontals. The nasals are not as noticeably tapered for most of their length as in this form, however. The extreme anterior end probably extended beyond the adjacent portions of the premaxillae, contributing to the dorsal part of the narial opening. In both PU 16239 and PU 16240, crushing has opened the lateral nasal sutures (Figs. 2 and 4) on one side or the other.

INTERNARIAL

This bone is well defined in *C. gigas* (Fig. 6). It is shorter than the overlying

nasals, beginning somewhat ahead of them and continuing forward to about the level of the maxillo-premaxillary suture. The narial passages were divided, at least along this portion of the skull. An anterior cartilaginous extension may have also existed and functioned in separating the chambers completely. A small tuber at the extreme tip of the floor of the opening that may have served as an anchor for this extension suggests this.

PREFRONTALS

These are centrally located bones suturally united along the median and form the upper anterior border of the orbits and a very thick portion of the face. Suturally attached at the side is the lachrymal, which forms a continuation of the anterior orbital rim. The prefrontals expand gradually in width along the lachrymal edge, then narrow along the maxillary edge. At the anterior extremity, they are divided by the intertonguing nasals.

LACHRYMALS

The lachrymal is a small triangular element. Its posterior side is part of the forward orbital rim, as noted above. The rim is nodular in texture in this area. Above, this bone meets the prefrontal. Along its lateral margin, it embraces the maxilla in front and the jugal behind.

JUGALS

In dorsal aspect, the jugals match *C. laramiensis* more nearly than *C. natator* in that the extent of their forward projections are about the same. The anterior wedge of this bone penetrates the maxilla. Its dorsal edge joins the lachrymal and continues posteriorly to complete the lower margin of the orbit and eventually meets the postfrontal behind the orbit. Laterally, it lies above the posterior extension of the maxilla whereby the suborbital arch is constituted.

Beyond the orbit, the jugal swings outward and joins the quadratojugal in an oblique posterior suture—the jugal being internal to the quadratojugal at the ends. The angle of this suture apparently has been reversed in ventral aspect for *C. natator* (Russell, 1956; Fig. 2, p. 7).

FRONTALS

These bones meet along the median and form a dorsal continuation of the orbits. The frontal joins the prefrontal in an interlocking step-like suture dorsal to the orbit, and the parietal in similar fashion posteriorly. Laterally and behind the orbit, it lies next to what has been called the postorbital (Brown, 1905 and Russell, 1956) but is herein interpreted as the postfrontal. This will be discussed below. The surface of the frontal is deeply sculptured with the most characteristic feature of ornamentation on the head. About two thirds of the way back from the front of this element is a lateral projection or tubercle that is more or less opposite its mate on the other frontal (Fig. 6). The bone is sharply depressed between the ridge bearing this feature and its lateral border. The bone is thickened to form the internal orbital wall. Along all suture contacts, the bone thins to more normal thickness.

POSTFRONTALS

The postfrontals (Fig. 6) in *C. gigas* resemble those (postorbitals) of *C. natator* (Russell, 1956) in that they run from the posterior edge of the orbit to the supratemporal opening contacting both the frontals and parietals along their superior margins. As compared with bones more median to them, the surfaces are relatively smooth except for some heavy striations just behind the orbits. Laterally, a strong union with the jugal is achieved by omitting most of the postorbital contact with this bone. Posteriorly, the postfrontals and the
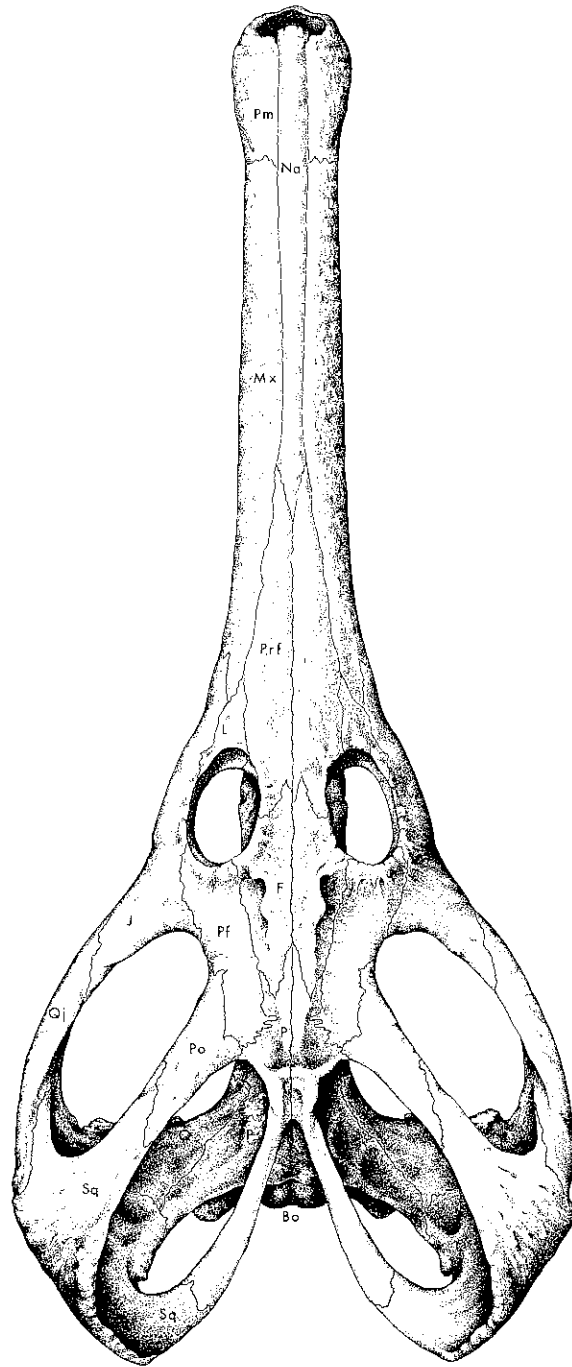
Fig. 6. Restoration of the skull of *Champsosaurus gigas* in dorsal view. Bo, basioccipital; F, frontal; J, jugal; L, lachrymal; Mx, maxilla; Na, nasal; P. parietal; Pf, postfrontal; Pm, premaxilla; Po, postorbital; Prf, prefrontal; Q, quadrate; Qj, quadratojugal. Based on PU 16239 and PU 16240.

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postorbitals meet obliquely.

POSTORBITALS

The bones posterior to the postfrontals and making up the anterior portion of the supratemporal bar are considered to be the postorbitals (Fig. 6 and p. 52). They are flat and smooth. The postorbitals are separated from the postfrontals by a Z-shaped suture in both external and internal views. At their anterolateral extremity, they retain connection with the jugals ventrally. As seen in figure 4, they taper rearward and form a long, oblique junction with the squamosals.

PARIETALS

In *C. gigas*, PU 16240, the skull is opened along the heavy interparietal suture. Here the exposed contact area, which can be observed in sagital section (Fig. 4), is very thick; and a minor crest is developed. The posterior end of the midline, where the crest projects upward and is the highest, is not well preserved in PU 16239. However, a slight medial depression, as has been described in other forms (Brown, 1905; Russell, 1956), is indicated forward. In PU 16240, no such depression is apparent. Instead, between midline and the outer edges, the bones are concave. Sutures between these elements and the postfrontals and frontals are very sinuous in nature. The parietals do share a short suture also with the postorbitals at the hindermost point of the postfrontals. Behind the level of the postfrontal, the inner side of the superior temporal opening is formed; and a posterior projection, although not well preserved in either specimen, was present for contact with the most posterior portion of the squamosal.

The oblique ridge on the inner wall of the superior temporal opening, presumably for demarcation of different temporal muscle areas as noted by Russell (1956),

is sharply defined in PU 16240. Ventral relationships between the various bones are obscured in the present skulls, but it would seem that they were not too unlike those of their dorsal patterns.

The inner wall is exposed in PU 16239 (Fig. 2), although the sutural contacts are indistinct.

At its base, the parietal appears to be bound to at least two elements: the squamosal (prootic of Russell, 1956) posteriorly, and a second bone forward, which has been referred to as the prootic (Fox, 1968) and epipterygoid (Russell, 1956). Demarcation of this forward bone in *C. gigas* is vague, and neither is there good evidence of a neomorphic segment like that reported for *C. natator* (Fox, 1968). The presence of the columellar-shaped "epipterygoid" as described by Fox (ibid.) is uncertain also. The anterior edge is a smooth arch to which the supposed anterior cartilaginous portion of the braincase adhered. On the posterior ends, they overlie a small supraoccipital of uncertain configuration.

SQUAMOSALS

As indicated above, the posterior contact of the lateral wall of the parietal is either with the squamosal or prootic, depending on interpretation. Based on the evidence offered by *C. gigas,* however, the sutures are not well enough preserved to argue the point. The bone areas in question are badly distorted in both skulls. A small foramen (pterygoquadrate foramen) is present in both skulls along the preserved suture.

The squamosals occupy the posteriormost part of the skull and contribute the rear support of the bars defining both temporal openings. They present three long diagonal sutural unions with the quadratojugal, postorbitals, and the parietals respectively. Below the level of the temporal fossae, they are continuous with the

quadratojugals, quadrates, and the parietals/prootics that form a broad, flat ventral plate giving the head its characteristic shape. The opisthotics (exoccipitals of Brown, 1905) lie in close contact also. Posteriorly, the outer rims of the squamosals are smoothly rounded.

QUADRATOJUGALS

In *C. gigas,* PU 16240, this bone is presented as a thin, flat bar between the jugal and the squamosal that forms the outer side of the infratemporal opening. Ventrally, it also merges with the quadrate in a well defined suture immediately behind the articular facet for the lower jaw.

QUADRATES

The quadrate is completely immobile, forming as it does an integral part of the ventral plate of the temporal region. It is interior to the quadratojugal and anterior to most of the squamosal. Its anteromedian end blends into the posterior pterygoid ramus. Ventrally, it is overlapped by the distal end of the opisthotic. Sutures in the vicinity of its inner border are not clear in either skull, as noted. The broad surfaces of this bone are thin and smooth. Along its anterior edge arises a stout, articular condyle for the lower jaw. This feature is elongated transversely and depressed obliquely through its center.

SUPRAOCCIPITALS

As indicated above, this small solitary bone cannot be described accurately in any of the present skulls because of distortion and fragmentation of the skulls.

EXOCCIPITALS

The exoccipitals surmount the basioccipital to form the sides of the foramen magnum. They are largely preserved in the type (Fig. 8) and show most of the relationships. Each is constricted above its base. Presumably, the upper, inner ends of these bones met the supraoccipital and carried posterior projections for contact with the atlas. Lateral to the foramen magnum are deeply incised areas along the exoccipital-opisthotic fusion. Deep within these areas are a pair of foramina for posterior cranial nerves, X and XII, according to Fox (1968).

OPISTHOTICS

Orientation of these elements is clearly shown in the type also (Fig. 8). They originate at the level of the exoccipital contact, which is much higher up on the occipital region than in other forms. They angle downward and rearward to lie in close opposition to the squamosals (prootics of Russell, 1956) and the quadrates. The dorsal squamosal sutural surface on this bone is very broad and partially extended over the outer, upper end of the exoccipital. Its outer end is broadly squared.

BASIOCCIPITAL

This element consists of a massive, rounded occipital condyle that is set out by transverse depressions above and below. There is a central groove that runs for most of its vertical length. Dorsally, the basioccipital affords a foundation for the lateral occipitals between which it contributes the floor of the foramen magnum. The somewhat deformed element is seen in PU 16239 and PU 16240, and a relatively undisturbed condition is seen in SMM P71.2.1 (Fig. 8). Its basal posterior projections are steeply inclined and deflected caudad. The amount of rearward projection probably reflects age as development of these projections is greater in larger specimens. The hinder margins have prominent, striated areas that distinguish them from the tightly fused overlying parasphenoid sheath.
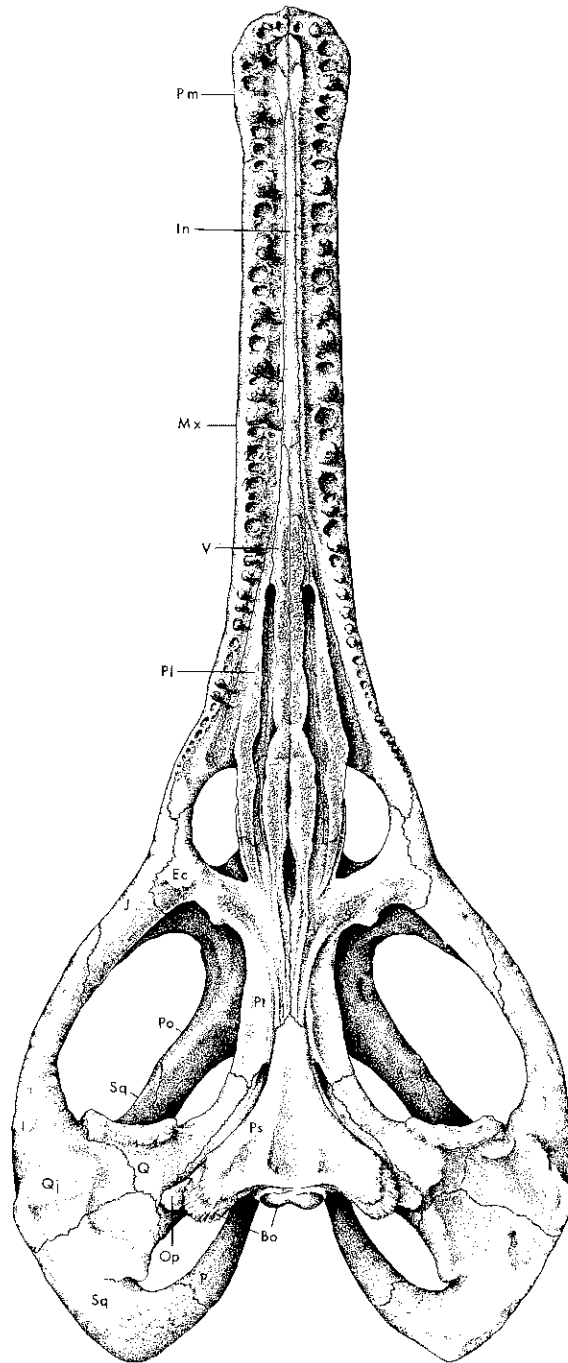
Fig. 7. Restoration of the skull of *Champsosaurus gigas* in ventral view. Bo, basioccipital; Ec, ectopterygoid; In, internarial; J, jugal; Mx, maxilla; Op, opisthotic; P, parietal; Pl, palatine; Pm, premaxilla; Po, postorbital; Ps, parasphenoid; Pt, pterygoid Q, quadrate; Qj, quadratojugal; Sq, squamosal; V, vomer. Note the conical shape of the maxillary and premaxillary teeth and the shallow pits for their reception. Based on PU 16239 and PU 16240.

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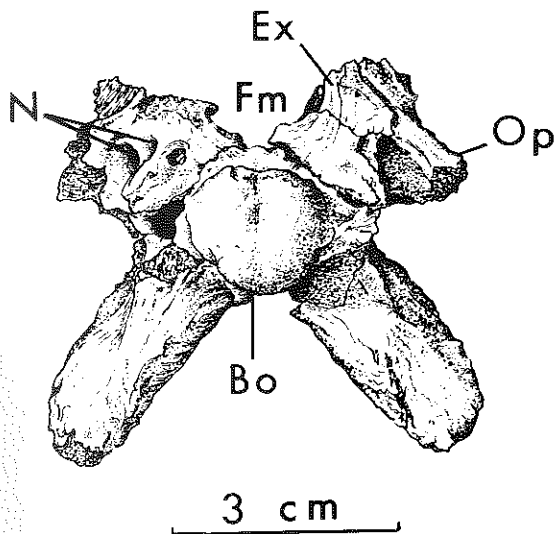
Fig. 8. *Champsosaurus gigas*, type specimen SMM P71.2.1. Occipital region of the skull. Bo, basioccipital; Ex, exoccipital; Fm, foramen magnum; N, openings for cranial nerves; Op. opisthotic.

BASISPHENOID

The basisphenoid is completely concealed ventrally or is lacking in the present material. The lateral gaps between it and the pterygoids are present but have been closed by lateral compression; hence, any view of the internal structures, as seen in *C. natator* (Fox 1968) for example, is unavailable. In PU 16239 and PU 16240 (Figs. 3 and 5), the parasphenoid narrows rapidly toward the front and makes an acute insertion between the pterygoid ends. Dorsally, portions of the above skulls, seemingly contiguous with the basisphenoid (basisphenoid of Fox, 1968 and post-optics of Russell, 1956), are preserved in a crushed condition. It is best shown in PU 16239 (Fig. 2) as an anterior extended trough on the floor of the braincase.

PTERYGOIDS

The pterygoids are outlined in ventral aspect in figure 7. They differ some from those of other described species in the path of the sutures. Their midline opposition is incomplete at the distal end where they split from one another and branch laterally to make a long overlapping contact with the quadrates, and at about the level of the ectopterygoids where an elongate interpterygoid vacuity is present. In specimen PU 16240, the anterior suture with the palatine is just visible (Fig. 5). It enters from the palatine vacuity and arches anteromedially. Its relationship to the vomer is simple and direct to midline. The interpterygoid vacuity is bordered on either side by two tooth-bearing ridges that diverge forward. One is at the edge of the opening, the other at the lateral border of the bone. A restored view is available in figure 7.

ECTOPTERYGOIDS

This structure in the form of a bar separates the palatine vacuity from the temporal opening. Its proximal sutural definition is indistinct in both specimens and appears to be completely ankylosed with the pterygoid. Attachments to the jugal and maxilla, on the other hand, are very bold and in the form of a lateral buttress. As in other species, a keen ridge on the ventral surface of the pterygoid is continuous onto this surface and changes in that teeth are borne here on the ridge. This ridge begins far back on the pterygoid and follows the expansion of the element to remain lateral to the two anterior tooth-bearing ridges mentioned earlier.

PALATINES

The palatine fills the space between the posterior maxillary projection and the vomer. It narrows forward to about the level of the last occurrence of palatal teeth and ends in a point. Laterally, it forms about half of the wall and roof of the in-

ternal narial opening. Its suture with the vomer passes approximately through the center of this opening and the posterior trough into which it opens. A tooth shagreen continues atop a narrow lateral elevation on the outside of this bone from a similar elevation on the pterygoid behind. Teeth are numerous and more nearly dispersed like *C. laramiensis* than other species.

VOMERS

The vomers lie in juxtaposition from about half way along the medial length of the maxillae to the level of the forward edge of the palatine vacuity. At their extreme tips, their lateral edges converge to touch the internarial bone. At about midlength, they are constricted and continue rearward as a narrow elevation dividing the internal openings of the nostrils. The elevation descends gradually to the level of the posterior palate or the floor of the narial openings. In forming the medial half or so of the narial trough mentioned above, they join the palatines laterally in the bottom of the trough and extend posteriorly together until intercepted by the pterygoids. Just above the narial openings, the vomers briefly embrace the palatines. Vomerine teeth are present along a central row throughout most of the length of the bones except for the most anterior tips.

MANDIBLE

A single, lower jaw-half of *C. gigas* is represented in PU 16239 (Fig. 9). It lacks only the end of the angular and the articular. This portion is, however, conveniently preserved in the type SMM P71.2.1. The jaw is long and slender and looks much like that of the rest of the group, although the symphysis is somewhat longer. The single jaw preserved is flattened so that in dorsal view it is straight.

DENTARIES

The dentary comprises most of the length and lateral area of the mandible. It unites with the opposing half of the lower jaw along a symphysis that covers close to the anterior half of the length of the jaw. A deep Meckelian groove runs the length of the symphysis a bit below longitudinal center. Anteriorly, the groove becomes shallow and fades into the distal alveolus. The dentary bows ventrad to the region of the posterior point of the symphysis and rises posteriorly to join the surangular. The union with this bone is obscured but was probably in the striated area. The very smooth surface beyond this is believed to be mostly surangular. Medially, it is overlain by the splenial, and aside from the symphysis is exposed only along the dorsal rim of the jaw. A single row of teeth is present on the rim and decreases in size from front to rear. The last few remain just beyond the level of the coronoid.

SPLENIALS

The splenial is about half the length of the dentary and lies, for the most part, internal to it. It contributes to the symphysis that posterior portion beyond the deep Meckelian groove and runs caudad to meet the dentary along its lateral surface and above until it is separated from this element by the anterior prong of the coronoid internally and by a wedge-shaped projection of the angular, laterally. The splenial terminates ventrally in a short diagonal suture with the angular just beyond the level of the Meckelian notch. It is quite smooth on its exposed surface.

CORONOIDS

The coronoid is an exaggerated diamond-shaped piece interposed between the posterior reaches of the dentary and the splenial on the inside of the mandible. Medially, it covers a dorsal portion of the
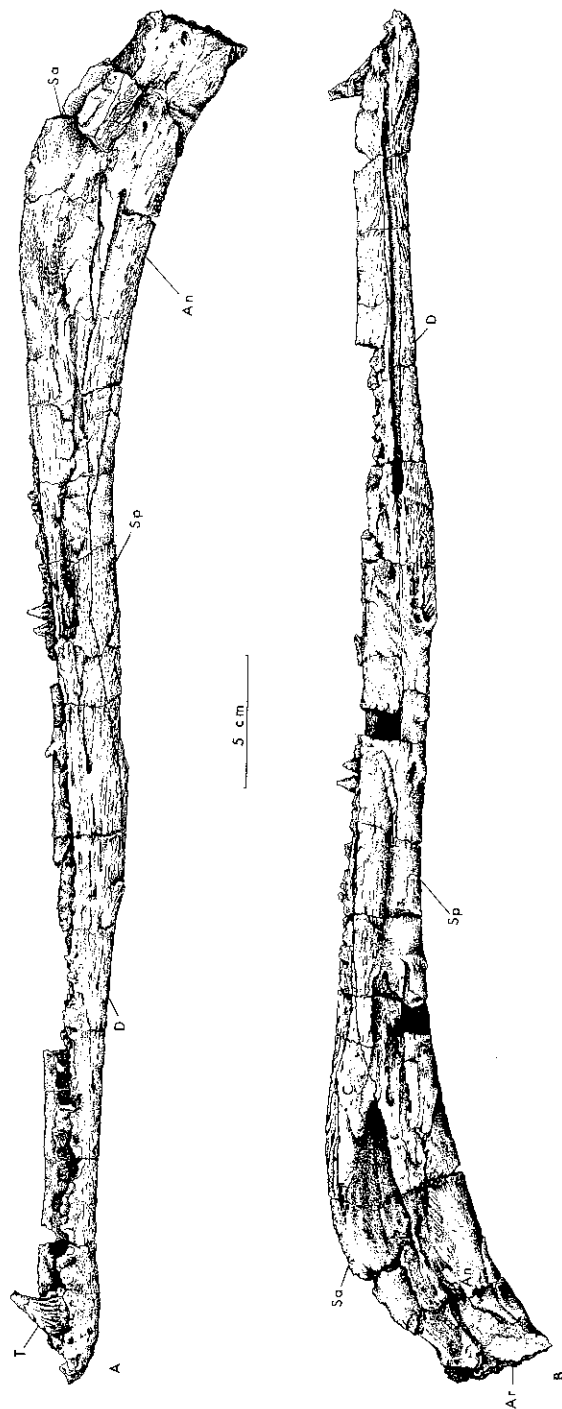
Fig. 9. A. Lateral view of left mandible, *Champsosaurus gigas*, PU 16239. B. Internal view of same. An, angular; Ar, articular; C, coronoid; D, dentary; Sa, surangular; Sp, splenial; T, tooth, note recurving, crenulated base and marginal notching of jaw for skull teeth.

surangular, and its lower posterior side forms the upper rim of the Meckelian notch, which enters at an acute angle rather than as the rounded notch seen in some forms.

SURANGULARS

This element is located dorsally at the rear end of the jaw. The surangular bears characteristic striations for muscle attachments upon its dorsal edge including the front end where it enters between the coronoid and dentary. The bone is thin and smooth elsewhere. Its union with the dentary is not clear but is suspected to resemble that of other species wherein the suture between these elements angles ventrad from the striated area across the outer surface. This bone encloses the dorsal half of the articular on its lateral surface. Medially, it has the internal flange mentioned by Russell (1956) that extends in front of the articular and nearly meets the angular coming around from below.

ANGULARS

This element also resembles its homologues closely, making up the lower posterior border of the jaw from the rear surface of the splenial to the articular. A well preserved extremity of the jaw in the type, SMM P71.2.1, shows that the extreme posterior extension of this bone overlay the internal suture between the surangular and articular but failed to reach the extreme angle of the jaw, which was formed above by the surangular and below by the articular. Dorsally, the angular extended forward along the base of the surangular and dentary until it merged with the splenial-dentary suture.

ARTICULAR

This element as preserved in the type contributes the posteriormost edge of the jaw. Most of it, however, is internal to the surangular and angular. A large articular facet is provided on a posterodorsal enlargement to match a corresponding facet as described for the quadrate.

POSTCRANIAL SKELETON

ATLAS-AXIS COMPLEX

Except for portions of the neurocentra, this complex is complete in the type (Fig. 10). As indicated, the type is regarded as a small adult and shows essentially adult development of features.

The atlas had four parts. The two major portions, the pleurocentrum and the hypocentrum, are preserved. The pleurocentrum, as seen in its fullest development in SMM P60.2004 (Fig. 11), is a key piece in this complex. It is longer and heavier than that of other forms. It furnishes major support with a wide, flat posterior articular face for the axis. Its narrow base also has a flat face that is angled slightly caudad and expanded laterally to meet a similar expansion on the axis hypocentrum. Just ahead of this and below its main anterior face is a transverse notch that is faceted along its lower border for reception of the crescent-shaped hypocentrum of the atlas. The main anterior face spreads laterally to furnish support and space for the bases of the neurocentra. It also develops a central process that enlarges with age and engages the occipital condyle above. The hypocentrum is made up of articular facets behind, above, and forward. The anteroventral surface of this piece is curved rearward and forms an irregular contact surface that abuts the combined forward edges of the axis hypocentrum and the above noted surface of the pleurocentrum. The ventral projection mentioned for an immature specimen of *C. laramiensis* (Brown, 1905) is not present; nor is the subsequently expanded modification of this

projection indicated in the adult as it is in *C. laramiensis* (Brown, ibid.). There is only a small, irregular edge in its place. Together, the pleurocentrum and the subordinate piece form a loose socket affair for articulation with the occipital condyle of the skull. The axis pleurocentrum is the largest portion of the complex—about one third longer than the pleurocentrum of the atlas. The centrum is of normal form posteriorly. The anterior surface has two articular facets wherein the main face is divided into a large, superior portion to join the atlas and a lower portion that is set back but still looks forward to support its hypocentrum (Fig. 10). The sides of the centrum are concave and ventrally roughened. The diapophyses are located near the center of the length of the bone and are directed straight outward. The neural canal is quite wide. Figure 12 shows the crescent-shaped hypocentrum with its large dorsal facet and concave rear face. The partially preserved neurocentra appear the same as in other species having only a slight median crest but well developed zygapophyses.

CERVICALS

(3-9). The cervical series of *C. gigas* containing nine vertebrae is shown in figure 10. A large specimen, the eighth vertebra, is shown in figure 13 and illustrates the diagnostic form of a squared centrum having anterior and posterior faces parallel to one another and noticeably depressed sides. The anterior half of the series differs in presenting a profile of smaller centra with nonparallel articulating faces. This is especially noticeable in the third vertebra. Parapophyses and diapophyses are prominent on all and are deflected rearward. The former migrates in position on the lateral side of the centrum from the anterior perimeter of the vertebra where it is inconspicuous to a more central position where it is obvious, and finally merges with the diapophyses on the last and largest cervical. The latter feature is strongly developed throughout the series.

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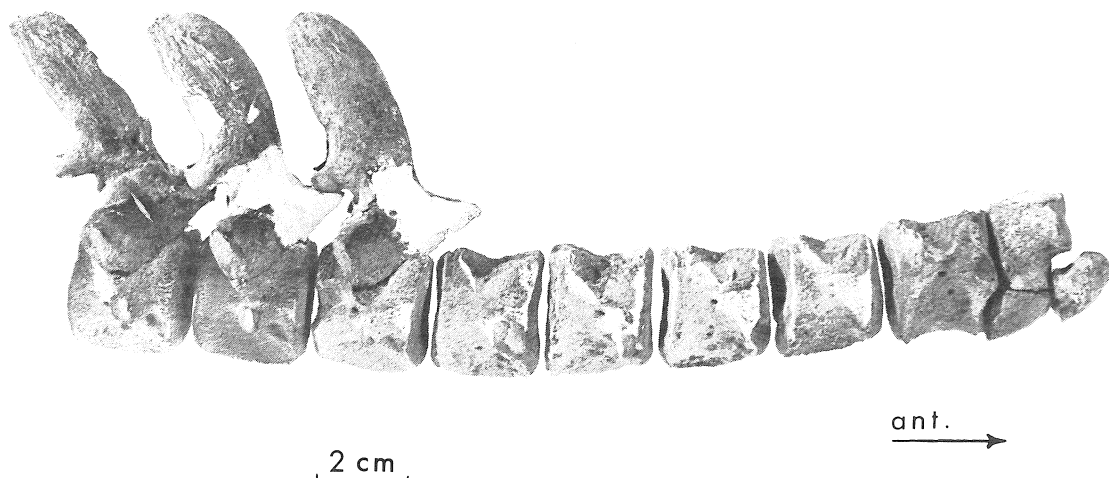
Fig. 10. *Champsosaurus gigas*, type specimen SMM P71.2.1. Lateral view of cervical vertebrae.

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A

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A

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B
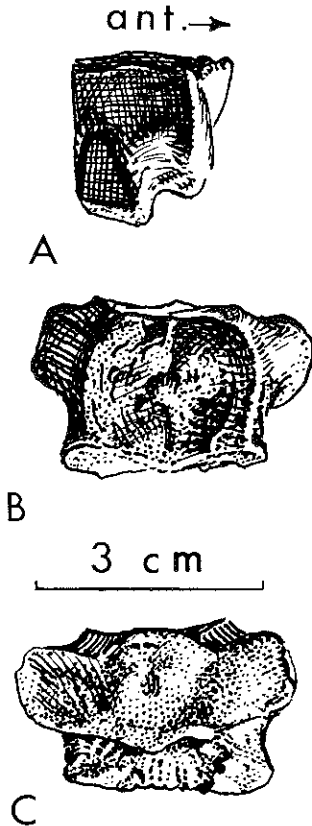
Fig. 11. Atlas pleurocentrum of *Champsosaurus gigas*, SMM P60-2004. A. Lateral view. B. Posterior view. C. Anterior view.

Fig. 12. *Champsosaurus gigas*, type specimen SMM P71.2.1. A. Ventral view of intercentrum of axis. B. Posterior view of same.

A ventral carina is present in *C. gigas* but less salient by comparison with some species. Maximum development of this feature is on the seventh and eighth vertebrae.

The neural arch is wide and carries well developed anterior and posterior zygapophyses. The neural spine is relatively narrow, long, and pitched rearward. The leading edge curves and at its highest point develops a narrow facet for ligament attachment. This is expanded into a wider facet at the posterodorsal aspect of the spine, giving the spine a slightly smaller terminus. A small curious element believed to represent the intercentrum of the third or fourth vertebra is shown in figure 14. By way of further analysis, this element could

have been associated with any adjacent pair of anterior caudal vertebrae as their intercentra had not been modified into chevrons (ref. p. 58). General description is that of a very small, wedge-shaped piece tapering at both lateral extensions and having one well developed central facet for contact with a centrum (Fig. ibid.).

DORSAL VERTEBRAE

Seventeen dorsals are preserved in the type (Fig. 15). This is the normal number for the species. They are more uniform in size than the cervicals but show a slight decrease in size posteriorly. The sides of the centra are depressed as well, and stout paradiapophyses exist throughout. The

Fig. 13. Cervical vertebral centrum of *Champsosaurus gigas*. A. Ventral view. B. Dorsal view. C. Lateral view.

Fig. 14. *Champsosaurus gigas*, type specimen SMM P71.2.1. A. Ventral view of "intercentrum." B. Lateral view of same.
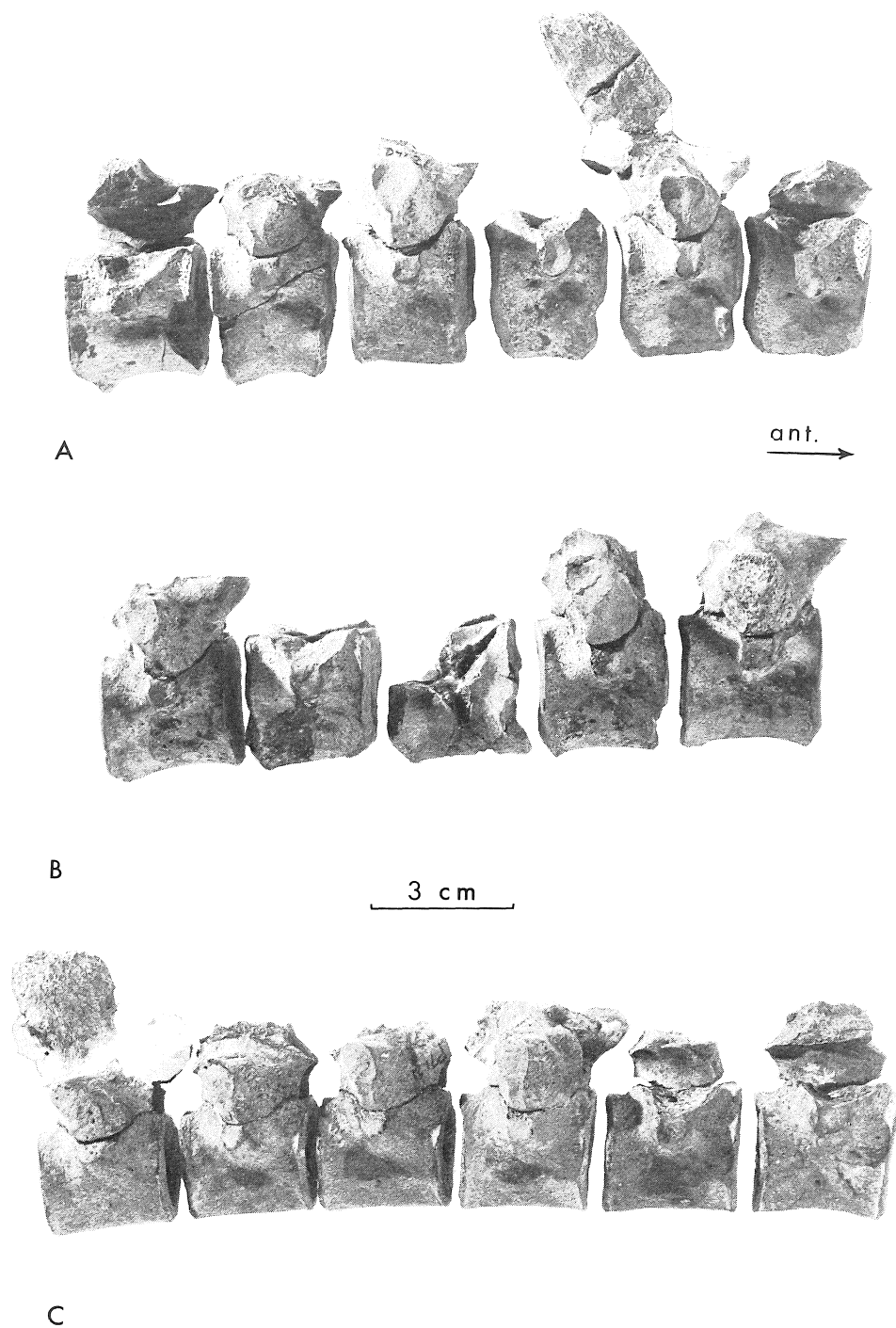
Fig. 15. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. First through sixth dorsal vertebra. B. Seventh through eleventh dorsal vertebra. C. Twelfth through seventeenth dorsal vertebra. All numbers refer from right to left. Note pathological condition in A and B near ventral intervertebral areas.

first three look straight outward; the remainder become increasingly angled caudad.

The anterior two thirds of the dorsal series in the type show marked deformation of the centra, probably due to injury. However, the ventral carina are clearly continued into the series from the neck region, being quite distinct on the first four elements.

Much of the material of the neurocentra is present but fragmented. In figure 15 note the second dorsal vertebra in which the zygapophyses are of modest size. The anterior ones face up and are mildly tipped out; whereas, the posterior zygapophyses face down and are angled inward. The neural spine is long, squared off dorsally, and directed rearward. The last dorsal vertebra has broad zygapophyses that are nearly in opposition to each other anteriorly and "back to back" posteriorly with a steep ventral pitch. The neural spine is wider and shorter than the one in the anterior bone. It is vertical and expanded appreciably at its distal extremity. Small processes near the posterodorsal corner are also present but not to the extent that they are in the sacrals and anterior caudals. There is a gradation of the neurocentral features between these two extreme vertebra. The spines on the last few are more or less erect and swollen distally.

SACRAL VERTEBRAE

The sacrum consists of three fused centra. This portion of the column is preserved in excellent condition in the type (Figs. 16 and 17). The centra are not as compressed dorsoventrally as they are in older and larger individuals, e.g., SMM P60.2004 (Fig. 18). Of the present sacrals of *C. gigas*, the absence of overlap of the paradiapophysial surfaces of the second centrum with the first centrum, and the definite overlap of the last with the second centrum is a constant condition. It would seem otherwise in other species (ref. p. 58). The diapophyses look directly outward toward the iliac blades. Each neural arch is broad and supports a stout spine. The first is erect and slightly shorter than that of the last dorsal ahead of it. The second and third spines are expanded rearward along their posterior edges. A pair of lateral processes located posterodorsally, as seen in the last dorsal, increase in prominence to the last sacral, continue in the first few caudals, then gradually fade. The zygapophyses are essentially like those of the posterior dorsal vertebrae.

CAUDAL VERTEBRAE AND CHEVRONS

Twenty-five caudal vertebrae are present in the type and are represented by various elements from the tail in figure 19. This is probably about one half of the total number. Caudals are also present in lesser numbers in USNM 20521 and SDSM 53508. In USNM 20521, the first five elements are present in sequence. No definite chevron facets are noted on the third vertebra. If a chevron was present, it must have been indeed loosely fixed and probably reduced in size. In any event, the base of the tail may be said to consist of the first three vertebrae. Figure 20 illustrates the second caudal vertebra of the type.

Sutured ribs are in evidence in the type, as well as USNM 20521, on the first ten-eleven vertebrae. It would seem from both that one or two more uncoossified ribs also exist. Lateral processes may have extended to about the fifteenth or so vertabra. The neurocentra remain stout with strong zygapophyses. Coossification of neurocentra with the centra in *C. gigas* is established at about the level of the twelfth vertebra. From this region, ribs and sepa-

5 cm
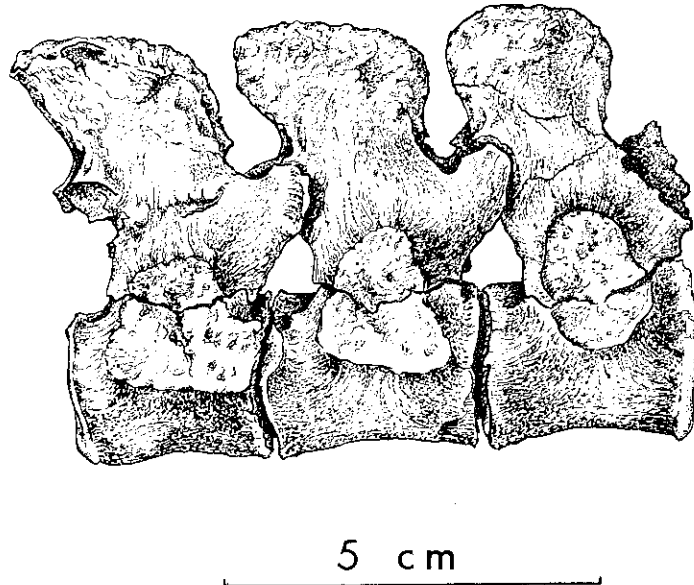
Fig. 16. *Champsosaurus gigas,* type specimen SMM P71.2.1. Right lateral view of sacral vertebrae.

rate neurocentra are not distinguishable; and the remaining caudals become simplified in form. The zygapophyses on these are much reduced and finally lost, the posterior ones disappearing first. The neural spine thins and loses its distal expansion by the medial caudals. In the distal elements, the neural spine is decreased further; and the sides of the centra become laterally and ventrally ridged. Chevrons continue to the end of the series. Typical medial and distal chevrons are illustrated in figure 21.

RIBS

CERVICAL RIBS

Unfortunately, little is known of the cervical ribs in *C. gigas*. The type presents a number of fragments belonging to anterior ribs. These indicate the presence of at least four, short, Y-shaped ribs that curve posteriorly and are of the type illustrated in figure 22 for *C. laramiensis*. At

least one has an anterior spike positioned between the capitulum and the tuberculum. In this case, the spike is double-pronged, as it is only to a very subtle degree in the smaller species. As in other forms, the tubercle is larger than the capitulum. The posterior cervicals are mostly lacking but an uncinate is indicated among the fragments present.

DORSAL RIBS

Dorsal ribs are borne on seventeen vertebrae. Nowhere are the peculiarities of the ribs of this genus better observed than in *C. gigas*. The dorsals are heavy, mildly arched, and show a fusion of tubercle and capitulum, the former becoming greatly expanded over the latter. Mild pachyostosis persists throughout the series. The distal end is swollen and abruptly terminated in the longest ribs. The first three ribs are thin distally and expanded into an uncinate projection (Fig. 23). From the fourth through the eleventh rib, there is a pro-

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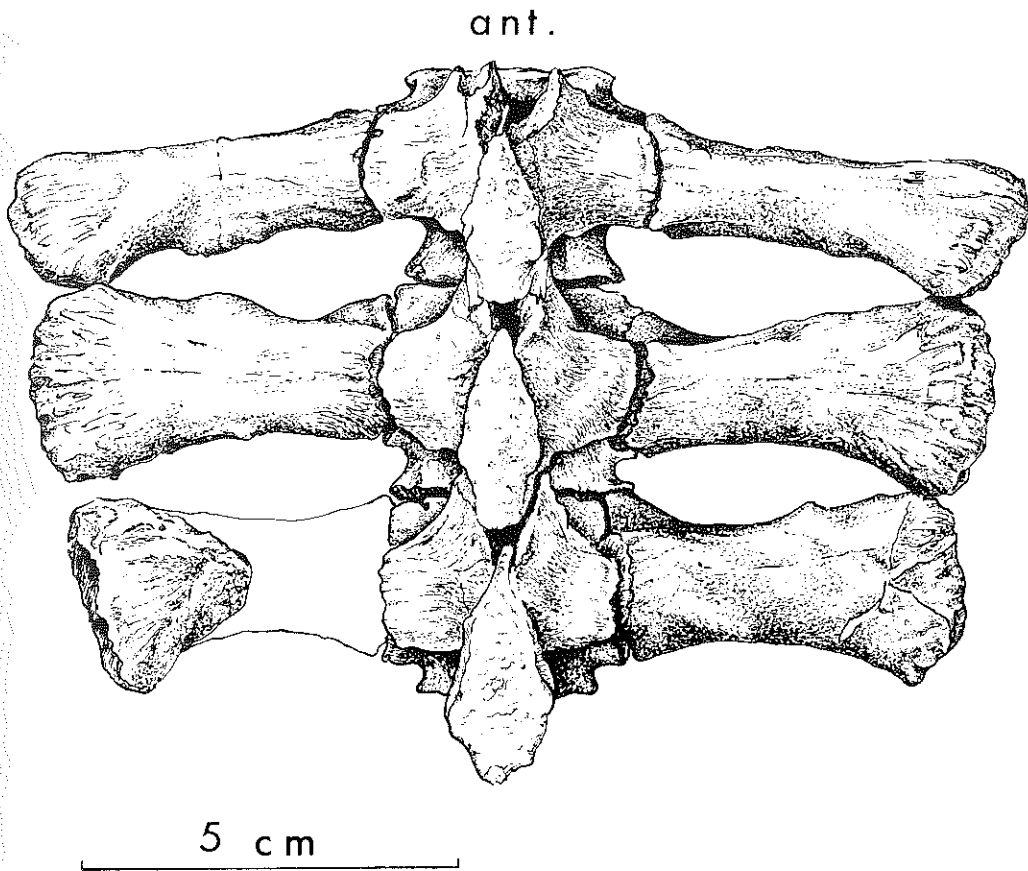
Fig. 17. *Champsosaurus gigas*, type specimen SMM P71.2.1. Dorsal view of sacrum.
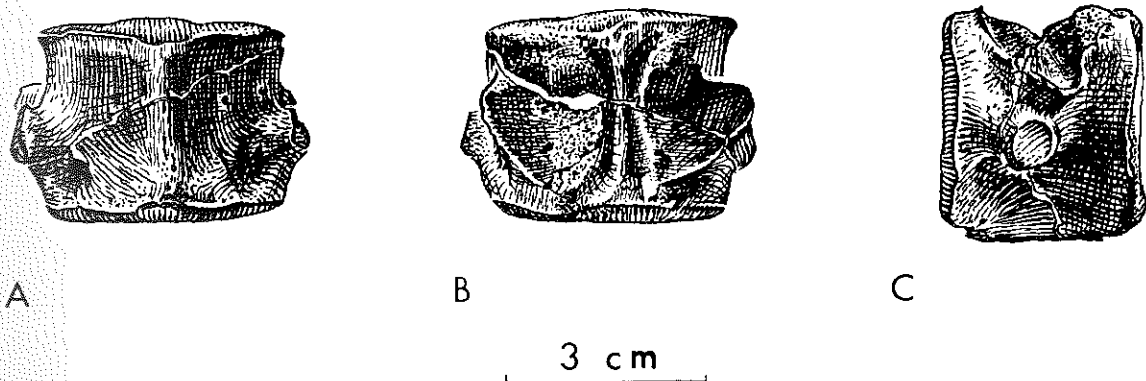

A   B   3 cm   C
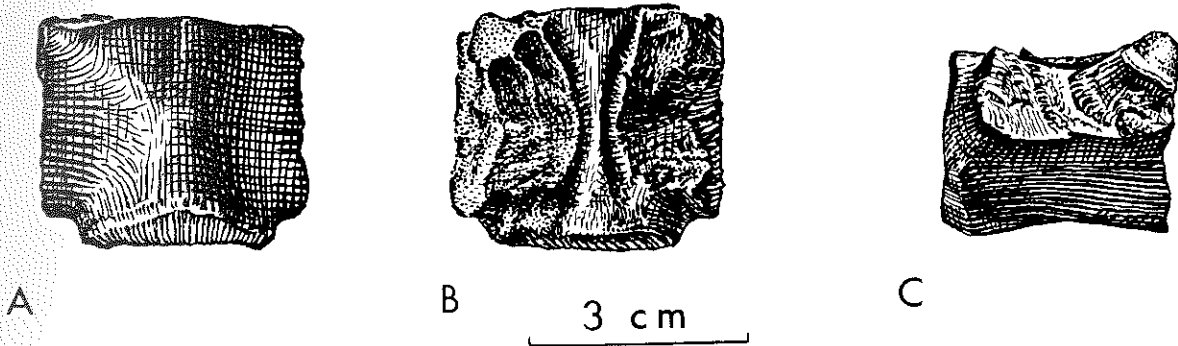
Fig. 18. Sacral vertebral centrum of *Champsosaurus gigas*. A. Ventral view. B. Dorsal view. C. Lateral view.

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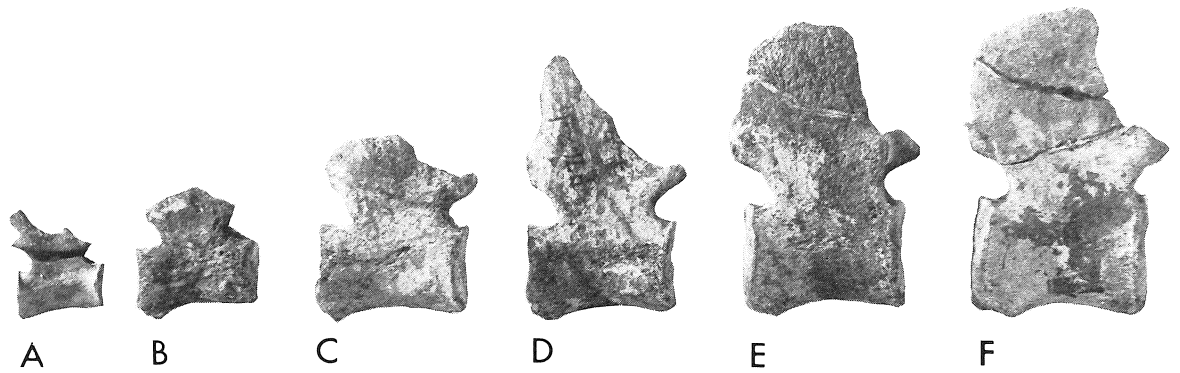
Fig. 19. *Champsosaurus gigas,* type specimen SMM P71.2.1. Lateral view of caudal vertebrae from various regions. A.-D. Distal vertebrae. E. and F. median vertebrae.

3 cm
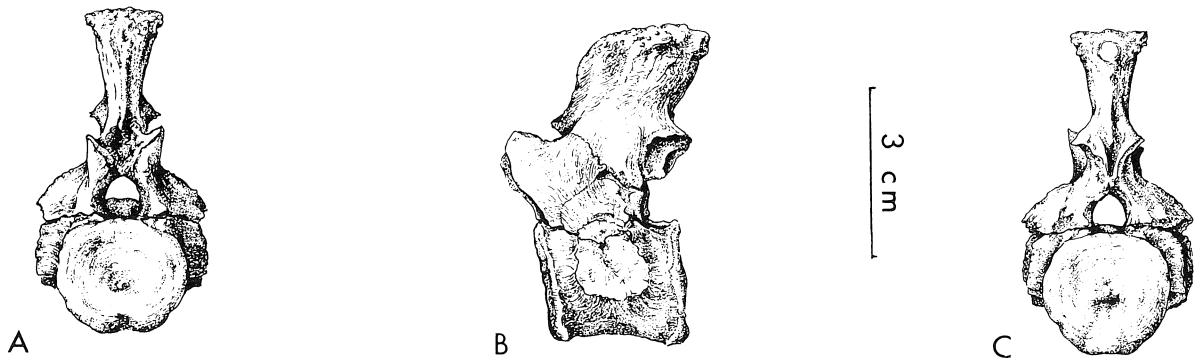
Fig. 20. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. Anterior view of second caudal vertebra. B. Lateral view of same. C. Posterior view of same.

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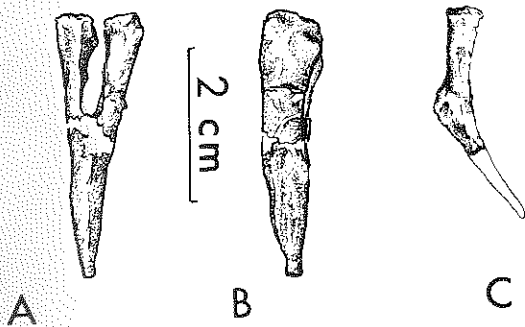
Fig. 21. Chevrons of *Champsosaurus gigas*. A. Anterior view of proximal element. B. Lateral view of same. C. Lateral view of distal element.

nounced incising believed to be the result of pressure erosion induced by internal organs—the lungs (ref. General Morphology, p. 76 and Figs. 58 and 59). Ribs 12 through 17 are simple with reduced distal swellings and gradual reduction in length toward the sacrals (Fig. 24). Unlike other forms, all retain a strong facet at the distal extremity for cartilaginous attachment.

SACRAL RIBS

Of the three sacral ribs of the type (Fig. 17), the first is the longest and narrowest. It is curved rearward and expanded distally (Fig. 25). It joins the first sacral vertebra in an excavation formed at the meeting of diapophysis and parapophysis.

All ribs are compressed from above and below along their shafts, are slightly ridged in front and behind for most of their lengths, and are similarly united with the vertebral column.

The second or middle rib is greatly enlarged distally, especially in older individuals, to increase contact areas for ilium and adjacent ribs (Figs. 17 and 26). This is the stoutest rib of the sacral triplet. The last rib is much like its predecessor except the proximal articulation is greater in that the anterior parapophysial portion is long-

er and overlaps the posterior edge of the second centrum. The distal expansion is also different because of the thinning of the end into a posterior flange carrying only a narrow facet that is directed rearward and outward but not for direct contact with the ilium.

CAUDAL RIBS

Unlike the caudal vertebrae, the ribs in this section cannot be conveniently differentiated by region. They are all similar in form and show a uniform gradation in size from the first, which is the largest, to the tenth. They angle ventrad and are strongly curved caudad, especially the first few. Their bases join the centra on broad, centrally depressed surfaces. The first five are shown in USNM 20521 in figure 27. Figure 28 illustrates the first caudal rib of the type in ventral aspect. Note the lateral rugosities and distal facet, which diminish rapidly.

PECTORAL GIRDLE

In the type SMM P71.2.1, all elements are represented with only portions of some lacking. It differs from other forms primarily in magnitude.

SCAPULAE

The scapulae are both incomplete in the type SMM P71.2.1, but a near complete restoration is possible because of the presence of complementary portions between the two. The scapula differs from most others in that its distal end is markedly expanded anteroposteriorly into a hatchet-shaped blade (Fig. 29); whereas, in most other forms it is nearly uniform in width for its length. In this respect, it is close to that seen in *C. laramiensis*. However, in both species, there are some individuals possessing a blade that is not expanded distally. This may be an immature characteristic or an expression of sexual dimorphism (ref. p. 62, General Morphology).
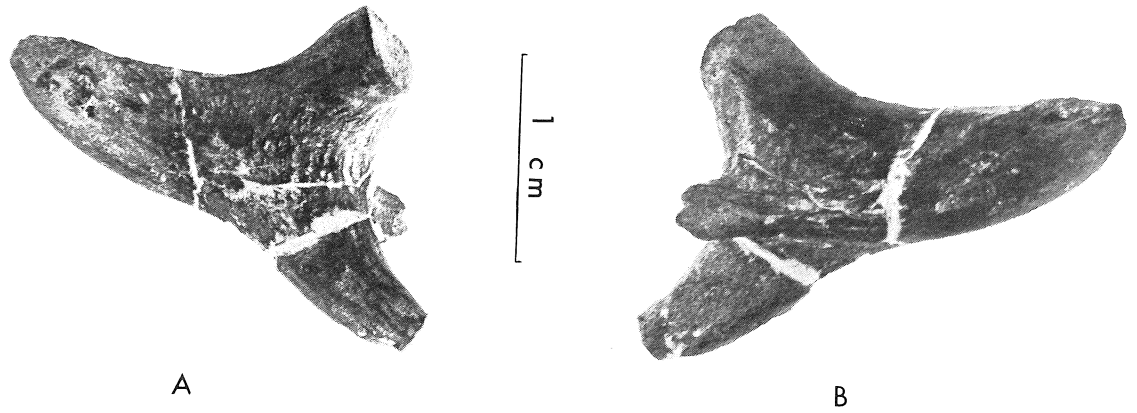
Fig. 22. Left anterior cervical rib of *Champsosaurus laramiensis*, juvenile. A. Internal view. B. External view.
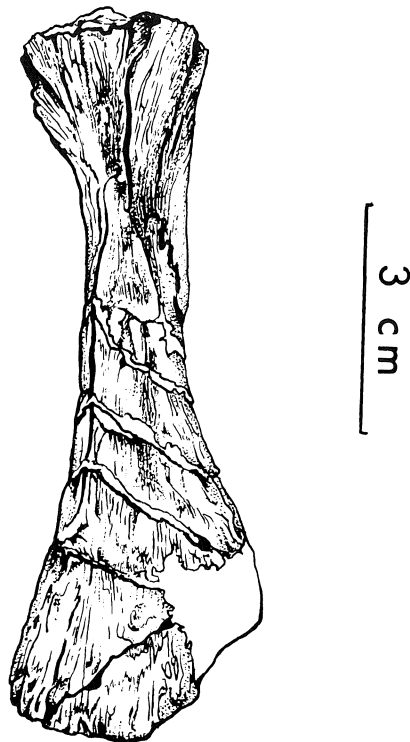
Fig. 23. Anterior dorsal rib of *Champsosaurus gigas*, SDSM 53508, with uncinate process restored.

Fig. 24. *Champsosaurus gigas,* type specimen SMM P71.2.1. Last six ribs (Nos. 12-17). All except the largest are from the right side of the animal. These are the only dorsal ribs other than the first three having no incising for the lungs.

The blade is thin and more or less the same thickness, except for the anterior edge, in the region of contact with the clavicle, which is heavier. Near the base of the blade, the bone swells and two pointed tubercles are present on the lateral and posterolateral surfaces. The base of this bone turns rearward into a massive expansion consisting of a posterolateral face that forms the anterior half of the glenoid cavity and a larger irregular surface medial to it that matches a similar area on the front edge of the coracoid. Medially, the scapula is incomplete but is reduced to a thin plate that follows the curve of the clavicle.

CORACOID

Like the other ventral girdle elements, portions of this bone are frequently found with specimens that are fragmented. The blade is often shattered or otherwise warped because of its thinness. The coracoid of SMM P60.2004 is shown in figure 30. It reflects this condition of being shattered and is actually concave below and convex above, which is the reverse of the normal condition. Its shape is like that seen in *C. laramiensis* but is distinguished from other species by its well developed infraglenoid process. It is a large, flat bone thickened anterolaterally to form the large, centrally excavated surface of the posterior

3 cm

3 cm

A

B
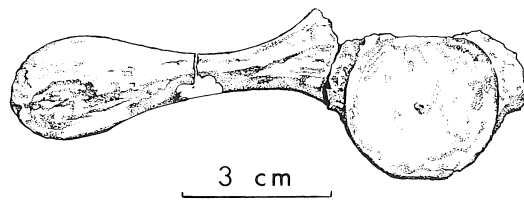
Fig. 25. Anterior view of first sacral rib of *Champsosaurus gigas,* SMM P60-2004.
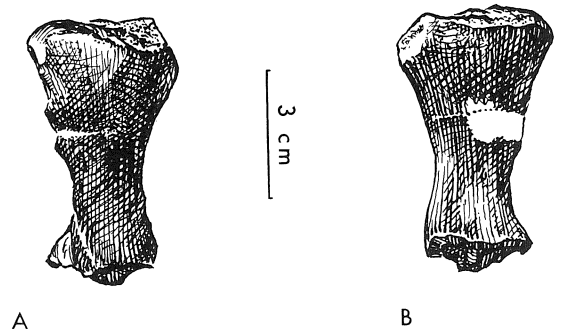
Fig. 26. Middle right sacral rib of *Champsosaurus gigas,* SMM P60-2004. A. Dorsal view. B. Ventral view.

2 cm
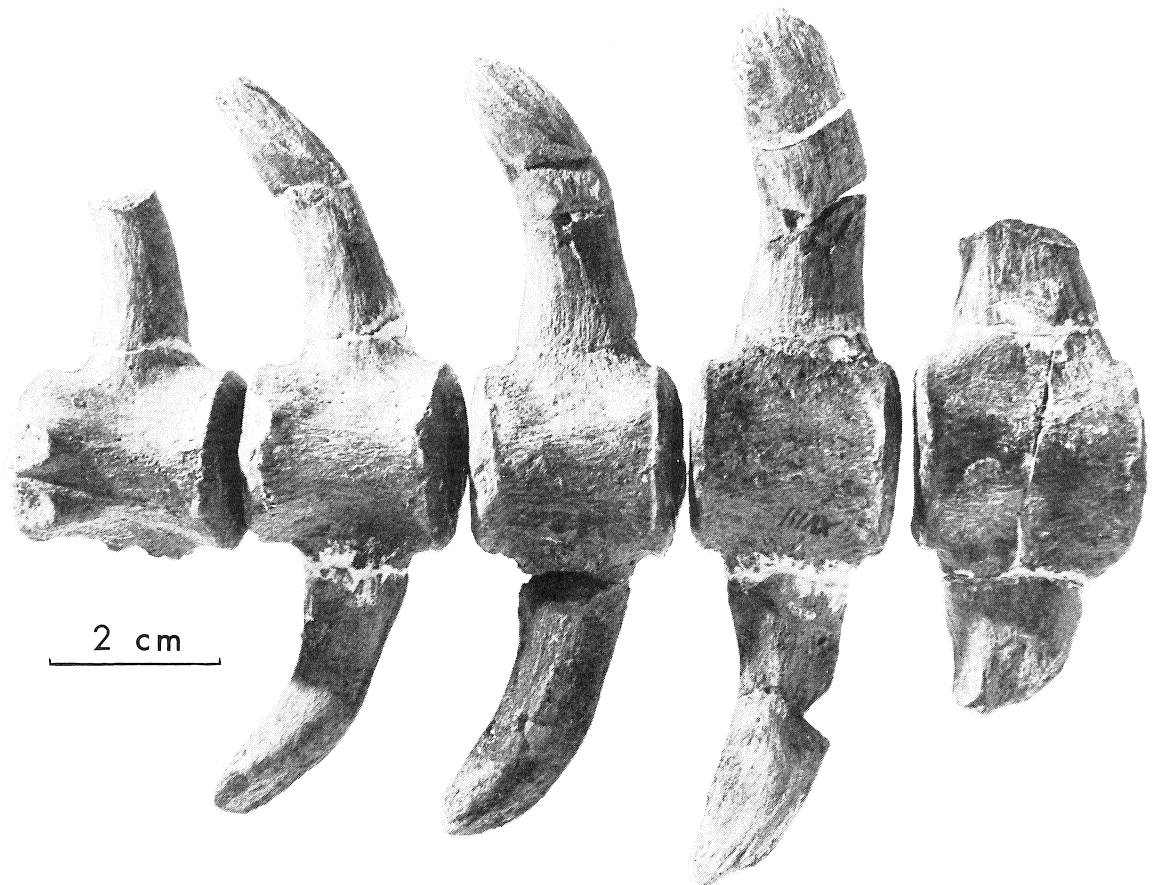
Fig. 27. First five caudal vertebrae and ribs USNM 20521.
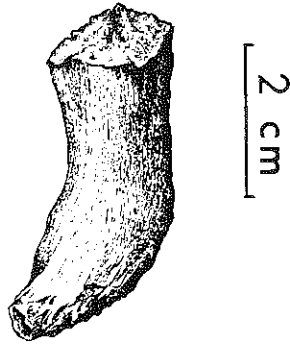
Fig. 28. *Champsosaurus gigas,* type specimen SMM P71.2.1. Left first caudal rib in ventral view.
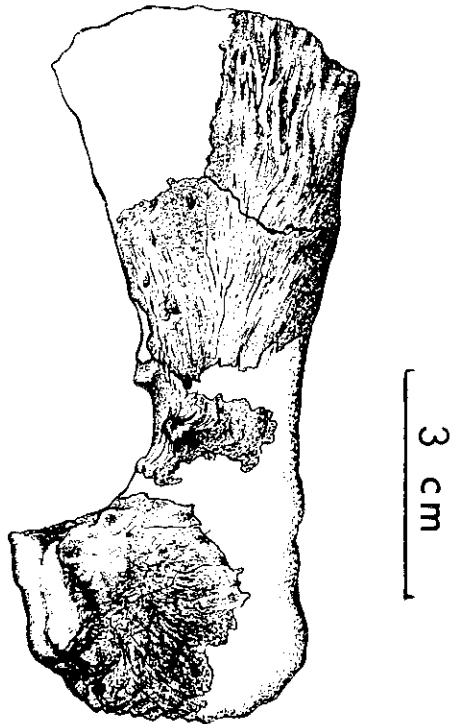
Fig. 29. *Champsosaurus gigas,* type specimen SMM P71.2.1. External view of right scapula, partially restored.

39

half or so of the glenoid fossa and a smaller rugose area medial to it for union with the posterior flange of the scapula. The internal rim of the plate has a broadly curved cartilaginous border.
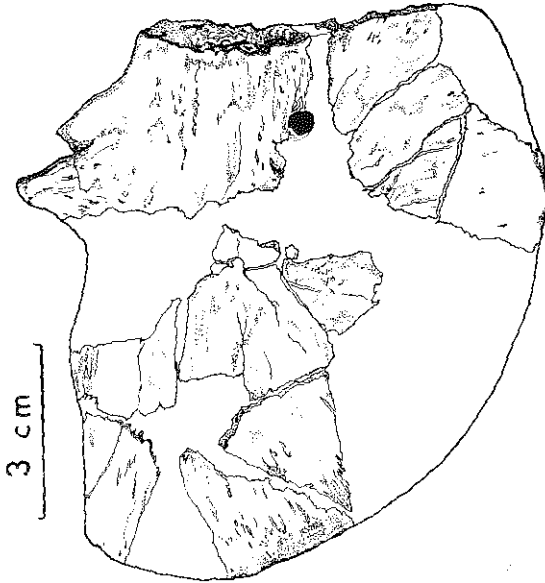
Fig. 30. Left coracoid of *Champsosaurus gigas*, SMM P60-2004, in dorsal view, partially restored.

CLAVICLE

Both clavicles are present in the type (Figs. 31 and 32). They form a wide, flattened, U structure across the anterior part of the chest. Their bases lie anteroventrally to the interclavicle, being joined to it by heavy interlocking sutures. Their front edges form the leading edge of the pectoral girdle, and at midline touch one another at the extreme forward tip of the interclavicle. In dorsal view (Fig. 32), the clavicle is strongly flared rearward to accommodate the wide interclavicle branch. The upright arm of the clavicle is narrow by comparison with the horizontal portion and is coarsely striated laterally where it engages the anterior border of the scapula.

INTERCLAVICLE

The most complete interclavicle is represented by the type (Fig. 33). Unfortunately, most of the central blade is wanting. The transverse portion is massive. In overlying the horizontal portion of the clavicle, it bulges upward and spreads laterally almost to the base of the upright arm of the clavicle. At the center of the transverse portion, the front edge is depressed and projected forward and nearly covers the junction of the proximal tips of the clavicles. The large posterior blade is intact for only about an estimated one third of its length. However, indications in SMM P60.2004 are that the blade was generally straight-sided, somewhat serrated, and not as expanded as in some forms. Near its distal end, it was constricted and drawn out into a point. The normal blade is gently concave dorsally. Ventrally, sutural surfaces occupy the transverse area; and the central blade is smooth. An interesting pair of small foramina are located one on either side of midline just behind the clavicle contact area.

FORELIMB

The forelimb is preserved in the type as well as partially in SDSM 53504 and USNM 20521. A forelimb to hind limb ratio may be expressed as 100/135 for this species.

HUMERI

The humerus (Fig. 34) is a stout bone with a slender shaft and wide expansions at both extremities—the distal end always somewhat greater than the proximal. The shaft is twisted about 85°. This bone is not as massive as that of *C. ambulator*. Its proximal end also differs from this species and *C. laramiensis* in lacking a prominent entotuberosity. The ectotuberosity, as well, is less pronounced but is partially separated from the head. A deltopectoral crest

running down from its edge is only mildly developed. Distally, the humerus closely resembles *C. laramiensis*, having a large radial condyle and a lesser entotuberosity and entepicondyle. A deep ectepicondylar sulcus is developed adjacent to the radial condyle.

RADII

Figures 35 and 36 illustrate the radius, which bears no important morphological distinction from other species. The upper end is greater than the lower in surface area. The shaft has the characteristic curve of the group and shows a ridge on its external surface.

ULNAE

The ulna is very heavy proximally and reduced and flattened distally (Fig. 36). The most outstanding aspect of this bone is its high, acute olecranon, which is in contrast to the lower silhouette of some species. The radial facet is smooth and centrally depressed. The shaft is constricted and carries a trace of a ridge distally on its ventral side. The distal articular surface is slightly rugose and convex in shape.

CARPUS AND MANUS

The forefoot of *C. gigas* is represented by numerous unassociated elements; unfortunately, no carpals are included. From what can be observed, its structure adheres closely to that illustrated for *C. laramiensis* in figure 52 and referred to on page 66. No attempt at a formula is possible with the present materials.

PELVIC GIRDLE

The upright ilium as well as the ventral plate-like ischium and pubis are preserved for the most part in most of the present specimens including the type.

ILIA

The ilium of the type is shown in figure 37. This specimen is unweathered and gives a good detailed view of the striated areas both internal and external. The base is broad with anterior and posterior surfaces that angle ventrad to receive respectively the pubis and ischium. Laterally, there is a large, smooth concavity that contributes the upper part of the acetabulum. Above this is a roughened buttress. The posteriorly projecting iliac blade is ovoid in form without parallel edges. At the anterior base of the blade, a small tubercle projects inward. The length of the blade closely approximates the height of the entire bone.

PUBES

The pubis (Fig. 38) is a smooth, rectangular plate that has a deep sulcus along its anterior edge and a straight posterior border that is in close contact with the ischium for its entire length. Proximally, it is angulated for union with the anterior slope of the base of the ilium and to form the anterior portion of the acetabulum. The plate projects forward from the acetabular area and expands to form a large, rugose, downturned lip presumably for attachment of ambiens or pubotibialis muscles. Distally, the pubic plate thins and is truncated to form the interpubic symphysis. An obturator foramen is located toward the heavy end of the plate.

ISCHIA

The ischium (Fig. 38) is a smooth, triangular plate roughly the size of the pubis. Its anterior edge abuts the posterior edge of the pubis in a straight contact. Its posterior border angles rearward toward the median from the acetabular area and is strongly tuberculate about two thirds of the way from the acetabulum. This feature is acutely developed for a large tail ligament and tendon. The proximal apex of the bone is thickened for union with the posterior slope of the ilium base and to form

3 cm

Fig. 31. *Champsosaurus gigas,* type specimen SMM P71.2.1. Anterior view of the dermal shoulder girdle elements.

the posterior portion of the acetabulum below. Medially, the plate is truncated to form the interischial symphysis. The median margin is dorsally swollen at about midlength to lend transverse structural support.

HIND LIMB

The hind limb was recovered in the type and in SMM P60.2004. As already indicated, its length appreciably exceeds that of the forelimb. This suggests a greater use of the hind limb for the giant species, perhaps related to the hypothesized lunging behavior mentioned elsewhere in this paper.

FEMORA

This bone (Fig. 39) is long and expanded at each end. The shaft is twisted some 80° and has an open S shape. The proximal articular surface is broad and occupies the entire oval head. The internal trochanter is much like that seen in all other forms with the exception of *C. ambulator*. It is connected with the head by a narrow neck on the postaxial side of the bone. It is coarsely striated on its sides as well as in the deep intertrochanteric fossa. The distal articular face is somewhat greater in size than the proximal face, occupying the entire broadly rounded end of the bone.

TIBIAE

This bone is characterized by a greatly swollen upper end, which is ovoid and slightly domed, and consists of articulating area entirely (Fig. 40). The shaft is slender and has minor development of a longitudinal distal ridge on the fibular side, but the marked proximal ridge of some species is inconspicuous. The distal end is strongly reflexed toward the fibula and abruptly cut by a broad, flat, astragular facet. Below this, the shaft is terminated in an oval articular surface about one third that of the upper end of the bone.
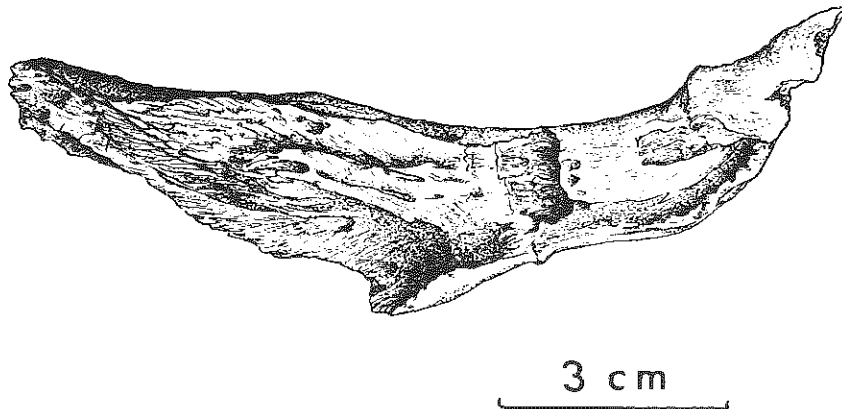
Fig. 32. *Champsosaurus gigas,* type specimen SMM P71.2.1. Dorsal view of right clavicle.

FIBULAE

The fibula is paddle-shaped. Figure 40 illustrates the element of the type specimen. The upper end is simple, being slightly swollen and rounded off as an articular area. The shaft is nearly straight and of similar thickness throughout. About midway on the tibia side, there is a longitudinal groove paralleling a short, low ridge that is opposite the longer ridge on the tibia noted above. The shaft begins to expand about three fifths of the way down and finally quits in a wide, arcuate surface having a tapering area laterally and a small oval area that is mildly excavated and turned medially to embrace the astragalus. The anterior side is convex and the posterior, flat in the type, and only perceptibly concave in SMM P60.2004— a very large animal.

TARSUS

Two of the four component elements of the tarsus are preserved in the type—the astragalus (intermedium) and a smaller distal bone. Both are somewhat eroded. The astragalus is also present in SMM P60.2004 in an uneroded state (Fig. 41).

This bone is essentially the same as that in *C. laramiensis,* except for size. Articulating surfaces surrounding the margin, except for a brief space between the tibia and fibula, are expanded a bit more; therefore, a concavity of the dorsal and ventral sides is deeper. In the type, there is no suggestion of the usual perforating arterial foramen on the lateral dorsal edge as there is in the larger specimen. Proper orientation of the single distal tarsal is uncertain. Its shape is subangular; and the one reduced, nonarticulating surface is concave.

PES

Like the tarsus, only minor portions remain. From both feet, parts of seven or eight metatarsals are represented. Metatarsals II-IV match those of other species nicely. Number V, shown in figure 42, presents the most diagnostic shape of all. This bone is shorter than the others in the series as far as known. Its upper end spreads out laterally for a distance more than half that of the total length of the bone. It has a wide obtuse crown for association with the calcaneum proximally and a flat medial facet, which is directed to
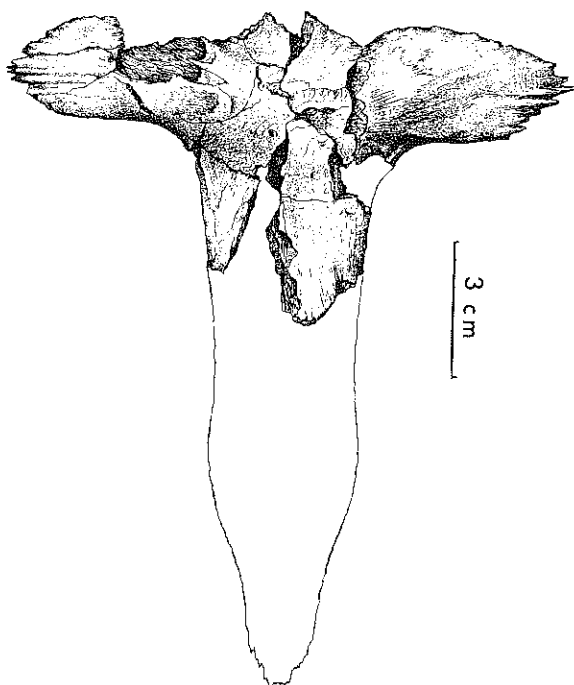
Fig. 33. *Champsosaurus gigas,* type specimen
SMM P71.2.1. Dorsal view of interclavicle with
posterior portion of blade restored.

the outer distal tarsal. The dorsal side has a low, central ridge and the ventral side, a shallow proximal excavation. The distal extremity is only a bit wider than the shaft; and there is a smooth, simple ovoid, articular area. There is also a small ventral expansion of this area with a small tubercle above it. Of the dozen or so remaining phalanges, all have normal terminal flaring and facets. A long, fluted, claw-like ungual akin to that of other species is also noted.

GASTRALIA

The gastralia segments, judging from the various specimens at hand, were well distributed over most of the ventral surface of the body from the pelvis to the anterior dorsal region. Figure 43 shows sections of these rod-like elements from various parts of the body. Each element is made up of a stout, median segment with a slight bow and a lateral pair joined to it at each end by overlapping contacts.

The medial segment is grooved for about one fourth of its length at each end on its anterior side. This is to accommodate the corresponding feature on the posterior side of the inner end of each lateral segment.

The posterior surface of the longer composite elements is incised longitudinally probably as a means of better alignment with adjoining elements or intervening cartilage.

Measurements of the postcranial skeleton of *Champsosaurus gigas* are given in the following table. All measurements are of maximum dimensions unless otherwise indicated.

Fig. 34. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. Postaxial view of right humerus. B. Pre-axial view of same.
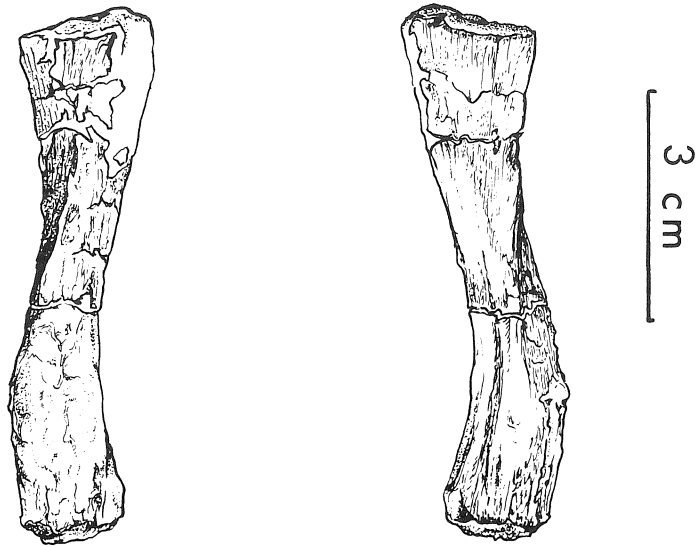
Fig. 35. Left radius of *Champsosaurus gigas*, USNM 20521.

A

B
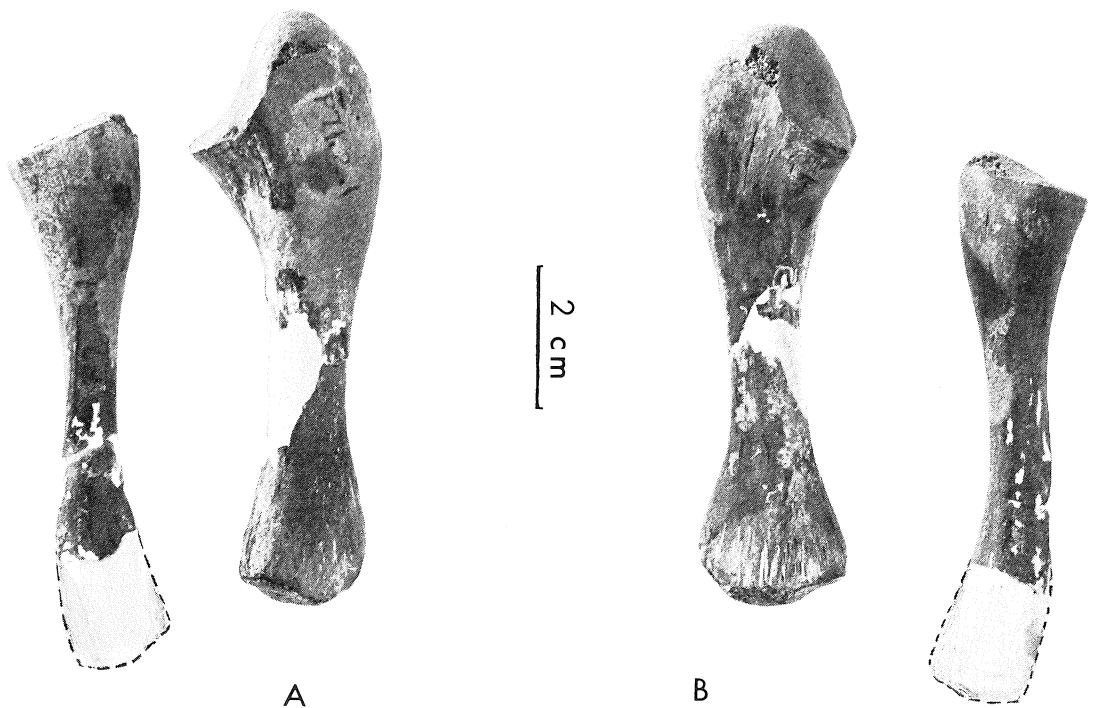
Fig. 36. *Champsosaurus gigas*, type specimen SMM P71.2.1. A. Dorsal view of left foreleg. B. Ventral view of same.

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Fig. 37. *Champsosaurus gigas*, type specimen SMM P71.2.1. A. Internal view of left ilium. B. External view of same.
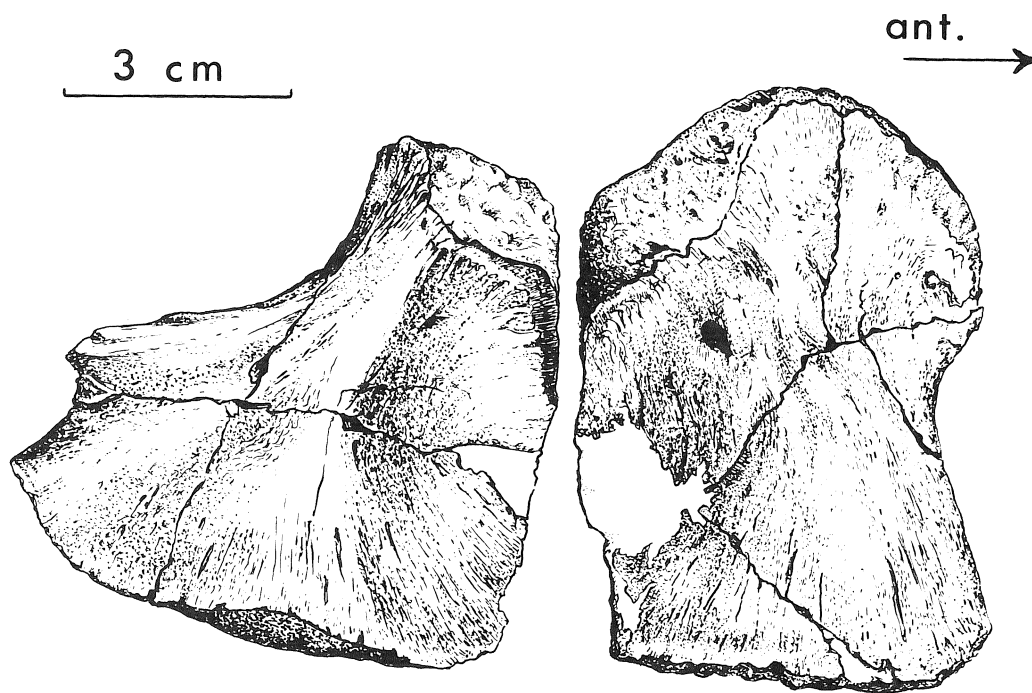
Fig. 38. *Champsosaurus gigas*, type specimen SMM P71.2.1. Dorsal view of left side of puboischiadic plate.

5 cm

A

B

Fig. 39. *Champsosaurus gigas*, type specimen SMM P71.2.1. A. Postaxial view of ~~right~~ left femur. B. Preaxial view of same.

Fig. 40. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. Ventral view of rgiht tibia and fibula. B. Dorsal view of same.

Fig. 41. Astragalus of *Champsosaurus gigas,* SMM P60-2004.

Fig. 43. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. and B. Ends of lateral portions of gastralia. C. Central bar of same.

Fig. 42. *Champsosaurus gigas,* type specimen SMM P71.2.1. A. Dorsal view of right metatarsal V. B. Medial view of same.

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TABLE 1.

	Height of Centrum at anterior end	Width of Centrum at anterior end	Length of Centrum
Champsosaurus gigas, type SMM P71.2.1 Cervical Vertebrae			
atlas	20.2 mm.	28.8 mm.	19 mm.
axis	26.9	22.2	24
third	24.8	26.1	24.1
fourth	24	27.6	25
fifth	26	27.7	24.3
sixth	27.2	29	24.7
seventh	26.1	29	25.9
eighth	25.9	28	26
ninth	26.1	29	26
Dorsal Vertebrae			
first	26.7	30.6	26
second	28.5	31.8	27
third	29.2	31.5	25.6
fourth	28.5	31.2	27.4
fifth	30.9	30.8 (est.)	27.1
sixth	28.6	30.7	28.5
seventh	28.2	29.6	28.5
eighth	28 (est.)	31.7	28
ninth	28.7 (est.)	31.5 (est.)	29
tenth	29	32.5	27
eleventh	28.1	29.5	28.4
twelfth	27.6	28.9	28.8
thirteenth	26	29.9	29
fourteenth	26	28.6	28.7
fifteenth	25	27.6	28
sixteenth	24.7	27.9	28.3
seventeenth	23.5	27.6	28
Sacral Vertebrae			
first	23	26	28
second	21.9	28.7	27.2
third	21.1	28.8	26.1
Caudal Vertebrae			
first	20.6	23	25

Height of last cervical vertebra including neural spine............................... 73.2 mm.
Height of second dorsal vertebra including neural spine............................ 74.8
Height of last dorsal vertebra including neural spine................................ 62
Height of middle sacral vertebra including neural spine............................. 57.2
Height of first caudal vertebra including neural spine.............................. 56
Total length of cervical series including atlas and axis............................. 227
Total length of dorsal series.. 469
Total length of sacral series.. 81
Length of first sacral rib... 53.9
Length of second sacral rib.. 51.6
Length of third sacral rib... 49.7
Length of first caudal rib (along outside curve)................................... 55.4
Height of scapula... 90.8 (est.)

TABLE 1.—Continued

Width of shoulder girdle at clavicles.. 180 mm.
Height of ilium... 63.5
Width (at base).. 29
Length (blade)... 63.4
Width of pubis... 80.6
Length (along inner border)... 59.4
Width of ischium... 70
Length (along inner border)... 68.7
Width of pelvic girdle (at ilia)... 180.4
Length of humerus... 142
Greatest dimension at proximal end... 48.8
Greatest dimension at distal end... 53.4
Length of radius... 72   (est.)
Length of ulna... 82.1
Length of femur... 178.3
Greatest dimension at proximal end... 36.4
Greatest dimension at distal end... 42
Length of tibia.. 123
Length of fibula... 115.7

C. gigas, SMM P60.2004

Total length of dorsal vertebral series.. 561
Total length of sacral series... 96.3
Length of first sacral rib.. 67
Length of second sacral rib... 61.2
Length of third sacral rib... 56   (est.)

C. gigas, SMM P60.2004

Length of first caudal rib... 57.2
Width of coracoid (blade)... 94.9 (est.)
Length (blade) 87   (est.)
Height of ilium... 78.9
Width (at base)... 33.2
Length (blade) 78.8
Width of pubis.. 105   (est.)
Width of ischium.. 91.2
Length .... 90.7 (est.)
Width of pelvic girdle (at ilia).. 240
Length of femur... 207.4
Greatest dimension at proximal end... 46.5
Greatest dimension at distal end... 50
Length of tibia... 140.6
Length of fibula.. 136

GENERAL MORPHOLOGY

As well as the general review of skeletal morphology, one aim of this study has been to isolate juvenile and adult characters. Further separation of age variations from individual variations was attempted. The results of the latter are limited owing to the lack of materials of certain sized individuals and the intergradation of age and individual character variations. Certain trends were found, however. These are discussed below.

SKULL

Osteology of the skull has had adequate description by Brown (1905), Russell (1956), and Fox (1965), in addition to that attempted for *C. gigas* in the present paper.

Relatively few skulls of *Champsosaurus* are known, and these show a remarkable consistence in form. The minor differences that do exist are largely variations in the shape of some bones. These are expressed by sutural patterns and are presumed to indicate differences between various species. Age variations and individual variations found among those of comparable age cannot be determined reliably for the skull. Therefore, only brief note will be made regarding the variations observed.

Notable among these are the prefrontal, which is longest in *C. natator* due to the manner of joining the nasals, and the jugal, which is also extended farther forward than in other species. The relative length of the snout remains unaffected, however.

Most interesting of all of the skull elements are the postfrontals and postorbitals. These bones show the most variation in shape, being elongated in some forms, abbreviated in others. Proper identification of these two elements is also a point of conjecture lying as they do with only one contributing to formation of the posterior orbital rim and the other to the anterior part of the temporal bar (Fig. 6).

In the champsosaurs, the postorbitals may have spread to the entire posterior border of the orbit and excluded the prefrontals completely from the orbit as interpreted by Brown (1905); or, as in the case of *C. natator* (Russell, 1956), displaced the postfrontal from the orbit as well as separating it from the frontal.

On the other hand, the prefrontal may have, in retaining its more normal association with the frontal, encroached upon the position of the postorbital to the extent of eliminating it from the orbital rim. With exaggerated expansion of the temporal region in this form, it would seem more convenient to have stretched the postorbital into the base of the temporal bar away from the orbit and pressed the postfrontal, a more medial element, into

service as the sole contributor to the posterior orbital rim and as the major dorsal support of the jugal. The postorbital, in any case, still retains its ventral contact with the jugal.

With normal relationships of these elements in a less modified skull, the postorbital is lateral to the postfrontal, and, as pointed out by Romer (1956, p. 105), normally makes up part of the temporal bar. These elements have been interpreted in this light in the present paper.

Details of the braincase are not clear in any of the specimens of *C. gigas;* hence, no discussion beyond what has been described for this species in the previous section will be made.

MANDIBLE

Lengthening of the distal jaw may be related to age as is probably the slight dorsad flare of the extreme tip as shown in figure 9 and Russell (1956, p. 38, Plate VI) for *C. natator*. This is not as noticeable in small jaws.

POSTCRANIAL SKELETON

The postcranial skeleton of *Champsosaurus* is of modest proportions ranging from a few feet to upwards of eight feet in length and presenting a somewhat crocodilian-like appearance. In this section, an attempt has been made to review the general osteology and separate juvenile and adult osteological characters. Features in one or the other groups are expressed largely as a matter of proportion and degree but are, nonetheless, important considerations in understanding the group as a whole.

The postcranial skeleton affords ample points of comparison not only between young and adult stages, but, to a limited

extent, of variations occurring among individuals of approximately the same age.

In regard to individual variations, the picture is not easily diagnosed. Conditions such as discussed under the various headings in this section are encountered and may be indicative of variations not solely governed by age. Designation of certain ontogenetic states, e.g., juvenile, young adult, etc., was arrived at in part by observing the relative numbers of various-sized individuals present from a single horizon. The average-sized specimens comprising the majority were probably young breeding adults and are regarded as such for this analysis. In all situations encountered where champsosaur remains occur in large numbers, immature specimens, including the extremely small, are represented. This indicates that both young and adult forms occupied the same habitat and that the young were hatched or born in the immediate vicinity of the normal habitat of the adult.

A second criterion applied in judging the relative age of a specimen employs proportional comparisons between small, average-sized, and large specimens. It was found that the limb length and individual limb bone ratios within a species nearly match regardless of age (Table 2). However, limb bone extremities do change in proportion with age. The long bones and girdle elements of the young are also straight or flat, depending on the element considered, and are relatively featureless; whereas, homologous elements of the adult become quite expressive of features and curvature. Other bones, such as vertebrae, show delicate structures like the ventral carina that become merely heavier and less acute with increasing age.

Another difference indicative of age is the amount of layerng found in the periosteal portion of the long bones and ribs

TABLE 2.

C. laramiensis	No. 982 (adult) from Brown (1905)	Juvenile, SMM P65.3.1
length of humerus	120 mm.	77 mm.
length of ulna	75	47
length of radius	73	47.2
length of scapula	92	67
length of coracoid	68	47.5
width of coracoid	65	41.2
length of femur	144	93.5
length of tibia	107	69.5
length of fibula	98	64.5
humero-femoral ratio	.83	.82
ulna-humeral ratio	.63	.61
tibia-femoral ratio	.75	.73
length of 1st dorsal centrum	25	17
height of 1st dorsal centrum	23	14.2
width of 1st dorsal centrum	26	17.6
length of 1st sacral centrum	25	15.6
height of 1st sacral centrum	19	13.1
width of 1st sacral centrum	25	15
length of 1st caudal centrum	24 (?)	15.5
height of 1st caudal centrum	15	14.9
width of 1st caudal centrum	16	15.6

(ref. p. 78).

In this work, the words "young," "juvenile," and "immature" are used interchangeably to describe nonadult conditions or individuals. The term "subadult" is used to indicate a form that is older than these but not possessing strictly adult features.

VERTEBRAL COLUMN

CERVICAL VERTEBRAE

(Atlas-axis complex). As stated (Parks, 1927), the atlas and axis are of great determinative value. In the context of determining species, this has not proved to be the case. However, in determining relative age of a particular specimen, it does have value.

The atlas is known only in *C. laramiensis, C. ambulator,* and *C. gigas.* It is partially known in *C. natator.* The axis is represented in the above two former species and partially in the latter two. Of the various homologous elements making up the atlas-axis complex, a constancy of shape and form is the rule. Greatest exceptions are

the proportional disparities between small (young) and adults. For example, regarding the pleurocentrum of the atlas, the whole forward face changes. The anterior projecting process on the superior surface is a prominent feature in the adult and almost nonexistent in the juvenile. The anterior articular face widens in the adult and becomes prominent (Fig. 11). This unit of the atlas is described in further detail for *C. gigas* in the preceding section and may be applied to all species. Of the three remaining units comprising the atlas, a pair of neurocentra (neural arch) and an intercentrum (hypocentrum) are similar in form wherever known. Their form is simple and considered primitive. Each is separate from any other unit. Each half of the neural arch is formed by a unit that is more or less T-shaped in profile. Arching across to midline, the anterior arm meets the exoccipital forming the superior segment of the atlantal ring and provides a protective shield for the spinal cord. The other arm of the T is directed caudad and forms good articulation with the anterior

zygapophyses of the axis. The stem of the T angles downward and diminishes as it contacts the hypocentrum. Medially, the stem of the T is expanded forming a solid articulation with the laterally expanded surfaces of the anterior side of the pleurocentrum. The lower segment of the atlantal ring is formed by the wedge-shaped intercentrum. This is an interlocking piece adding to the support and control of the neck. Articulation facets cover the entire posterior surface of this element (for contact above with the pleurocentrum and below with the intercentrum of the axis), superiorly at each extremity (for contact with the neural arches—neurocentra), and anteriorly in a concavity for union with the occipital condyle (Fig. 12).

The axis is less complicated, having only three separate units: centrum, neural arch, and intercentrum. The centrum only is preserved in *C. gigas* (refer description, p. 27). This unit of the axis regularly has three articular areas in the same places and occupying proportionally equal areas in each species. The anterior surface has a large superior facet for union with the pleurocentrum of the atlas. Below this is a smaller facet that is set in and looks anteroventrally in both young and old individuals. In *C. gigas*, it appears to have a more forward facing attitude. In figure 10, the profile of this unit is shown. In anterior views (Fig. 44), the centra of young and adult specimens are shown to differ also. In the juvenile, there is a more acute base and a suggestion of a ventral carina. The adult does not have this condition as the ventral surface is squared off. The neural arch arises from the lateral diapophysial sutures on the dorsal surface of the centrum, the bases of which are much expanded and indeed characteristic, and the most readily recognizable feature of champsosaur vertebrae.

As preserved in *C. laramiensis* and *C. natator*, the neural arches differ only slightly from each other. The characteristic features of this unit are a very slight neural crest that is directed posteriorly to form the post zygapophyses and a short forward projection that reduces to a narrow wedge and supports the anterior zygapophyses. The intercentrum of the axis fills an intervertebral position ventral to the main articular facets for the atlas pleurocentrum (odontoid) and the axis centrum. Its expanded posterior face, which is concave to a greater degree in younger animals, embraces the corresponding inferior facet of the axis. Dorsally, it contacts the axis pleurocentrum and its intercentrum at its forward extremity.

CERVICALS (three to nine)

There are judged to be nine cervicals in all species of the group. However, a complete series is known for *C. laramiensis, C. ambulator,* and *C. gigas.* The cervical centra are subcylindrical and more or less isometric, having three axes of nearly equal length. If anything, they are a bit dorsoventrally compressed and concave on the sides. There is a gradual increase in size posteriorly. The oblique faces of the centra, mentioned by most authors, account for the modest dorsal curvature of the neck—especially noticeable near the front. In life, great mobility was provided by the reflexed perimeters of the articular faces of the centra, as noted by Brown (1905). There is a ventral carina that is more salient in certain species. Brown's (ibid.) cervical carina are very pronounced in *C. laramiensis,* reaching their greatest development at the seventh vertebra, then decreasing to the eleventh vertebra. Figure 45 illustrates the series in a subadult. This feature is also impressive in very young specimens of this species (viz., SMM P.65.3.1, mounted skeleton, Fig. 46). The
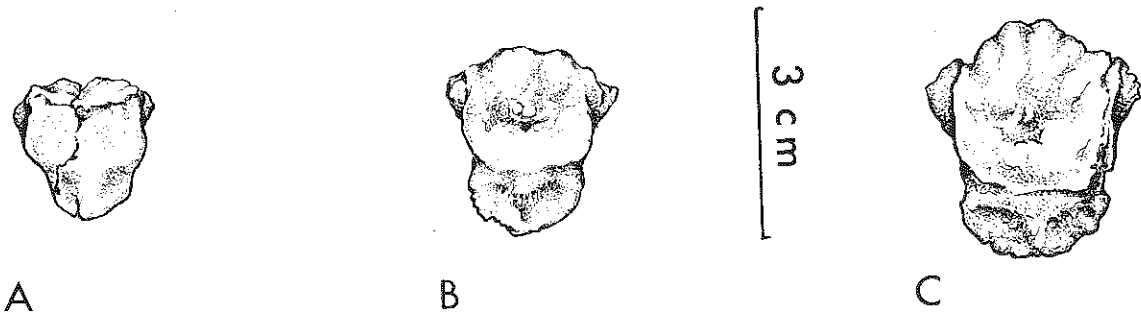
Fig. 44.   Anterior view of axis pleurocentrum in: A. *Champsosaurus laramiensis,* juvenile. B. *C. natator,* subadult to young adult. C. *C. gigas,* mature adult.

feature diminishes with increasing age. In examination of numerous specimens of *C. gigas,* some very young, the ventral carina was found to be much less pronounced.

Diapophyses are well developed and also increase in size from the front towards the rear of the column. Parapophyses, Brown (ibid.) states, begin on the fourth vertebra in *C. laramiensis;* other authors, (Russell, 1956), note their appearance on the fifth vertebra of *C. natator.* Actually, capitular articulation areas (parapophyses) are found throughout the cervical series with the exception of the atlas, which bears no rib, and the axis (Fig. 10). They

do not become well defined until the fourth or fifth vertebra where there is no longer a contiguity with the anterior face of the centrum. They gradually increase in prominence and finally merge with the diapophyses at about the beginning of the dorsals.

Occasionally, one or both parapophyses on the ninth vertebra may be confluent with the diapophyses; or one or both may still be separated on the tenth vertebra. This condition seems to be independent of the relative age of the individual and within the realm of normal variability. Intercentra have been mentioned for the first five cervicals (Brown, 1905). These
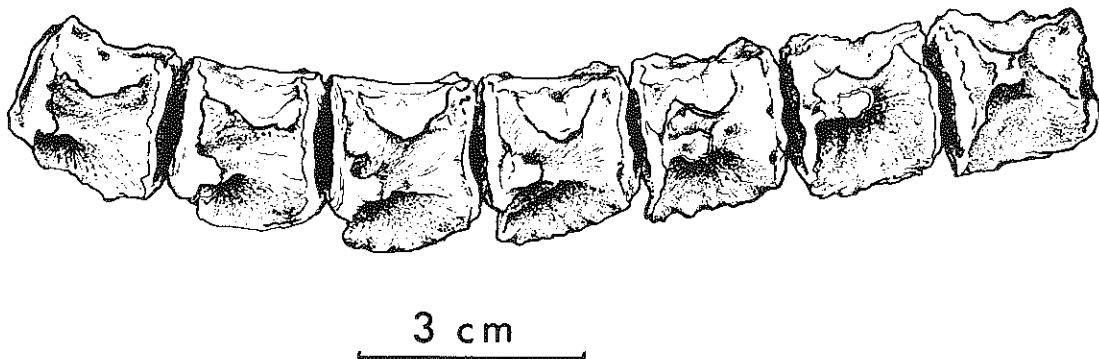
Fig. 45.   Cervical centra 3-9 of *Champsosaurus laramiensis,* juvenile size.

were obviously very small elements and perhaps to a large extent cartilaginous. There is evidence that the intercentra, a rather primitive feature, were retained in the full cervical series. Figures 45 and 46 show juvenile aspects of the ventral carina wherein the anterior portion of the carina is carried far forward and ventral to the intervertebral space and spread presumably to accommodate the intercentrum. Subsequent development of the main articular faces overgrew and displaced the intercentra with the possible exception of the first few elements. As indicated in the type (Fig. 14), a single "intercentrum" is preserved and believed to represent that of the third or fourth vertebra.
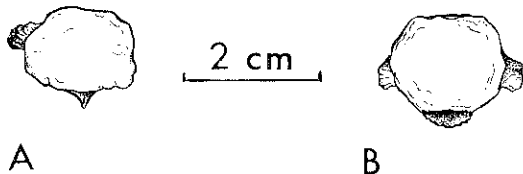

Fig. 46. Anterior view of cervical centra, *Champsosaurus laramiensis*, juvenile specimen. A. Anterior cervical. B. Posterior cervical. Note modification of carina in B.

Neurocentra are heavy with a large canal that is higher than it is wide. Zygapophyses are strong. Anteriorly, they tip outward; posteriorly, they tip slightly inward. The neural spines are long and narrow. The extremities are rounded, and there is a distinct ligamentous facet at the posterior point. The last is the heaviest and most nearly resembles that of the squared first dorsals.

DORSAL VERTEBRAE

The dorsal vertebral series appears to be stable in a number of elements. All species have seventeen dorsals although a complete set is unknown for *C. albertensis*

(Parks, 1927). The dorsals (Fig. 15) are usually circular in section with slight dorsoventral compression posteriorly. The articular faces are amphiplatyan. There is no marked change in the length of the centra from front to rear. The sides are always slightly concave, and prominent parapophyses are situated a little ahead of center on the first few centra. These gradually move back along the sides and are always confluent with the diapophyses, with the possible exception already noted for the first vertebra. Unlike the cervicals, the first few dorsal diapophyses look straight out, not caudad. Any reference to the degree of concavity as being diagnostic of species seems hardly valid. It is more likely a condition of individual variation.

The neurocentral suture is an outstanding part of the superior surface of the centrum as it fills most of the surface area on either side of a centrally constructed neural canal floor. It is positioned more forward on the centrum.

A ventral keel or carina is observed on the first few dorsals of all species. According to Brown (1905), only the first dorsal of the adult has it; but juveniles carry it on the first four vertebrae. From the present materials of *C. laramiensis*, it was found that carina occur on the first few vertebrae of adults, although some are very much reduced and rounded; hence, the condition appears to be a variable one. As further evidence in adults of *C. gigas*, the feature can be very rugose or smooth and varies in extent between the first and the middle of the fourth vertebra.

Brown (ibid.) indicates a shift in the attitude of the parapophyses from an outward facing position in the anterior region to a rearward, oblique position in the posterior vertebrae. A shift of this kind takes place in *C. gigas* at about the level of the

third dorsal, a point at which the ribs are no longer confined by the shoulder girdle and the body begins to bulge outward. At this point, also, the tighter radius of the juvenile rib accounts for a more slender body form (Fig. 47, A). Body bulge increases with size and perhaps varies between sexes. Individuals of modest proportions (subadults), however, seem to have acquired most of the bulge that is to be attained. In *C. gigas,* at the level of the third rib, it is judged that the trachea became bifurcated forming paired bronchi.

The remainder of the neural arch is a massive structure similar to that described for the cervicals. The canal is reduced in size and more circular. There is no marked break in neural spine shape or pitch between the neck and trunk regions. Spines are best developed anteriorly and decrease in height and angle to a vertical blade near the middle of the series. In juveniles there is much less erectness of the blade, and it remains constantly pitched rearward throughout the column (Fig. 47, B). "Squaring off" of the spines with age gives the blade its upright orientation.

SACRAL VERTEBRAE

General form of the sacral portion of the column is a flattened set of three vertebrae fused together. The first is the largest. The last is more circular in cross section as well as being the smallest of the three. The ventral surfaces are broad and flat—more so in adults. Brown (1905) states, "Sacrals consist of two true sacral vertebrae and a sacrocaudal." The basis for this observation is the lack of fusion of the third vertebra of the sacrum triplex to the second (middle) centrum, and the fact that the distal rib end on the "sacrocaudal" is only in partial contact with the ilium. A similar condition is also found in the mounted skeleton of *C. laramiensis,* SMM P65.3.1, which is an immature animal. All adult specimens examined in this study show evidence of a firm joining (fusion) of the third and second sacral centra. The third sacral rib, as well, is changed by adulthood and makes substantial contact with the ilium. No distinction of a "sacro-caudal" in any species seems justified.

The areas of insertion (diapophyses) for the rib heads are large-sized on all three vertebrae and are located toward the front of each centrum. An ontogenetic trend is separation of the ribs from one another as effected by lengthening of the sacrum. In young animals, e.g., *C. laramiensis,* the last two ribs at their proximal ends overlap upon the centrum in front of their own. In other words, the middle rib is partially supported by the first centrum as is the third rib by the middle (second) centrum. In larger specimens of this species, the overlap between the first and second centra is lost; and in the largest specimens, the overlap between the second and third is sometimes lost. In *C. gigas* and *C. albertensis,* the overlap condition between the second and third is retained in all specimens examined—a condition that would lend additional strength to the column at this point. The neurocentra are well formed, as in the dorsals, with stout spines that are greatly thickened at their tips—a feature established at an early age. As best shown in *C. gigas,* the spine extremity becomes complicated with lateral processes and a posterior facet. The spines are erect in adults and swept back in juveniles.

CAUDAL VERTEBRAE AND CHEVRONS

A complete caudal series is unknown. Estimates of the number of vertebrae run from 36 upward. It would seem that a dozen or so should be added to this number to complete the series. The caudals have been divided into as many as four types by Brown (1905), Parks (1927), and others according to the presence of
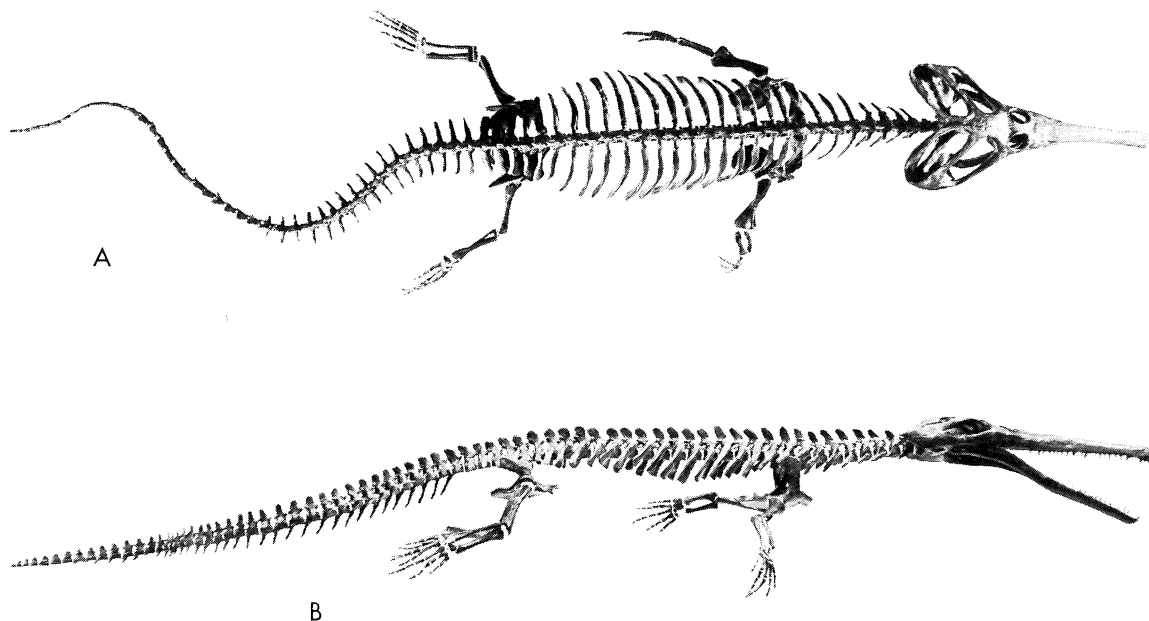
Fig. 47. A. Dorsal view of *Champsosaurus laramiensis,* SMM P65.3.1. Mounted skeleton of juvenile. B. Lateral view of same. Total length of specimen along vetebral column including skull: approx. 1610 mm.

chevrons, rib attachments, and type of neurocentral joining. Because of inconsistence in a demarcation between types, it seems best to consider the tail by regions. The first region, or the base of the tail, consists of the first two or possibly three vertebrae and is the only region that bears no chevrons. A loosely attached chevron, however, may have been present on number three in some. Neurocentra and ribs here are suturally united to the centra.

The second region of the tail begins with the third or fourth vertebra and may extend through the fourteenth.

According to Brown (ibid.), ribs are carried on the first twelve vertebrae only. His number thirteen has no trace of a rib or lateral process. Parks (1933) indicates eleven on an interrupted sequence. Further evidence shows variability in the extent of ribs. In some specimens of *C. gigas,* for example, as many as fourteen or fifteen vertebrae may have carried ribs or lateral processes. The last few of these, however, were not suturally joined to the centra and may not constitute "ribs." Coossification of rib and centrum occurs between the level of the ninth through fourteenth vertebrae. Coossification of the neurocentra and centra also occurs within this range but not perforce at the same point. In C. *gigas,* the tenth neurocentrum and the ribs are still attached suturally. In some *C. laramiensis* they are already fused on the ninth. In SMM P63.13.1 of the same species, they are not. The neurocentrum fuses in *C. gigas* at about the eleventh or twelfth vertebra; and the ribs—it is estimated from their size in the eleventh vertebra—remain uncoossified beyond this point, perhaps only to the twelfth vertebra. Beyond this, sev-

eral smaller lateral processes persist. Figure 19, E and F, shows persistent lateral processes on what are considered to be near the fifteenth caudal vertebra. The remaining caudals of *C. natator* after eleven are alike (Parks, 1933). The arrangement in *C. albertensis* is uncertain, although it appears that lateral processes or parapophyses extended to the fourteenth or so.

A third region of the tail, beginning between the ninth and fourteenth vertebrae, is noted as having the neurocentra and ribs coossified with the centra. Ribs are lost around the twelfth through sixteenth, wherein begins a fourth region, including all remaining elements. A heavy dorsal fin was a feature shared by the first dozen or so vertebrae in life. Beyond this, the distal expansion of the neural spine is drastically reduced; but a thin fin probably remained.

RIBS

CERVICAL RIBS

Ribs are borne by all cervical vertebrae except the first. The absence of parapophyses (Parks, 1933 and Russell, 1956) on the first few vertebrae does not reflect the absence of ribs. All ribs are divided proximally into a small capitular head and a larger tuberculum. As the parapophyses climb on the centra and progress rearward, the lower head moves in beneath the upper. The ribs increase in length until the eighth (last), which is disproportionately longer and heavier than the preceding ribs. The first rib is simple, smooth, and rather straight. The succeeding elements are curved rearward and angle ventrad. Along the anterior surface of each rib is a ridge that ends proximally in a small spike between the capitular and tubercular processes (Fig. 22). This feature exists on ribs one to five in *C. laramiensis*, two to eight in *C. natator*. It is missing on the sixth in *C. albertensis* and preserved only on numbers two and three in *C. gigas*. The form of the cervical rib varies. Only in *C. natator*, *C. laramiensis*, and *C. gigas* is there a posterior uncinate prominence. In the first, the uncinate is present from the sixth through the last cervical. It is suspected to be similar for the latter two also.

DORSAL RIBS

Most interesting of all the ribs are the dorsals. All vertebrae in this series have ribs. They are rather heavy elements with single heads, except occasionally the first in immature animals. In the young of *C. laramiensis*, (Brown, 1905) and SMM P65.3.1, there is a slight separation into two articulating heads. This situation can be expected in the young of all species. The tubercular facet is always confluent with the capitular by the second dorsal and becomes very broad in older individuals as well as superior in position to the lower head. It is especially noticeable in *C. gigas* wherein its area is twice that of the capitular area in the region of the longest (7th-8th) dorsal rib.

The general shape is a stout shaft that curves gently caudad and is twisted medially and somewhat swollen distally. All terminate abruptly. There is a keen ridge both in front and behind. This is especially marked on the proximal half of the shaft. The distal extremity is fluted usually with numerous open canals in the periosteal surface. The first few ribs are flattened against the body rather than swollen distally in *C. natator*, *C. laramiensis*, and *C. gigas*. With this terminal modification, a posterior uncinate process develops, which is simply a continuation from the cervicals. With proper alignment, the uncinate process actually projects more upward than posteriorly. The uncinate gradually moves down the blade and diminishes. This feature, when present, is an indication of maturity; in *C. laramiensis*, at least, it is

totally lacking in juvenile skeletons. It is probable that the appearance of this feature is correlated with the time at which major body bulge is being attained or "subadult" size.

In *C. natator* (Russell, 1956), the uncinate is distinct on the ninth and tenth ribs but rudimentary on the eleventh and lost in the remainder. A complete set of dorsals for an adult of *C. laramiensis* is not available, but a prominent uncinate is indicated by the flared tip of what is considered to be the eleventh adult rib in SMM 64.10.1, by comparison with *C. natator*. An even stronger uncinate is preserved on what is taken as the tenth rib in *C. gigas* (SDSM 53508, Fig. 23). The eleventh rib also of this species (USNM 20521) has an incipient process nearly at the base of the shaft of the same rib. The twelfth rib shows no sign of the feature. Corresponding elements in *C. albertensis* and *C. ambulator* (supposedly adults) are more uniform in shape, and none show expanded extremities or uncinates.

At about the level of the third or fourth rib, there is a general lengthening of the ribs; and they become directed more rearward from their bases. The lengthening is accompanied by a lateral spreading and widening of the rib cage. As noted above, it is within this anterior region of the body that the lungs also expand. This development is believed to be responsible for the modification in the form of incising observed in certain forms. It is seen in large specimens of *C. laramiensis* (adults) and in all individual ribs of *C. gigas* examined (possibly all adults). The incised area occupies up to one third the length of the visceral surface of the rib starting slightly above the distal end. It is best developed on the longest (7th-8th) rib. Incising is inclusive of ribs four through at least number eleven—nearly one half of the total dorsal length of the series. It is esti-

mated to cover nearly the same extent in the smaller species also. As the ribs become more robust with age, incising becomes deeper. The last six ribs (Fig. 24) are simple and without visceral incising. A ridge persists on both front and rear edges. The anterior ridge covers essentially the entire length of the shaft. Brown (1905) indicates that the last three are without cartilaginous attachments. These are distinct in all specimens as having reduced distal ends that may have been unattached. However, some attachment is indicated, at least in *C. gigas*, by the existence of small but well marked facets (ref. p. 22).

SACRAL RIBS

The sacrum contains three ribs. It is their nature to be consistent in the function of support as all engage the ilia at their distal ends. The overall result is a strong pelvic bridge. The shape of the sacrum with ribs in place is square. A juvenile characteristic is a tapering form (Fig. 48) mainly because of the underdeveloped last rib. The center rib is the largest of the
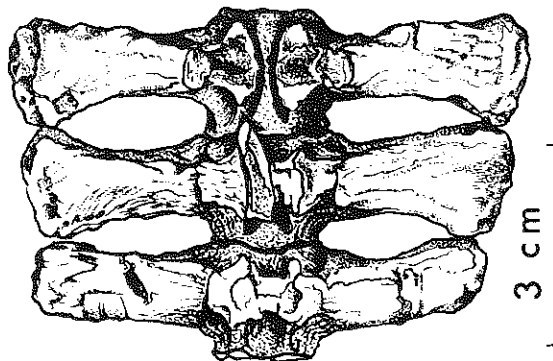

Fig. 48. Dorsal view of the sacrum, *Champsosaurus laramiensis*, SMM P65.3.1. Mounted skeleton of juvenile.

three and lends most support. Ontogenetically, the third rib becomes more involved and eventually shares about equally in support of the pelvis. This seems to be especially true in *C. gigas* and *C. albertensis*,

the largest species in which the base of the third rib retains its minor overlap condition onto the second centrum. The base of the third rib actually becomes larger than that of the second rib. Its distal end enlarges as well but never quite reaches the size of the second rib.

The first rib is curved backward (Brown, ibid.). It is also thinned on the forward border and projected forward on its distal end. A similar shape prevails in all species. This bone in *C. gigas,* however, has a more distinct backward hook with little thinning of the border and projecting of the distal end. The second rib, as noted, is most uniform throughout the developmental growth stages. The third rib shows changes; viz., in the very young, this bone is straight or may arch weakly forward, and the proximal end shows most expansion. As stated above, it overlaps the posterior part of the second (middle) centrum. The distal and proximal ends expand appreciably in the subadult stage, and on the rear edge there appears a prominence that migrates with age outwardly. As a result, larger specimens show a distinctive flare at the most posterior distal corner of this bone.

CAUDAL RIBS

Distribution and comments on the caudal ribs within their respective regions of the tail are made elsewhere. Figure 28 shows a typical caudal rib with its distal and proximal attachment areas.

PECTORAL GIRDLE

The pectoral girdle forms a shield affair over the anteroventral portion of the body. It is composed of scapulae with short, outwardly spreading, upright blades; ventral disc-like coracoids; and an elongate interclavicle that is tied firmly to the endochondral elements by a pair of stoutly curving clavicles. Ventral interconnecting cartilages evidently were present in life.

SCAPULAE

The scapula consists of a short, vertical blade that is generally uniform in thickness and width but varies to an expanded hatchet-shaped blade in some individuals of *C. gigas* and *C. laramiensis.* Because of sampling limitations, it is difficult to judge if this variation is one of age or individuals. In *C. laramiensis,* for example, the uniform blade is a character of the youngest specimens. Large individuals have a pronounced broadening of the distal end. In *C. gigas,* a similar condition exists. However, a thin, unexpanded blade also occurs in the adult stage. From what can be determined from these individuals, there is an accompanying condition in which there is slighter development of the limb bone extremities and girdle elements. This leads one to suspect that some expression of sexual dimorphism exists in the skeleton.

In all specimens, the suprascapular border truncates the blade in a gentle arc. Anteriorly, the edge of the blade provides a small, roughened surface for attachment of the vertically inclined end of the clavicle. Below this at the anteroinferior angle of the bone is developed an acromial process. The inferior end of the scapula consists of a short, anterior, subcircular blade that curves inward (following the curve of the clavicle) toward the medial interclavicle and in life probably had cartilaginous connections with both of these elements. The posterior portion is thickened externally and thinned medially for reception of a corresponding surface on the coracoid. In one form (Russell, 1956), a fusion of these bones is reported; yet none of the materials examined showed this. The forward portion of the glenoid cavity is formed laterally adjacent to the coracoid surface. The height of the blade increases very little with age; whereas, the inferior portion expands noticeably.

CORACOIDS

A major component of the ventral pectoral shield, the coracoid, is positioned behind the scapula. As indicated above, its outer anterior portion is heavy as it forms the posterior half or better of the glenoid cavity and the adjacent scapular connection. Immediately posterior to the glenoid fossa is a prominent laterally projecting infraglenoid process that is the principal structure of variation among species.

In *C. natator*, this process is continuous with the glenoid surface (Fig. 49) and, consequently, of little prominence. Neither is it an oustanding feature in *C. albertensis*. In *C. laramiensis, C. ambualtor,* and *C. gigas,* it is bold and located well apart from the glenoid surface at all ages. (Fig. 30). The remainder of the bone is a large, ovoid plate that reaches nearly to the interclavicle to which it was most likely joined by cartilage in life. A supracoracoid foramen is located near the scapular border about at the center of the element in all species.

CLAVICLES
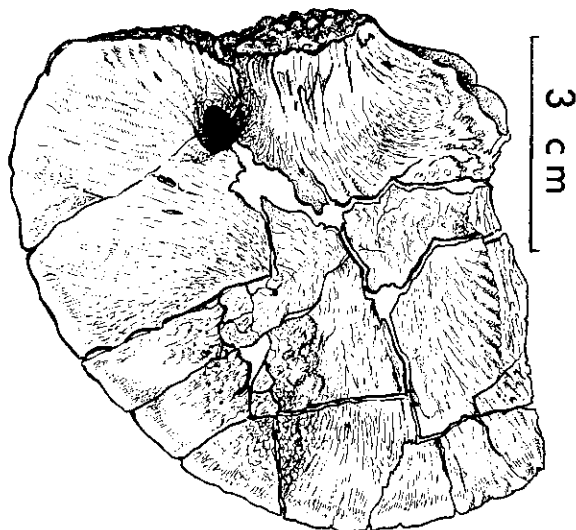
The shaft-like right and left clavicles

Fig. 49. Right coracoid of *Champsosaurus natator* in dorsal view.

unite with the median interclavicle about at the level of the eighth rib and tie the girdle together. These elements are stout throughout, thinning at their ends. As it reaches the base of the scapula, the shaft of the clavicle is twisted and becomes coarsely striated as it turns dorsad to lie in close contact with this element. Medially, the horizontal portion is striated and expanded for a solid interlock with the cross arm of the T-shaped interclavicle.

INTERCLAVICLE

The shape of this bone is that of a T. When united with the clavicles, its cross arm extends to form a channel (Fig. 31) that gives *Champsosaurus* its characteristically flattened chest. The stem of the interclavicle projects rearward into a blunt point and shows variations of length and shape among species. The stem is thin dorsoventrally, concave above, and except for its anterior end has a cartilaginous border surrounding it.

FORELIMB

Structurally the forelimb bones, as the hind limb bones, exhibit a condition of the compact periosteal bone that is generally nonvascular. This condition in which canals are sparse or absent is typically lepidosaurian (Gans, et al., 1969, p. 61). A second condition found at middiaphysis is also lepidosaurian in character in that it resembles the condition found in lizards wherein the cancellous trabeculae are greatly limited and in some specimens almost totally absent. Ratios between the front and rear limb lengths of both adults and subadults give an idea of the relative lengths that one might expect in various species. The number of specimens available for this analysis was small because both forelimbs and hind limbs are not often preserved intact and together, therefore, imposing obvious limitations. From a total of

nine suitable skeletons (7 adults and 2 juveniles), ratios of 100/125 – 100/135 were found. Extrapolation on several less complete specimens suggests similar ratios. In each case, the hind limb is longer (all measurements perforce exclusive of the foot). Three specimens of *C. gigas* account for the greater ratio of 100/135. Both the femur and epipodials become noticeably extended in this form. *C. natator* is the only species without complete enough material for a determination. *C. ambulator* appears to have been the shortest limbed form as judged from a single skeleton (Brown, 1905).

HUMERI

Morphologically, this bone has diagnostic value in specific differentiation. Humeri of four species are compared in figure 50. This is a stout bone with a narrow shaft that is ovoid in cross section. The shaft is twisted causing the ends to align 45° – 85° with one another. The most commonly observed

arrangement is around 80°. This condition is variable. A deltopectoral crest is a salient feature on the shaft in *C. ambulator,* mildly developed in *C. laramiensis* and *C. gigas,* but nearly lacking in *C. natator* and *C. albertensis.* The extremities of this bone are widely expanded but vary considerably among adults. The proximal end or head is always shorter in breadth (widest dimension) but thicker in width than the distal end. A large, articular surface is available proximally. Ento- and ectotuberosities are developed to a greater or lesser degree and most often continuous with the head. Brown (1905) notes a distinct separation of these tuberosities from the head in *C. ambulator* as well as in an immature specimen of *C. laramiensis.* This is found to be variable in the young and not a unique condition. At its distal end, the humerus is compressed dorsoventrally with the limb extended in a horizontal plane. The articular surface covers the entire end. In one
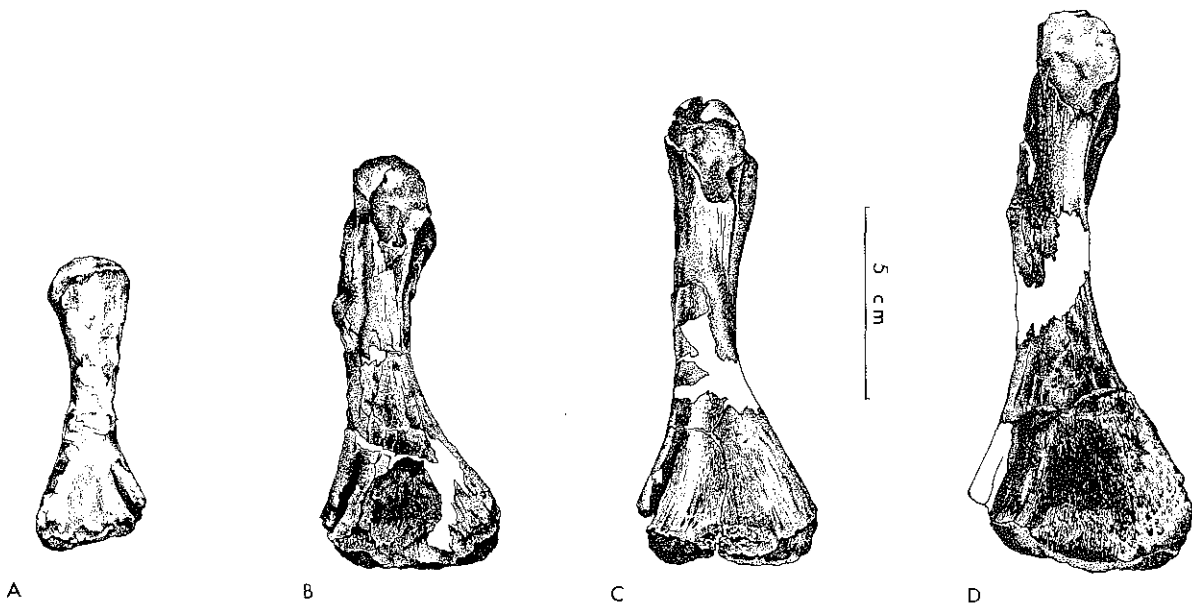

Fig. 50.   Humeri of four species of *Champsosaurus.* A. *C. laramiensis,* juvenile, B. *C. ambulator.* C. *C. natator.* D. *C. gigas.* All in preaxial view.

form, *C. ambulator,* the radial condyle is robust indicating the emphasis of support on this supposedly more ambulatory form. The feature is only moderately developed in other species; and in *C. natator* and *C. albertensis,* there is very slight development. Immediately above the radial condyle is an ectepicondylar sulcus instead of a foramen. This increases in depth toward the distal end to where it nearly penetrates to the ventral side but is unknown to actually do so. The sulcus becomes deeper with increasing age. It is distally closed, or nearly so, in *C. ambulator* but remains open in other species. Its status in *C. albertensis* is uncertain (Parks, 1927). The remainder of the articular surface varies somewhat in breadth. Centrally, there is a mild swelling—the entotuberosity. This is lacking in juveniles. Posteriorly, the entepicondyle extends up the side of the shaft a bit. Ontogenetic development of these aspects of the humerus is illustrated for *C. natator* in figure 51.

RADII

The radius (Fig. 35) is not a diagnostic element. It is a rather fragile bone well over half the length of the humerus in all species with expansions at each end. The upper end is the largest—ovoid and flat, or slightly excavated to fit the condyle of the humerus. The lower end is convex and more circular in cross section. The shaft has a distinctive twist, probably related to the posture of the foot (Romer, 1956), and a ridge on its external surface.

ULNAE

The ulna (Fig. 36) is essentially equal in length to the radius, heavier, and generally just as undiagnostic. There is a heavy proximal end of subtriangular form in cross section. The olecranon is large and of modest elevation in all except *C. gigas* where it is exaggerated in height. It is least obvious in *C. natator.* The shaft is flared on its internal side at the head to provide a radial facet. The shaft narrows
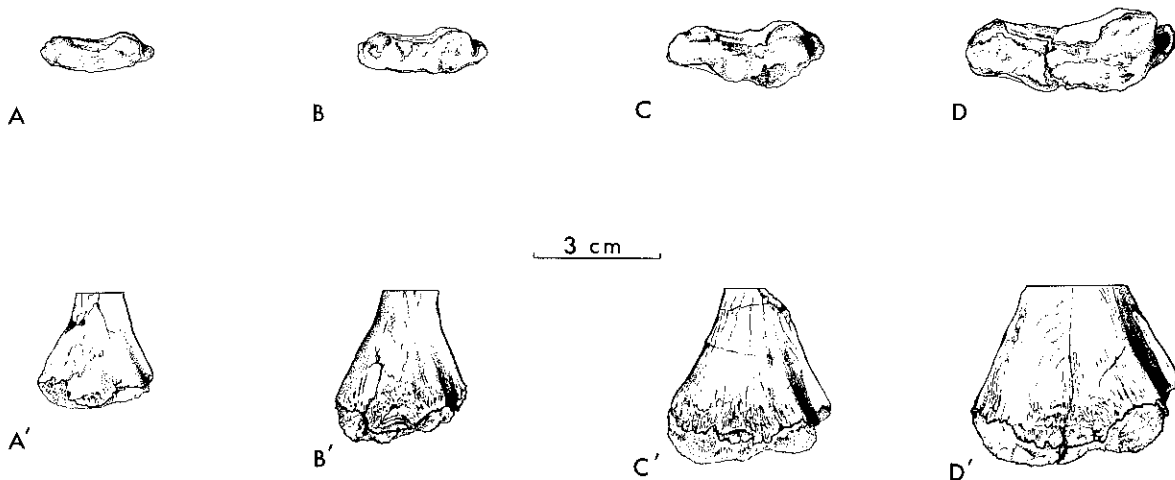

Fig. 51. Ontogenetic development of the distal end of the humerus in *Champsosaurus natator.* A-A'. Young, has simple articular surfaces, ectepicondylar sulcus incipient. B-B'. Larger juvenile, beginning to develop radial condyle. C-C'. Subadult, shows all condyles. D-D'. Adult, full development of condyles; ectepicondylar sulcus deep.

rapidly below this and becomes flat dist-
ally. It expands slightly near its extremity
and supports a low ridge near the tip on
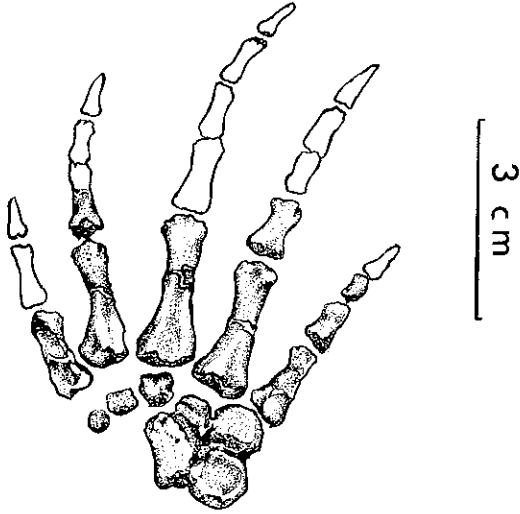the ventral surface. The articular area is
simple and mildly convex.

Fig. 52.   Restoration of forefoot of *Champsosaurus laramiensis*, SMM P65.3.1.

Fig. 53.   Foreleg and foot of *Champsosaurus laramiensis*, SMM P65.3.1., in situ.

CARPUS

Incompleteness of the carpus in aquatic
reptiles is not unusual (Romer, 1956, p.
378) because of imperfect ossifications of
the elements comprising this structure. A
fairly good idea of the carpus in *Champso-
saurus* has resulted, however, from the
present composite analysis.

Brown (1905) described five carpals:
the intermedium, an ulnar, plus three distal
carpals. The rest he dismissed as being
cartilaginous; therefore, not represented.
In *C. natator* (Russell, 1956), seven car-
pals are known: a radial, a centrale, the
ulnar, and four distal carpals. The present
forefoot of *C. laramiensis* (SMM P65.3.1,
Fig. 52) also contains seven carpal ele-

ments. Their interpretation as follows is
based largely on their original disposition
in situ (Fig. 53).

Of the three proximal elements of the
carpus, the radial is missing. It must have
been in accord, however, with that de-
scribed for *C. natator* by Russell (ibid.) as
being a flat, triangular bone fused to the
centrale at its distal end. The ulnar is a
squared bone with both dorsal and ventral
aspects concave. A rectangular-shaped in-
termedium separates the radial and ulnar.
It approximates them in size but is longer
and is rather flat and thin.

Articulated in situ (Fig. 53) with the
distal end of the ulnar is a smaller square
element that is considered to represent the
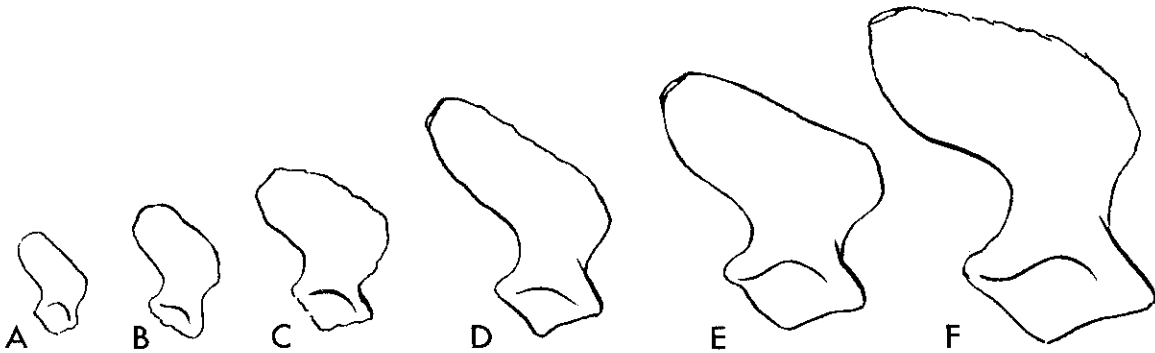
Fig. 54. Ontogenetic development of the ilium of *Champsosaurus*. A. Very young, probably not over one season old. B. and C. Juveniles, note increase in height of blade. D. and E. Older juvenile and subadult, blade first lengthens then "squares-off." F. Mature adult, blade becomes robust. In aged individuals the blade is heavier and rugosity increases. All figures are based on specimens of *C. laramiensis* except A., which is *C. natator*.

fourth carpal. It is slightly concave dorsally. The distal end is oblique, and strong articular areas are present on both ends.

A second bone about the same size and medial to this joins the oblique distal edge of the intermedium and appears to be a proximal centrale. A distal centrale seems also to have existed adjoining the lower end of the radial (Russell, ibid.). The three remaining, small distal elements in this specimen are the first, second, and third carpals increasing in size respectively. In light of the above, the fifth carpal and a pisiform member are still unknown. The total number of carpals was probably ten. The carpus, in general, is also unknown in *C. albertensis* and *C. gigas*.

MANUS

The manus is composed of five elongate metacarpals and five digits with apparent formulae of 2, 3, 4, 4, 3 and 2, 3, 4, 5, 4, as far as can be judged (Russell, ibid.). Figure 52 shows the arrangement of the manus in *C. laramiensis*. The metacarpals are flat dorsoventrally, constricted medially, and flared proximally. At their distal ends, they are only slightly expanded and

squared off as are the phalanges. These are simple in form and decrease in length distally. They are terminated abruptly. The unguals are claw-like and in life probably supported claws resembling those of crocodilians.

PELVIC GIRDLE

The pelvic girdle is a primitive structure with small but strong parts. It has a low silhouette because of a flat, ventral surface. All three elements of the pelvis share in formation of the acetabulum—the ilium contributing the greatest amount, the pubis and ischium about equally. The puboischiadic plate is penetrated by only a small obturator foramen.

ILIA

The ilium is in general like that described for *C. gigas* (p. 41 and Fig. 37). The blade shows greatest change in shape between species and age groups. The inner face has strong rugosities, the outer face much less and often with an inversion for axial and limb muscle attachments.

The ilium is a durable bone and, aside from vertebral centra, is one most fre-

quently preserved. Ontogenetic stages of this bone are illustrated in figure 54. Comparisons of individuals of assumed similar ages from different species show a growth pattern similar to that presented; hence, the proportions observed may be taken as a rough gauge of the relative age of an individual. Individual variation may involve the extent of rugosity or the size of posterior ligament facets on the blade of the ilium.

From the very smallest specimen and the young in general (A, B, and C, Fig. 54), there is a uniform, overall increase in height and length of the ilium. This is followed by a period in which the iliac blade elongates (D, Fig. ibid.). By the time the individual is subadult size, the blade "squares up" again (E, Fig. ibid.). In the largest individuals (F, Fig. ibid.), the blade becomes very thick and rugose. There is always a strong cartilaginous facet on the distal terminus of the blade and a small foramen just above the acetabular buttress.

PUBES

The pubis (Fig. 38) shows little variance from one species to another, and the description given for *C. gigas* is applicable to the group. Differences are mainly in the length of its medial border. For example, *C. ambulator* with a much extended internal border is easily distinguished from other forms in which the border barely stretches beyond the overall length of the bone. There is a "pectineal tubercle" at the forward end of this bone that is very subtly indicated in juveniles and only mildly in the average adult. In older specimens, however, it becomes an important feature that characterizes the bone (Fig. 55). Its best development is seen in the largest individuals of *C. gigas*.

ISCHIA

This element lends little by the way of diagnostic evidence for species determination, and about the only developmental change is in size and amount of tuberculation on the rear edge.

HIND LIMB

A most noticeable feature about the hind limb is that it is much longer than the forelimb. The normal ratio between forelimb and hind limb for *Champsosaurus* is about 100/125, holding regardless of age of the individual. In *C. gigas*, a ratio of 100/135 is attained and previously noted. The humerofemoral ratio of *C. gigas* is about 100/130. For its supposed closest kin, *C.*
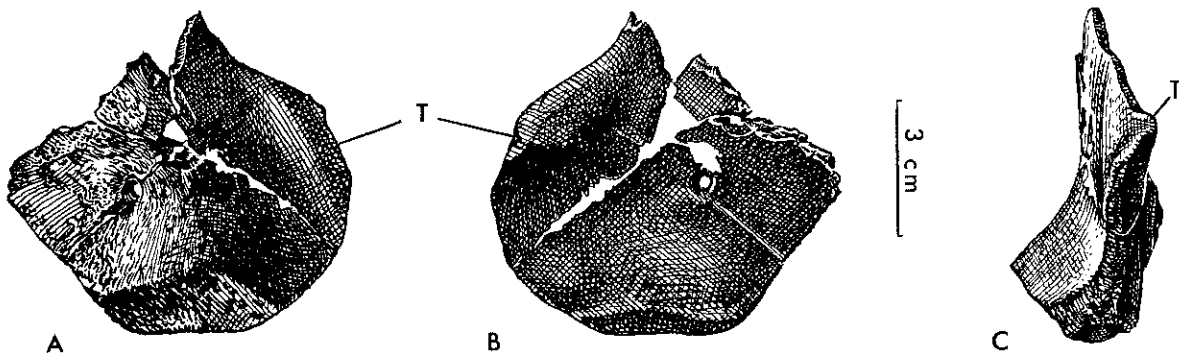

Fig. 55. Right pubis of *Champsosaurus gigas*, SMM P60-2004, showing pronounced development of anterior tubercle (T) in a very large individual. A. Dorsal view. B. Ventral view. C. Anterior view.

laramiensis, it runs close to 100/120.

FEMORA

The femur is a rather long, slender bone (Fig. 39). The mark of conservativeness is nowhere more evident than in this element. The degree of separation of the internal trochanter from the head has been considered important in differentiating species. Parks (1933) states that this separation is significantly greater in *C. laramiensis* and *C. ambulator* than in *C. natator.* Brown (1905) considers placement and its separation from the head descriptive, being lower on the shaft and not contiguous with the head in *C. ambulator.* The trochanter is a salient feature in all forms including the smallest specimens. The shaft of the femur is straight and modestly expanded at its ends in small individuals. It becomes curved and further expanded at its ends with age. At the proximal end, an articular head is well developed with a broadly rounded area of travel. The intertrochanteric fossa becomes deeper and its surface more irregular with age also. It is least pronounced in *C. ambulator.* Distally, the articular surface is broad and without distinctive condyles for the epipodials. It is oriented some 70° – 80° off the long axis of the proximal head.

TIBIAE

Expansions of the extremities in the adult are the most remarkable changes noted in development of the tibia. The shaft is slender and curved. Proximally, it is greatly swollen into a large, flat, articular region with little indication of a cnemial crest in any species. The opposite end of the shaft is curved toward the fibula, and the articular surface at this end is oval in shape and half or less that of the outer end in size. A somewhat concave, inner facet is present for union with the astragalus. The shaft bears a ridge on the fibular side that runs from a distal point about half way up. A second ridge occurs above this on the anterior face. It is best developed in *C. laramiensis* and *C. ambulator,* being very keen in juvenile specimens also.

FIBULAE

Unlike the tibia, the rod-like fibula shows only feeble swelling proximally. A small, oval, articular end is formed. Laterally, the shaft is striated near the end presumably for attachment of iliofibulatis muscles (Romer, 1956, p. 375). This bone is a bit shorter and straighter than the tibia. A short, low ridge appears on the shaft opposite the long ridge on the tibia. Distally, there is a wide flange on the shaft. Posteriorly, it is either flat or only mildly excavated. On its opposite side, it is convex. Two adjacent facets are present: one angled medially for contact with the astragalus and one laterally to receive the calcaneum.

TARSUS

Mobility of the hind foot appears to have been good as accomplished chiefly by the method of articulation between the tarsus and epipodials; viz., angle of attachment and the possible rotational capabilities between the two.

There were apparently only four elements comprising the tarsus: calcaneum, astragalus, and two distal tarsals. The tarsus is preserved in *C. natator* (Parks, 1933) and, but for one distal tarsal, in SMM P65.3.1, a juvenile specimen (Fig. Fig. 56). In other forms the tarsals are not fully represented and exist as isolated elements of uncertain affinities.

The calcaneum (fibulare) is a thin, flat, rectangular piece that is thickened medially for contact with the astragalus. Its proximal border has a narrow face to match a corresponding face on the fibula. Its distal margin is rounded and lies above the fourth

distal and fifth metatarsal. This bone in
C. laramiensis is more triangular in shape,
possibly due to its immature nature.

Adjoining the calcaneum medially is the
astragalus (intermedium of Brown, 1905,
and Fig. 56). This is a larger bone and is
slightly concave both dorsally and ven-
trally. A large, tibial angulation occupies
much of the proximal area. Just lateral to
this at a right angle is a similar although
smaller articular surface that is slightly
excavated to fit the fibula. These two sur-
faces of the astragalus are separated by
a small area that is the only nonarticulat-
ing surface on the margin of the bone.
Adjacent and below this is another broad,
articular surface for the calcaneum. In

Fig. 56. Right hind foot of *Champsosaurus lara-
miensis*, SMM P65.3.1., juvenile. Restoration shown in
outline.

most specimens, the dorsolateral edge is
interrupted by a foramen for the perforat-
ing artery. The rest of the margin remains
thick and becomes roughened distally.

PES

The length of the pes is about one third
longer than the manus. Metatarsals II –
IV are long, slender, and moderately en-
larged at both ends. Proximally, they are
flattened and somewhat wider laterally
than at the opposite ends. The articular
facets are more or less flat. Numbers I and
V are the shortest and stoutest. Each has
a wide spread to its proximal end, the fifth
being hook-shaped (Figs. 42 and 56) prob-
ably as a means of joining the compara-
tively narrow tarsus (Romer, 1956, p.
411). The formula for the pes is probably
2, 3, 4, 4, 3, as indicated chiefly by one
intact specimen figured by Parks (1933).
Numerous disassociated elements are
known and seem to be morphologically sim-
ilar throughout the group.

As in the manus, the phalanges are sim-
ple and have some indications of flexibility
between elements, especially distally. The
unguals are also claw-like.

GASTRALIA

Gastralia are well developed in this
group and obviously afforded considerable
protection to the underside of the body.
Unlike contemporary crocodilians, how-
ever, this was evidently their only "ar-
mor." No evidence of other dermal pro-
tection is known. Increase in weight and
bluntness of extremities with age are ap-
parent changes.

C. laramiensis is the only species in
which a fairly complete, juvenile skeleton
was available for analysis. In table 2
(p. 54), note that linear limb bone propor-
tions are nearly identical, vertebral centra
are quite similar, and the height of the
scapula is little affected by age. Differences

in the lengths of the radii and ulnae are due to lagging development of the olecranon on the latter. A comparison of an average-sized adult and a medium-sized juvenile of the same species shows this close agreement of proportions in spite of the individual age difference. In the case of the juvenile, proportions of an extremely young animal would show greater differences.

SOME ASPECTS OF FUNCTIONAL MORPHOLOGY

All evidence points to *Champsosaurus* as being an aggressive predator endowed with remarkable aquatic capabilities of movement and capture of prey. Related responsive functions are reflected in its hydrodynamically suited body form and its elongate, tooth-lined snout that had a slicing effect through water. A number of gross structural similarities to certain of the crocodilians are noted, and it would be expected that some behavioral parallels existed in life as well. On the other hand, competition between the two may have imposed certain restrictions especially upon the subordinate champsosaurs. Analysis of the present material poses what is believed to be some legitimate speculation on behavioral patterns for champsosaurs.

That extant habitats can in no positive way be regarded as equal to those of extinct habitats will not be argued. I shall, nevertheless, make some comparisons here on the premise that behavioral traits that would have been influenced by structural attributes, regardless of environmental pressures, might be determined.

There is little evidence contrary to the idea that crocodilians today inhabit environments similar to those that they and their champsosaur contemporaries occupied during their earlier history. They seem also to have been as diversified in their preference then, as now. These two reptiles are most often associated as fossils. Therefore, some insight into the mode of life of the extinct champsosaurs might be gained if we compare these two reptiles relating to an extent on known habits of living crocodilians.

Comparisons can also be made with phytosaurs in reference to skull architecture and possible related functions. As evidenced by their stratigraphic distribution and occurrence in a variety of lithologies, the champsosaurs were quite diverse in habitat preference. Their distribution is discussed elsewhere in this paper. From the geologic record of the phytosaurs, we surmise that some like tolerances of habitat prevailed as well (Colbert, 1965). However, the phytosaurs lacked some of the advancements, such as a secondary palate, that the crocodilians acquired to a considerable degree. Consequently, these less specialized types yielded their position to the better equipped crocodilians at the close of the Triassic—a time before the champsosaurs were part of the scene. Conversely, the appearance of the latter and their subsequent development seems to have wrought no critical pressures for change upon the crocodilians. Divergent behavior evidently accounts in large part for their rather lengthy coexistence.

Comparisons of phytosaur, crocodilian, and champsosaur skulls, in particular the nasal and optic regions, suggest the following kinds of related activities. By virtue of placement of the external narial aperture, it appears that the phytosaurs and crocodilians may have had similar means of obtaining food, relying on both olfactory

and visual equipment. The high placement of the external narial opening in the phytosaur skull is ideally situated for resting nearly in total submergence in water with little more than the nostrils and eyes protruding above the surface (Fig. 57, A), much like the posture managed by the crocodilians. The champsosaur skull, with its external narial opening at the terminus of the snout, could not lend itself to the practice of lying submerged immediately below and parallel to the surface of the water with its nostrils exposed to the air above. In effect, its long snout would be forced to break water at a considerable angle to the air-water interface in order to expose the nostrils. This would not have been an advantageous pose for stalking prey. Alternatives might have been a more terrestrial feeding habit or, much more plausibly, underwater detection and capture of prey. The marked dorsoventral streamlining of the skull with its dorsad eye location suggests a practice of "cruising off the bottom" or lying in wait at or near the bottom.

The crocodilian skull in figure 57, B presents the most effective arrangement of skull features for achieving dominance of the surface of the water with the accompanying behavior that the phytosaurs acquired to some degree and the champsosaurs probably not at all. Resting thus near the air-water contact, the crocodilian could avail itself of any opportunities that might come along. This behavioral character very likely had a profound effect on their success through time.

Olfaction and vision are most reliable telesthetic senses, hence, important in obtaining food both in and out of the water. For crocodilians, especially broad-snouted types that are generally more omnivorous, the ability to detect and recognize objects or events at a distance is vital to feeding. Crocodilians are known to rely on vision

and a keen sense of smell to locate a potential food source (Oliver, 1955, p. 176). The olfactory apparatus here is remarkably well developed. More piscivorous forms, such as, gavials, garfishes, and champsosaurs, may have depended less on this sense and perhaps in some cases to the exclusion of it completely in their quest for food. However, olfaction can be a primary means of detection underwater (Walls, 1967).

Gavialis has been compared to *Champsosaurus* by Romer (1956), Fox (1968), and others. The narial apparatus in the former is typically crocodilian. Fox (ibid.) and others suggest that the niche occupied by *Gavialis* was previously filled by the champsosaurs, as the appearance of the former during the Eocene coincides with the disappearance of the latter. Inasmuch as both were long-snouted and *Champsosaurus* may have had either nasal sphincter valves or highly vascularized tissues for prevention of water entering, it would seem reasonable that it did resemble the gavials in some of its underwater activities. However, a peculiar behavior for the champsosaurs—one that did not totally come to be mimicked by the gavials—is indicated by: the terminal location of the narial opening and its questionable olfactory function, the choanae only at midlength on the palate whereby inspired air would not be separated entirely from the mouth cavity as in the gavials with their more complete secondary palate, the vision more aquatic than aerial as in crocodilians, and other bottom type features.

The probable position that the head of *Champsosaurus* assumed while at the air-water contact to replenish its oxygen stores is suggested in figure 57, C. In this position, just the tip of the snout would be above the surface of the water while the mouth was closed tightly. In such a position, the animal could remain submerged almost entirely and, therefore, incon-
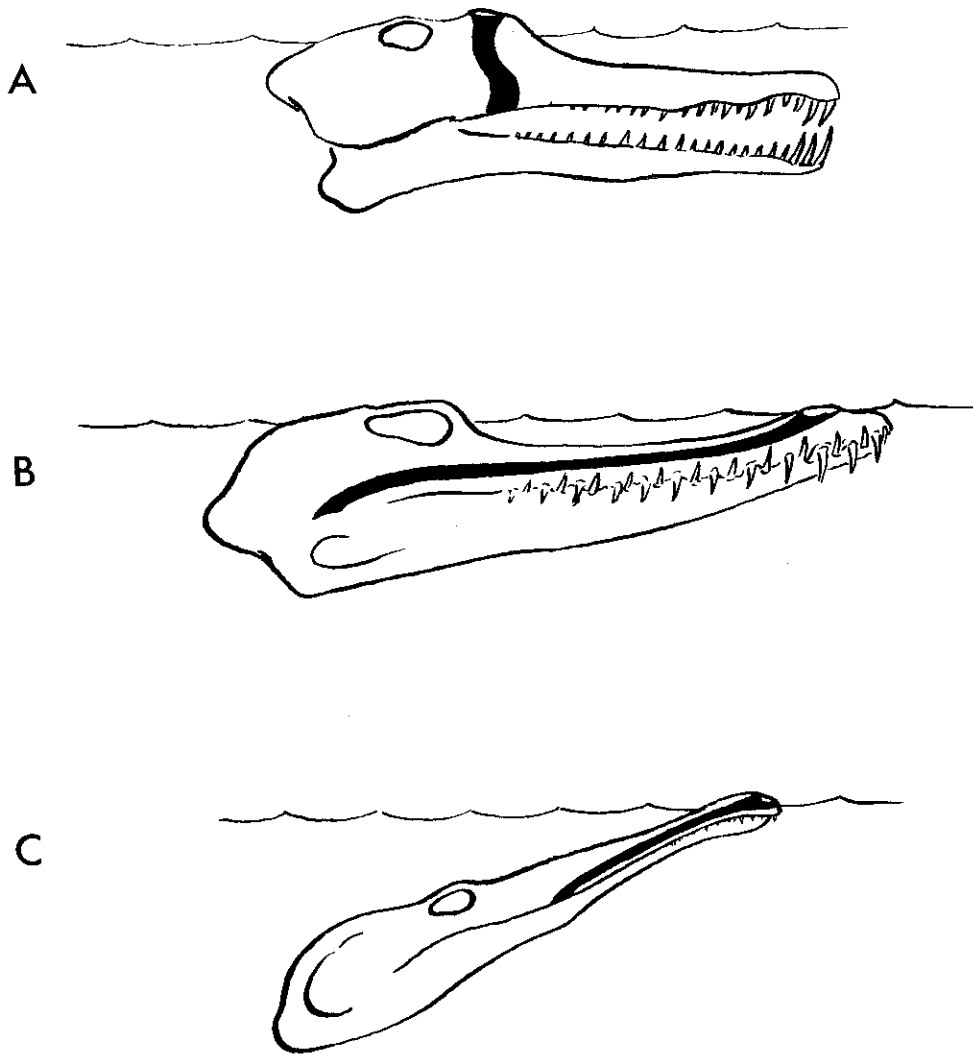
Fig. 57. Diagrammatic posture for the heads of: A, a phytosaur, B. a crocodilian, and C. *Champsosaurus*, while at the air-water interface. Nasal passages shown in silhouette.

spicuous.

A generalization that all species of this taxon were aggressive, underwater predators—"sight feeders," relying on visual detection of prey that would normally be restricted to relatively well-lit waters up to several meters in depth—seems sound. It should also be mentioned that hunting in dim underwater conditions may have posed problems dependent on the acuteness of vision. In this connection, the use of smell and even touch, as is known in some "hunting" turtles (Walls, 1967, p. 437), may have been required. Olfactory epithelium may have been present in ample supply along the airways of the long snout and could have been as vital as vision in locating prey.

The eyes of *Champsosaurus* were strategically placed for fairly good binocular vision. If vision was the main means of detection of prey, an aquatic vision quite unlike the specialized aerial vision of the crocodilian was present; or some means of accommodation to aquatic vision must have existed. No evidence exists in the fossil record. Discussion of the reliance on vision for location and capture of prey is presented by Walls (1967, p. 293) in which crocodilians are cited as having about 25° of binocular field of vision. This field is described as the spatial cone or zone within which separate monocular fields overlap. The highly predaceous snapping turtle *Chelydra* has about 38° of binocularity, according to Walls (ibid.). Most of the food of the snapper is animal, and half of this consists of fast-moving fishes; therefore, the need of good distance judgment is realized by its good binocularity. Measurements of visual angles in *Champsosaurus* are not possible, but estimates based on the position of the orbits suggest a decidedly more upward direction of visual fields and a binocularity exceeding that of *Chelydra* in that direction. This position could also provide a defense mechanism that, unlike that of its crocodilian contemporaries, is lacking in any other structural form.

RESPONSIVE FUNCTIONS

Of the champsosaurs, *C. gigas* is especially interesting in that it demonstrates certain morphological peculiarities of the group best. These are herein considered with an eye to their possible functional importance.

C. gigas is among the last of the genus to make its appearance. It is unusually large and has somewhat longer hind limbs than average. It also shows greatest pachyostosis of the ribs and, perhaps of most interest, is what is considered to be a specialization of the rib cage in which the visceral side of the dorsal ribs has been modified in conjunction with underwater behavior. It should be mentioned here that this specialization is not peculiar to the largest species; it is only best exemplified here. These characters favor the largest champsosaur as well as adults of some other species in the roll of specialized predators that would lie in wait near the bottom of a stream or pool instead of cruising or giving active pursuit, giving them the same effectiveness of smaller predecessors and perhaps the young of its own species.

Food procurement for the champsosaurs, in general, would not seem to have been difficult; but for very large forms especially, which are necessarily slower because of their bulk, an alternative means of securing food might have proven advantageous.

Expenditure of oxygen is rapid and commensurable to energy output in actively swimming animals. Certain reptiles are known to remain submerged in water for hours and even days. The advantages of

being able to do this and conserve energy at the same time are obvious. It is conceivable that *C. gigas* departed some from the more typical hunting pattern and stalked its prey by lying in wait at or near the bottom not unlike *Macroclemys*, the alligator snapping turtle. Without benefit of a distensible neck, the powerful hind legs might have aided in the seizure of prey by providing means of a quick lunge forward.

ried on by lungs, existed and was associated with the described modifications of certain dorsal ribs.

Regarding the plasticity and histological nature of bone, especially during ontogenetic development, the "fit" of ribs to lungs, as shown in the above figures wherein the ribs have conformed in shape and partially enclosed the lungs, would easily have been accomplished.
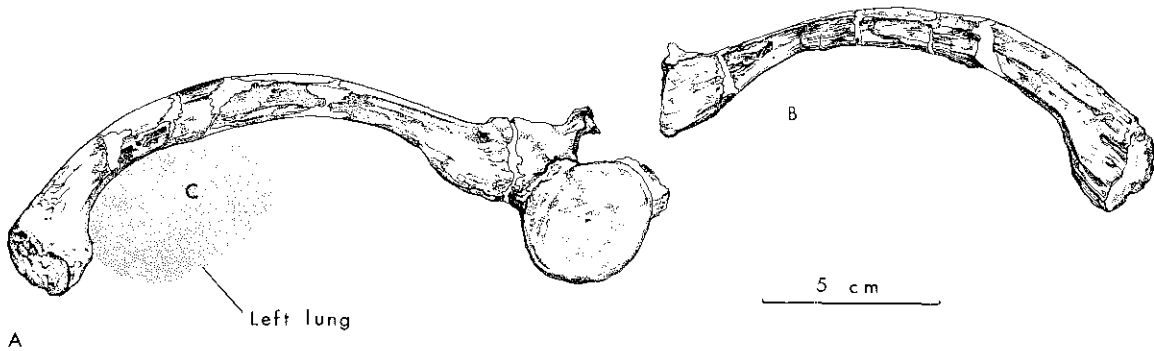

Fig. 58. A. Partial transverse section at level of the eight dorsal rib. B. Right seventh rib. C. Attempted restoration of lung position. All figures in posterior view. Maximum rib length and lung development is at the level of the seventh and eighth dorsal ribs.

A keynote to aquatic prowess of this kind is reflected in the configuration of the anterior part of the rib cage. Figure 58 represents a transverse section through the part of the skeleton showing the dorsal ribs and their internal incising. In this and figure 59, also, are shown restorations of the hypothetical lungs and associated respiratory apparatus. We do not know the shape of the lungs very precisely nor to what extent they conformed to the ribs. We can only speculate about more bizarre kinds of underwater respiration that may have existed and any possible hydrostatic functions that may have been present. From the evidence, it is my impression that a normal type of respiration, as car-

Incising of the visceral side is believed to have been caused by the existence of the lungs in close proximity to the ribs. It does not indicate a condition of pathomorphism. The feature is consistent in its occurrence in dorsal ribs four through eleven in *C. gigas*, showing most extensive development in the longest ribs, the least development in the anterior and posterior ribs (Fig. 59). Cross sections were made of numerous rib shafts of several specimens. Figure 60 illustrates diagrammatically a typical section through the incised area of a long, dorsal, adult rib. The cortex is layered and for the most part nonvascular in its outer zone but mildly vascular in its inner zone. Thin, circumferential, cortical
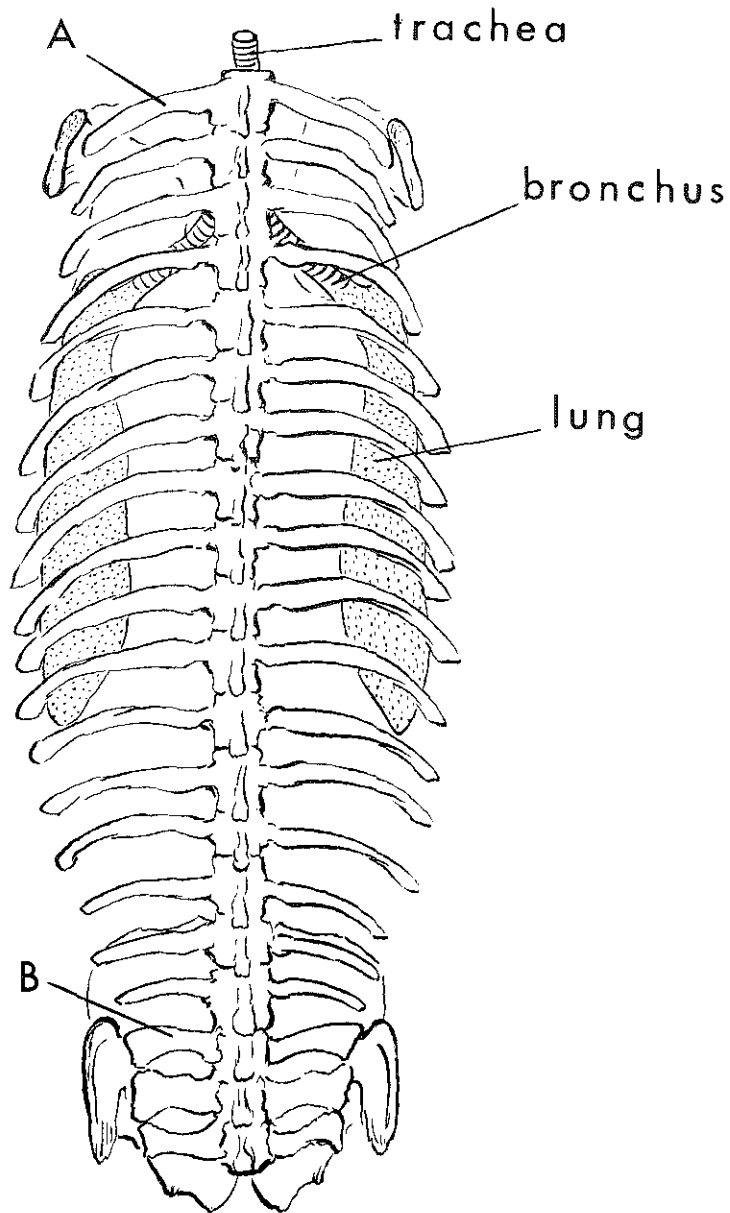
Fig. 59. Dorsal view of the rib cage of *Champsosaurus* with attempted restoration of the respiratory apparatus. Ribs indicate the presence of paired lungs of about equal length. Presumable the bronchi were well developed. A. First dorsal rib. B. First sacral rib.
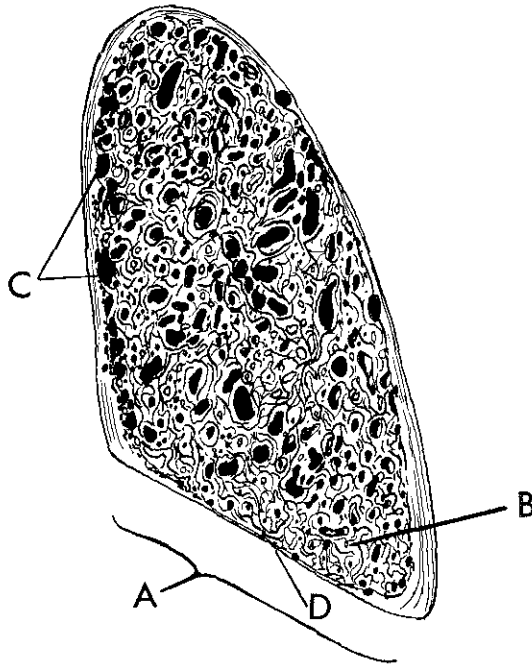
Fig. 60.   Diagrammatic cross section of dorsal rib of *Champsosaurus gigas.*   A.   Incised area of shaft.
B.   Compacted cancellous bone.   C.   Canals in endosteal region.   D.   Thin cortical bone layers of incised area.

laminae of the most recently deposited bone surround the shaft, the only lamellar bone present in the incised area (Fig. ibid. A). This very thin, cortical layer may often be missing in places, including the incised area, due to the effects of only minor weathering. The inner portion of the shaft or medulla is filled with noncompacted tissue having many cancellous spaces. Those near the endosteal margin are frequently enlarged into resorptive spaces. In the area of incising, the cancellous tissue is composed of compacted endosteal bone (Fig. ibid., B) indicating "drifting" of the cortex (Gans, et al., 1969) wherein cancellous material has been converted to compact bone. Resorption of bone in other regions, especially on the opposite side of the shaft, resulted in a gradual migration of the cortex to compensate, not only for the pres-

ence of the lung but for growth and the accompanying change in curvature of the entire shaft. This process of bone modification, or remodeling, by differential deposition and resorption of bone is the mechanism by which the incising of the ribs, such as, described for *Champsosaurus,* can be explained.

The dorsal rib of a juvenile, mounted skeleton, SMM P65.3.1, is shown in cross section through the area in which the adult rib is normally modified by incising (Fig. 61). In the juvenile bone, fewer periosteal laminae are present than in the adult. In the very young of crocodilians, only a single lamina is present (Gans, et al., ibid.). This layer of the present immature specimen is fairly heavy, nonvascular, and in other respects like that of the adult except where incising occurs. Compare with an adult
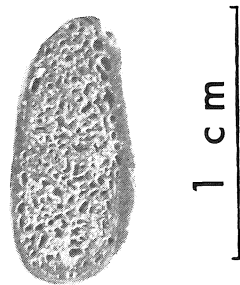
Fig. 61. Cross section of dorsal rib of juvenile champsosaur through area, which is modified by incising in the adult. Note the continuous uniform thickness of the cortical layer around the perimeter and the lack of compacted cancellous bone.
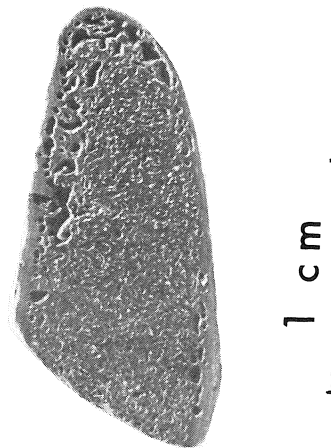

Fig. 62. Cross section of dorsal rib of adult champsosaur through incised area of the shaft. Note interrupted cortical layer (below at incising) and the amount of compacted cancellous bone.

specimen (Fig. 62). Note, also, the continuous cortical layer (Fig. 61) in the juvenile. The cancellous portion is uniform showing little compacted area.

Incising of the dorsal ribs evidently took place as maturity and expansion of the rib cage progressed. Materials are not available in sufficient quantity, however, to make a definite statement about the amount of age variation involved. As mentioned above, the feature is not exclusively that of *C. gigas*. It is present in the larger individuals of *C. laramiensis,* a possible ancestor from the late Cretaceous and early Paleocene.

In *C. gigas,* dorsal ribs four through eleven express the feature indicating the minimum length of the lungs. The condition was contrasted to a specimen of the American alligator, *Alligator mississippiensis,* SMM Z69.26.1, which upon dissection was found to have lungs that span the first through the eighth dorsal ribs. The bronchi branch at the level of the third

dorsal rib to enter the lungs on either side. The lungs of the alligator have a similar position adjacent to the ribs, which are of much lighter construction and more widely spread. *Champsosaurus* of somewhat similar build but with much heavier ribs and a narrower chest cavity simply compromised the form of the ribs for the oversized lungs it possessed.

It is well to note that merely increasing the size of the external dimensions of the lung, however, would not automatically bring about a proportional increase in their functional capabilities, as this is determined by the size of the alveoli as well as other factors. It does seem reasonable, however, to assume a certain increase of respiratory surface by enlargement of the total organ.

If we are to consider *Champsosaurus* as having behavior characters as proposed, we cannot overlook the potentials of its diving capabilities. The depths reached might not be excessive but would pre-

sumably exceed those frequented by croco-dilians. Any modification of respiratory apparatus that would prove beneficial should be noted.

Distensibility of the lungs is a point to consider. Any compression of the lungs by pressures caused by descending through the water, which would compress the chest cavity and consequently the lungs inward potentially to a state of full collapse, might be alleviated if the shape of the rib cage, viz., incised area, would not in effect allow complete collapse of the lungs by permitting some retention of lung shape. Prolonged diving or "bottom time" (suspension of breathing) may have been the rule for some species of the group. Such behavior is a widespread phenomenon among all classes of vertebrates. There are features common in many of these diving forms, as shown by Scholander (1964, p. 229).

One feature applicable to the present discussion is that of asphyxial defense. As stated by Scholander (ibid.), "The simplest conceivable mechanism for coping with a prolonged dive might operate through large oxygen stores and a great capacity for buffering carbon dioxide and other metabolic acids. The animal would then merely use these resources during the dive and recharge the stores in recovery."

The complete collapse of the lungs, which presumably takes place in certain deep diving mammals, offers no problem; for there is ample pressure available from the expanding air to force the lungs open upon ascent. This is possible because of the highly specialized alveolar system found, for example, in cetaceans. In reptiles, such total collapse would be fatal; therefore, a simpler mechanism for prevention of total lung collapse must have been in operation if *Champsosaurus* was indeed a "diver."

Many animals have devices that assist in accomplishing a prolonged submergence; such as, relatively high hemoglobin content in the blood, a larger blood volume, and a higher myoglobin concentration in the muscles—all of which increase oxygen stores. Scholander (ibid.) points out also, however, that during a prolonged dive the oxygen stores afford much less oxygen than necessary to maintain a predive level of oxygen consumption. However, modern animals are, and presumably extinct forms were, capable of remaining submerged for time periods several times longer than would be anticipated as judged from their basal oxygen consumption and the oxygen stores. This suspended breathing is a perfectly normal phenomenon of many modern animals. The enlarged lung capacity in *Champsosaurus* may have been an early attempt at increasing oxygen stores and complying in part with requirements for prolonged submergence.

Aquatic animals of widely divergent taxa show certain similarities of rib construction. Pachyostosis is a condition found to varying degrees of development in many forms including the champsosaurs. The reasons for this condition in diving animals is not entirely understood. The functional implications of a heavy (cancellous) rib as related to aquatic activities may be many. The condition in *Champsosaurus* may bear on metabolic and circulatory regulation, which in turn is a vital consideration in the responsive functions related to underwater activity suggested here.

The lungs of *Champsosaurus* occupied positions lateral to the esophagus and extended caudad on either side of the body. Whether or not they were posteriorly sacculated as in some living reptiles, e.g. chameleons, is unknown—nor if respiratory epithelium was present throughout. With paired lungs, the trachea must have bifurcated and sent one branch (bronchus) to each lung as depicted in figure 59, much

as in the American alligator. Their efficiency would presumably be augmented by their increased size and the condition seen in the ribs.

Coupled with considerable mobility of head and body and good sensory apparatus, the underwater behavior in which a prolonged bottom time was normal would seem to fulfill the basic requirements for successful predation by *Champsosaurus*.

CORRELATIONS AND DISTRIBUTION

Compilations of data on the geographic distribution of North American species comprising the genus *Champsosaurus* show a considerable range (see maps, Figs. 63 and 64). The principal champsosaur-producing strata lie in the western plains of North America along the eastern flanks of the Rocky Mountains from southern Alberta to New Mexico. Their remains are most conspicuous in the Cretaceous badlands of the Red Deer River of southern Alberta and the transitional Cretaceous and Paleocene beds exposed in the brakes of the Missouri River in Montana. Other localities scattered from southern Saskatchewan to New Mexico produce fewer numbers, most as unarticulated elements. Highly productive concentrations of specimens have been found in late Paleocene sediments ("Clarkforkian") of eastern Montana and western North Dakota. *Simoedosaurus* of the European Tertiary is considered congeneric and implies an even more cosmopolitan status for the group.

By their numbers, it would appear that their peak of development was during the span of Oldman through Hell Creek time (late Cretaceous) — a time when many other groups of reptiles also flourished. Greatest geographic range was attained during this and the earliest Tertiary time (map, Fig. 64). The Puercan (early Paleocene) is the only horizon, so far, that definitely documents more than one species.

Simoedosaurus in Europe is represented by one or more species in the late Paleocene, becoming rare by early Eocene (Sparncian) time. This suggests prior proliferation and earlier (pre-Tertiary) radiation, which led to entering Europe by way of a Laurasian land connection, probably during the late Cretaceous.

Giant forms like *C. gigas* and *Simoedosaurus* of the late Paleocene, as well as the North American short-snouted form and those of the basal Eocene in Europe, should then be considered as more specialized "climax" populations. The Cretaceous-Tertiary transition was perhaps uneventful, yet was unsuccessfully executed by many groups. It is interesting to ponder what environmental conditions may have existed and the extent of vested influence for survival or initiation of decline upon the champsosaurs. Colbert (1967) notes that the culmination of eusuchian evolution may have been attained also during the late Cretaceous.

The crocodilians and the champsosaurs apparently made an easy transition from Cretaceous to Tertiary time. If any difficulties were encountered in making adjustments to cooler or warmer Tertiary temperatures, whatever the case may have been, they left little visible impression on either form. Tertiary crocodilian populations were progressive in morphological development, and the accompanying refinements concerned with tolerance for temperature changes were successful. Speculation on the reasons for a seemingly uneventful

transition for both crocodilians and champsosaurs is not necessary. Suffice it to note that the environmental tolerances in living reptiles as shown by Colbert, et al., (1946) were likely similar to those of extinct forms that were making the transition.

As judged from the present materials, the greatest populations of champsosaurs inhabited coastal flood plains and swampy situations, later forms becoming more removed from any coastal areas but still remaining very aquatic. During their early development (late Cretaceous), there is evidence that they may have frequented salt marshes and estuarine waters, but perhaps not to the extent that certain crocodilians did. This is indicated by the succession of North American champsosaur species occurring in sediments interspersed between intervals of marine deposits belonging to the Pakowki and Bearpaw formations. For stratigraphic references, see Russell, 1967. Possible early Eocene marine associations are also indicated by the occurrence of champsosaurids in the Sparnacian, near Reims in Europe, which is deltaic in nature (Brinkmann, 1960, p. 120). The rather spotty record of specimens from marine transitional sediments, such as, the shales of the Oldman, Bearpaw, and Hell Creek formations, might be mentioned. Only a few bones have actually been recovered directly from marine facies, and these are suspected as being materials of redeposition; yet a proximity to salt water environments existed. The association of champsosaurs with remains belonging to other possible brackish types, such as turtles that may have ventured forth to lay their eggs upon land and in the process were detained permanently, is an interesting aspect of some latest Cretaceous horizons; viz, Frenchman and Hell Creek formations.

Cope's type species, *C. annectens,* is from the Judith River beds of Montana. Unfortunately, the record consists of fragmen-

tary material; hence, its correlative usefulness is small. Suffice it to note that this species represents a sizable population that existed near center of this group's geographic radiation. Populations persist throughout the Oldman and Edmonton as two recognizable species: *C. natator* and *C. albertensis,* respectively.

Intensive collecting of the marine Bearpaw shale in southeastern Alberta and the transitional sandy clays of the underlying Oldman deposits in this region turned up several specimens of *Champsosaurus.* As suggested previously, this material may have been derived from the Oldman originally. Nearly all are vertebrae lacking neural arches; and without more complete materials, the only choice is to refer it to *C. natator.*

Hell Creek and Tullock species from Montana and North Dakota are more easily separated. Brown (1905) described these, and in doing so stated that they were obtained from the lower strata of lignite above the "Ceratops Beds" in what is now Garfield County, Montana. Russell (1956) correctly observed that these species should be considered as Paleocene, coming as they do from the lignites, not Cretaceous. Brown's types undoubtedly originated from the Tullock (Paleocene) lignites that are so characteristic of the exposures overlying the Hell Creek at this locality. While collecting these deposits during several seasons, it became evident to the writer that *C. laramiensis* is found regularly in both the Hell Creek and Tullock; at least the Hell Creek form cannot be distinguished from *C. laramiensis* of the Tullock. It is clearly not *C. ambulator.* Remains from the younger rocks are generally less disturbed, especially in or adjacent to lignites. *C. laramiensis* is present in the Hell Creek as far east as the Missouri River in central North Dakota; and a femur, SMM P69.19.1, from the French-
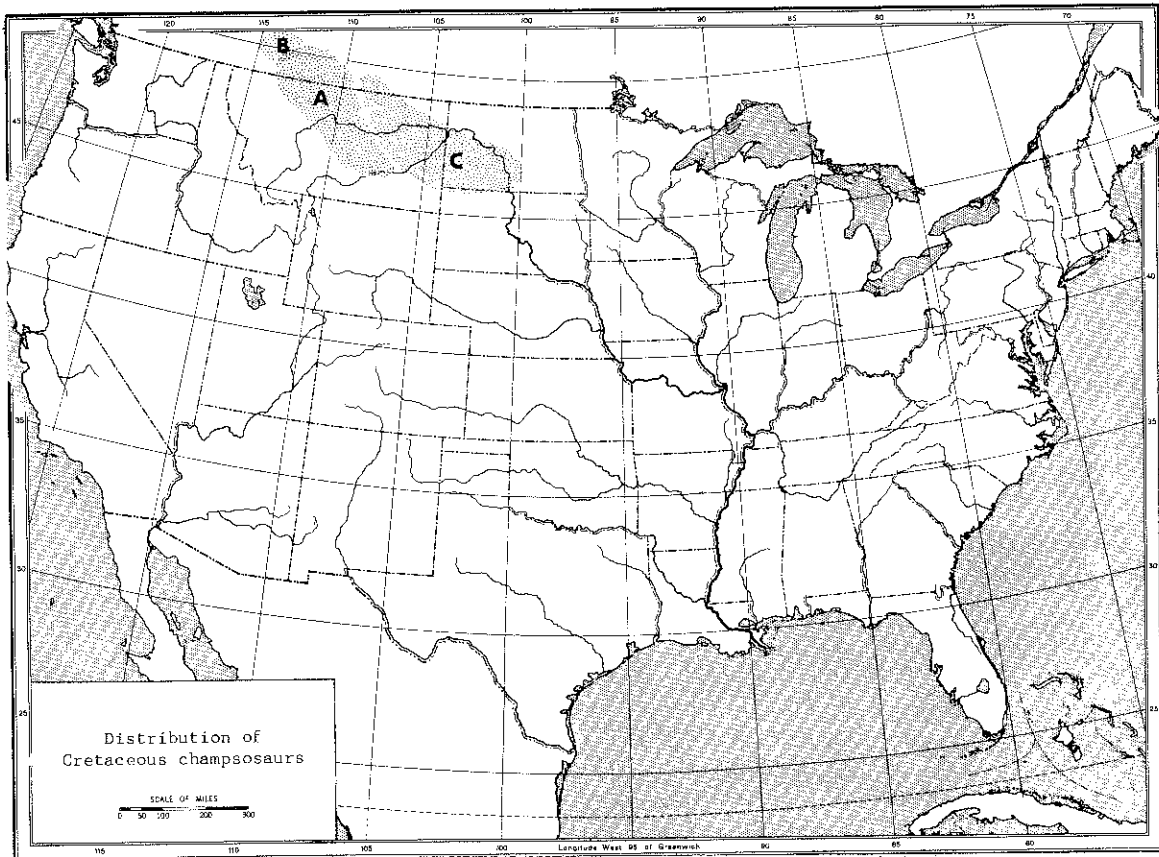
Fig. 63. Distribution of Cretaceous champsosaurs in North America. A. *C. natator.* B. *C. albertensis.* C. *C. laramiensis.* Stippled areas indicate approximate range within which champsosaurs have been found.

man of southern Saskatchewan extends its geographic range northward (Fig. 63).

Champsosaurus is also known from the Tiffanian-pre-"Clarkforkian" (circle fauna) and the Lebo formation of Montana. So far, all materials collected are small, badly eroded, vertebral centra, not sufficent for meaningful description.

As far as can be demonstrated, stratigraphic correlations by champsosaur remains are difficult for the most part. The limiting factor, of course, is that specific determinations depend on fairly complete materials. Some correlative application can be made, however, with one of the latest species.

C. gigas would appear to be suited as a "guide fossil," a means of identification, primarily because of its size and its relatively wide geographic distribution. *C. gigas* occurs in the following formations or as part of the following local faunas: Sentinel Butte and Tongue River formations, North Dakota; Ravenscrage formation, southern Saskatchewan; Bear Creek formation, Montana; Plateau Valley formation, Colorado; Olive fauna, Montana (Fig. 64), all of which are here noted as
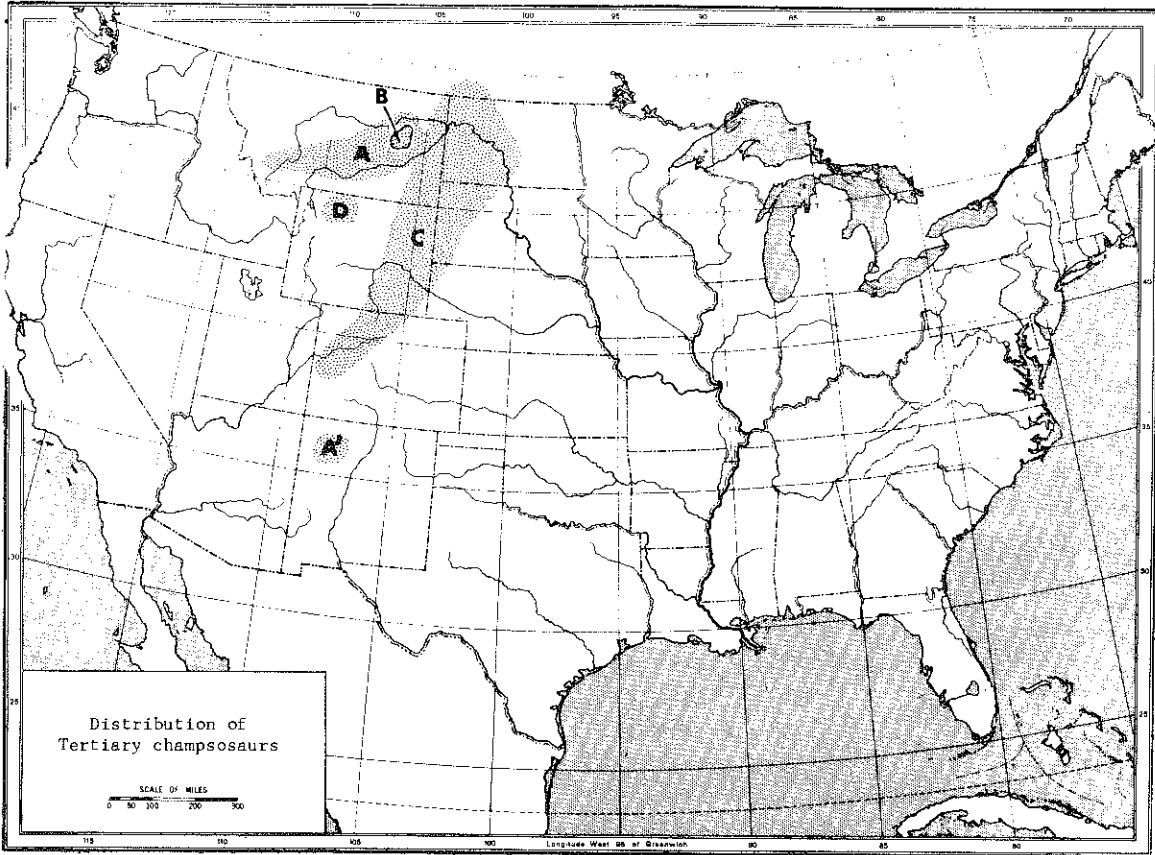
Fig. 64.   Distribution of Tertiary champsosaurs in North America. A. *C. laramiensis.* A'. *C. laramiensis* (?) B. *C. ambulator.* C. *C. gigas.* D. Short-snouted champsosaur. Stippled areas indicate approximate range within which champsosaurs have been found.

comprising "Clarkforkian" horizons. By early Eocene (Willwood), all the "large" champsosaurids are gone and only a short-snouted form remains.

An interesting generalization may be made with regard to relative abundance of champsosaurs and crocodilians. In almost every occurrence of champsosaurs, remains of crocodilians are also found. In their earlier history (Cretaceous and basal Paleocene), the champsosaurs were physically small but far outnumbered crocodilians in their occurrence together. By late Paleocene, the champsosaurs were larger, in some cases surpassing associated crocodilians in size. The crocodilians, however, are known from recorded materials as being much more numerous. This shift in balance through the Paleocene may have been governed by modification of behavior of the champsosaurs in order to survive competition or simply an indication of losing the struggle to survive in a changing environment.

PHYLOGENY

The isolated phylogenetic status of *Champsosaurus* as a specialized late-surviving eosuchian has remained unchanged by the present study. Recognition of ancestral stock from which it may have sprung will have to await further discoveries of new material. Present evidence would seem to place it in the uncertain position of being a derivative of some generalized primitive diapsid, possibly even a marine type, as could easily be inferred from the occurrence of some of the Cretaceous members of the group.

Within the champsosauridae, however, there exists some interesting possible connections that may, of course, be altered by subsequent discoveries of intermediate forms. It is obvious that the long-snouted "typical" *Champsosaurus* evolved in modest fashion giving rise to few remarkably similar species between Oldman and "Clarkforkian" time.

At some point during their development, a short-snouted variety was produced. In fact, it seems most reasonable to speculate that the long snout arose as a specialization toward a more aquatic mode of life out of the more generalized, short-snouted stock. At any rate, two distinct lines are in evidence.

A common North American origin seems most feasible, followed by separation during the Cretaceous with ensuing geographic radiation. The result was wide dispersal in North America and into Europe via a Laurasian land route. The long-snouted, perhaps more piscivorous, species became well established in the former land area by the late Cretaceous as did the short-snouters in Europe by late Paleocene times. Earlier Paleocene deposits are absent, and as yet no Cretaceous material has been found in Europe. This is due perhaps to the lack of work on the Cretaceous (D. E. Russell, 1971, personal communication). A short-snouted branch persisted in North America and is represented by the Polecat Bench (early Eocene) form. Both this and its European counterpart from the Sparnacian (also early Eocene), may be derived from *Simoedosaurus*, a relatively short-snouted champsosaur with an abbreviated mandibular symphysis from the late Paleocene of Europe, or in the case of the former, more likely from some earlier short-snouted simoedosaur-like form.

It is interesting to note the trend toward gigantism in both lines. This is best observed in *C. gigas* and *Simoedosaurus* of the late Paleocene—a point in time that marks broad development of the group. The rare lingering basal Eocene forms represent the rather abrupt culminative phase of champsosaurian evolution.

In attempting to relate the long-snouted species to each other on morphological grounds, difficulties were encountered. Lack of cranial materials from various horizons is a most unfortunate situation. However, with the following limitations in mind, some links seemingly valid at this

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C. gigas

C. ambulator

Simoedosaurs

C. laramiensis

C. albertensis
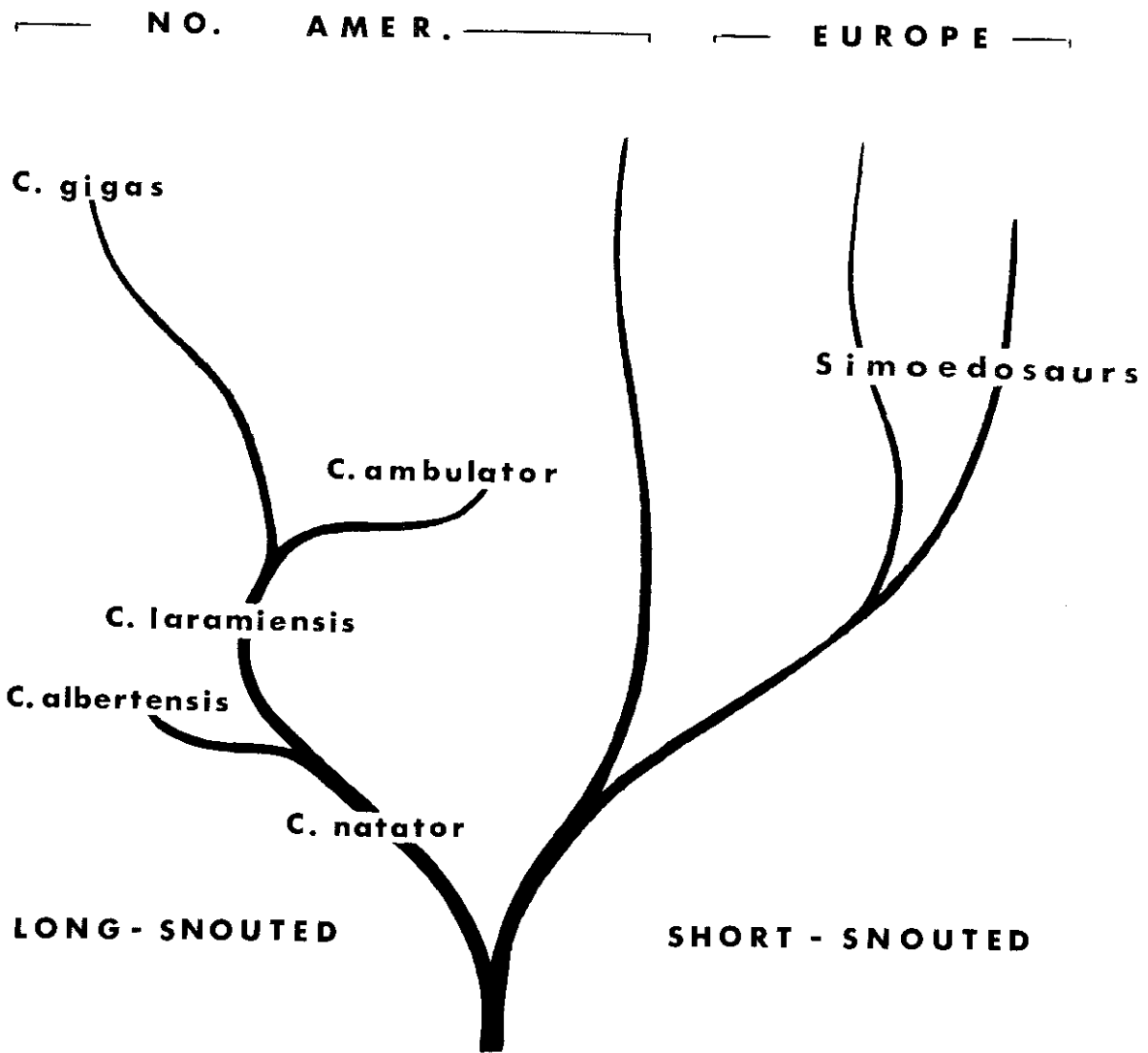
C. natator

LONG - SNOUTED

SHORT - SNOUTED

Fig. 65. Suggested phylogeny for the champsosaurs.

time are made: The vertebral column, other than the cervical and sacral series, is of little use in segregating specific characters (even these are of small use); the humerus and femur are diagnostic in most cases; the ribs that either possess or lack uncinate processes or visceral incising are of value; some girdle elements, especially those of the pelvis, show distinctions of importance, and limb length ratios as well.

The type species, *C. annectens,* is of little taxonomic use. It is here considered along with *C. natator* and *C. laramiensis* as part of a line that developed during the latter part of the Cretaceous. Features relating the latter two are found in the ribs. Both have uncinate features on the last few cervicals and the first few dorsals. The main dorsals are deeply incised (ref. p. 61) in the latter. It is suspected that incipient incising of ribs may have existed in *C. natator. C. albertensis* is thought to be a minor offshoot because it appears to lack the above features and has shortened epipodial elements. A tendency toward increase in the length of the hind limbs is noted from *C. natator* to *C. gigas.* In the latter, the hind limbs are considerably lengthened and rib incising very acute.

The Puercan (basal Paleocene) saw the persistence of *C. laramiensis* from the Cretaceous and the appearance of *C. ambulator* in the Tullock formation of Montana. This rather short-limbed contemporary of *C. laramiensis* is distinctive. Morphologically, it shows the greatest departure of any long-snouted species.

Present evidence indicates, however, that it was a small population as it is known from but a few specimens from a restricted area (Fig. 63). Brown (1905) suggests more ambulatory habits for it, which might explain its scarcity in deposits containing a relative abundance of other champsosaur remains. Structurally, it does not qualify as ancestral to later species and is probably best regarded as a short-lived side branch.

Relatively little champsosaurian material has been recovered between the Puercan and "Clarkforkian." These are, for the most part, small, isolated, vertebral centra and limb bone extremities, usually eroded, and not considered reliable enough for taxonomic purposes.

A suggested phylogeny for the champsosaurs is given in figure 65.

SUMMARY

In *Champsosaurus* we see a rather specialized reptile of uncertain ancestry but exhibiting sufficiently adequate evidence to retain its status in the lepidosauria.

The North American champsosaurs were primarily adapted to a dependence on underwater predation. This mode of life was carried out successfully in spite of the ever present potential of competition and perhaps predation from various crocodilians. An attempt has been made to demonstrate how they, by remaining conservative in their evolution and habits, might have managed to meet the challenge as a subordinate and, in turn, become a highly successful group. If any progressive trends can be sited, increase in overall size and in the length of the hind limbs might be noted, as well as a tendency to modify the rib cage in certain species.

Five species have been recognized in this work on the basis of new and reevaluated materials. This was facilitated by distinguishing juvenile and adult characters. In doing this, age variations became clearer; and to a limited degree, individual variations were brought out. As it turns out, most significant differences between species are found in the postcranial skeleton. Much of the information was derived from the large form referred to as the new species, *Champsosaurus gigas*.

A most interesting feature of this species is the incising found on the dorsal ribs that leads to observations about functional anatomy and the associated underwater behavior.

The unreliability of categorizing material on size is debated. Generally, it was found to be unwise; yet in view of the consistency of size difference between the late Paleocene species, *C. gigas* and other forms, there seems to be some validity in its application. On these grounds, it is suggested that *C. gigas* is of use as a "guide fossil" for the "Clarkforkian."

It would seem unfounded, as has been the practice, to regard *Champsosaurus* as strictly a freshwater type. Ample stratigraphic evidence is sited to indicate at least an early (Cretaceous) proximity to transitional marine (coastal and estuarine) environments. This undoubtedly had influence on distribution. The geographic range of the champsosaurs, not only in North America but in Europe as well, was appreciable and was apparently maintained throughout nearly all of their history. The middle Paleocene will, hopefully, be filled in with future discoveries. The apparent ease of adaptability and broad habitat tolerances would then also account for the wide dispersal and considerable success of the entire family.

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