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Anatomy and Relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming

GLENN WILLIAM STORRS

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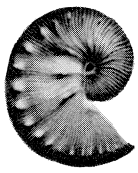

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LISTS OF ABBREVIATIONS

The following are lists of abbreviations that appear in the text and accompanying tables and figures:

Anatomical Abbreviations

a	angular
acet	acetabulum
adf	M. adductor femoris
bo	basioccipital
br	M. brachialis
bs	basisphenoid
car	carpus
cbr b	M. coracobrachialis brevis
cbr l	M. coracobrachialis longus
cf	M. caudofemoralis
cl	clavicle
cor	coracoid
cor ex	coracoid extension
cp	coronoid process
de	dentary
delt	M. deltoideus (undivided)
delt c	M. deltoideus clavicularis
delt s	M. deltoideus scapularis
dent or	dental orientation
ecpt	ectopterygoid
ect	ectepicondylar notch
ect f	ectepicondylar foramen
en	external naris
ent	entepicondylar foramen
eo	exoccipital
epic	epicondyle
ept	epipterygoid
ext	extensors
f	frontal
fe	femur
flex	flexors
fm	foramen magnum
f tib	M. femorotibialis
fo sub	foramina subcentralia
g	gastralia
gl	glenoid

h	humerus
ha	hypantrum
ho	hypospene
hyp	hyperphalangy
icl	interclavicle
if	M. iliofemoralis
ilc b	iliac blade
ilm	ilium
int	internal trochanter
intc	intercentra
isch	ischium
ist	M. ischiotrochantericus
itr f	intertrochanteric fossa
j	jugal
l	lachrymal
lat d	M. latissimus dorsi
M.	primary muscle
mx	maxilla
max can	maxillary caniniform
n	nasal
o	orbit
obt f	obturator foramen
op	opisthotic
p	parietal
p for	parietal foramen
pachy	'pachyostosis'
pal	palatine
par f	parietal foramen
pec b	pectoral bar
pec f	pectoral fenestra
pec r	pectoral rib
pect	M. pectoralis
pf	postfrontal
pif	puboischiadic fenestra
pif e	M. puboischiofemoralis externus
pif i	M. puboischiofemoralis internus
plt dent	palatal dentition
plv c	pelvic canal
pmx	premaxilla
pmx can	premaxillary caniniform
po	postorbital
pop	popliteal space
pp	postparietal
prf	prefrontal
pro	prootic
pt	pterygoid
ptf	posttemporal fenestra
pub	pubis
pvr	posteroventral ridge
q	quadrate
qj	quadratojugal
ret p	retroarticular process

sa	surangular
sac	sacrum
sac r	sacral rib
sac v	sacral vertebrae
sbcsc	M. subcoracoscapularis
sc	scapula
sc b	scapular blade
sch cr	M. scapulohumeralis cranialis
so	supraoccipital
spa int	spatium interosseum
sq	squamosal
st	supratemporal
stf	supratemporal fenestra
sub f	suborbital fenestra
sup	supinator process
sup c	M. supracoracoideus
sup f	supracoracoid foramen
sup l	M. supinator longus
sup r	supinator ridge
sym	symphysis
t	tooth
tem	temporal emargination
tar	tarsus
thor c	thoracic cavity
thy f	thyroid fenestra
tib c	tibial condyle
v	vomer
z	zygapophysis
za	zygantrum
zo	zygosphene

Taxonomic Abbreviations

A	*Anarosaurus*
Ce	*Ceresiosaurus*
Ch	*Chinchenia*
Co	*Corosaurus*
Cy	*Cymatosaurus*
D	*Dactylosaurus*
Ke	*Keichousaurus*
Kw	*Kwangsisaurus*
L	*Lariosaurus*
M	*Metanothosaurus*
Ne	*Neusticosaurus*
No	*Nothosaurus*
P	"*Pachypleurosaurus*"
Pa	*Paranothosaurus*
Pi	*Pistosaurus*
Pr	*Proneusticosaurus*
Rh	*Rhaeticonia*
Sa	*Sanchiaosaurus*

Se	*Serpianosaurus*
Sh	*Shingyisaurus*
Si	*Simosaurus*

Stratigraphic Abbreviations

Є	Cambrian
Fm	Formation
fms	formations
J	Jurassic
K	Cretaceous
K/J	undifferentiated Cretaceous and Jurassic
lmst	limestone
mbr	member
P	Permian
pЄ	Precambrian
P/C	undifferentiated Permo-Carboniferous
Q	Quarternary
ss	sandstone
T	Tertiary

Museum Abbreviations

BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
UW	University of Wyoming, Laramie
YPM	Yale Peabody Museum of Natural History, New Haven

Miscellaneous Abbreviations

Å	angstroms
cm	centimeters
Co	County
∂	molecular layer spacing distance
d	difference
E	east
km	kilometers
λ	wavelength of incident X-radiation
m	meters
mm	millimeters
mtn	mountain
N	north
PDB	Pedee belemnite isotopic standard
R	range
r-l	long spacing resistivity
r-s	short spacing resistivity
Sec	section
SMOW	standard mean ocean water isotopic standard
sp	self potential

T	tier
θ	½ angle between incident and diffracted X-radiation
W	west
WY	Wyoming

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151 PP., 62 FIGS., 4 TABLES, 1991

ANATOMY AND RELATIONSHIPS OF *COROSAURUS ALCOVENSIS* (DIAPSIDA: SAUROPTERYGIA) AND THE TRIASSIC ALCOVA LIMESTONE OF WYOMING

GLENN WILLIAM STORRS

ABSTRACT

The 'Nothosauria,' a traditional suborder of Triassic marine reptiles, is of interest because of its presumed relationships to both plesiosaurs and primitive diapsid reptiles. 'Nothosaurs,' placodonts, and plesiosaurs together form the Order Sauropterygia. The single described New World 'nothosaur' species, *Corosaurus alcovensis* Case, 1936, from the Alcova Limestone of central Wyoming, U.S.A., has long been incompletely known. Numerous new specimens supplement the holotype and virtually complete our knowledge of its skeletal anatomy. *Corosaurus* has been thought of as a traditional 'nothosaurid' and, indeed, has several plesiomorphic sauropterygian features. The relatively expanded appendicular girdles of *Corosaurus* are only superficially plesiosaur-like. The axial skeleton is generally conservative. A discussion of sauropterygian taxonomic characters, a review of 'nothosaur' genera, and a cladistic phylogenetic analysis using parsimony are presented by which a basal sauropterygian dichotomy is defined resulting in the monophyletic clades Pachypleurosauria and Nothosauriformes (new taxon). Plesiosauria and Placodontia are monophyletic groups within the Nothosauriformes. Consequently, the traditional 'Nothosauria' is paraphyletic. Shared derived characters indicate that *Corosaurus* is a valid genus within the Nothosauriformes. *Claudiosaurus* Carroll, 1981 is the closest known sister group to the Sauropterygia, both apparently derived from plesiomorphic diapsid reptiles.

Hypothetical musculature reconstructions and functional morphology suggest that *Corosaurus* and other large 'nothosaurs' favored a primarily limb-dominated method of aquatic locomotion partially analogous to that of plesiosaurs, while the small pachypleurosaurs may have relied more heavily upon tail-dominated propulsion. Structural differences in the appendicular skeletons of pachypleurosaurs, 'nothosaurids,' and plesiosaurs probably largely reflect the nearshore, possibly amphibious, behavior of the two former groups. Most 'nothosaurs' inhabited paralic marine environments within which a range of habitats is increasingly evident. Their plesiomorphic overall similarity is in part functionally mediated.

Close examinations of the geology and structural setting of the Alcova Limestone illuminate the paleoecology of *Corosaurus* and the biogeography of nothosauriforms minus the plesiosaurs and placodonts. Diverse paleontologic, sedimentologic, and geochemical evidences indicate a restricted, hypersaline marine embayment as in the German Muschelkalk. Stratigraphic analysis places the Alcova Limestone Member, Crow Mountain Formation, Chugwater Group, most probably in the uppermost Lower Triassic (Spathian).

KEYWORDS

Alcova, biogeography, Chugwater, *Corosaurus,* function, morphology, Nothosauriformes, 'nothosaurs,' Pachypleurosauria, paleoecology, Placodontia, Plesiosauria, review, Sauropterygia, Spathian, stratigraphy, systematics, Triassic, Wyoming.

ZUSAMMENFASSUNG

Anatomie und Verwandtschaftsbeziehungen von *Corosaurus alcovensis* (Diapside Reptilien, Sauropterygier) und der triassische Alcova-Kalk Wyomings

Die traditionelle Unterordnung 'Nothosauria' umfasst triassische Meeres-Reptilien, die als mögliches Bindeglied zwischen primitiven Diapsiden und Plesiosauriern ein besonderes Interesse verdienen. Zusammen mit den Placodontiern und Plesiosauriern bilden sie die Ordnung Sauropterygia. Der bisher einzige neuweltliche 'Nothosaurier,' *Corosaurus alcovensis* Case, 1936 aus dem Alcova-Kalk von Wyoming, war lange Zeit nur unvollständig bekannt. Zahlreiche Neufunde vervollständigen dieses Bild.

Corosaurus wurde bis jetzt als typischer 'Nothosauride' betrachtet. Er zeigt in der Tat mehrere morphe Sauropterygier-Merkmale. Dazu gehören die relativ breiten Schulter- und Beckengürtel, die denen der Plesiosaurier nur oberflächlich ähneln. Auch das Achsenskelett ist konservativ. Eine Übersicht über die taxonomischen Merkmale, eine Zusammenstellung bekannter 'Nothosaurier'-Gattungen, sowie eine kladistische Analyse nach Parsimonie-Kriterien lässt indessen innerhalb der Sauropterygier eine Dichotomie zwischen den monophyletischen Zweigen der Pachypleurosauria und der neu aufgestellten Nothosauriformes erkennen. Innerhalb der Nothosauriformes bilden die Plesiosauria und die Placodontia ihrerseits selbständige, monophyletische Untergruppen. Dagegen sind die 'Nothosauria' im traditionelle Sinn eine paraphyletische Gruppe. Innerhalb der Nothosauriformes ist *Corosaurus* durch abgeleitete Merkmale als selbständige Gattung ausgewiesen.

Die nächstverwandte Schwestergruppe zu den Sauropterygia als Ganzem wird durch *Claudiosaurus* Carroll, 1981 repräsentiert; beide werden von plesiomorphen Diapsiden abgeleitet.

Eine Rekonstruktion des Muskelapparates und funktionsmorphologische Merkmale zeigen, dass *Corosaurus* und andere grosse 'Nothosaurier' sich ähnlich wie die Plesiosaurier, im Wasser hauptsächlich mit Hilfe ihrer Extremitäten fortbewegten. Im Gegensatz dazu spielte beim Schwimmen der kleineren Pachypleurosaurier der Schwanz eine wesentliche Rolle. Unterschiede im Extremitätenskelett der Pachypleurosaurier, 'Nothosauriden' und Plesiosaurier deuten auf eine möglicherweise amphibische, küstenbezogene Lebensweise der beiden ersten Gruppen. Die meisten 'Nothosaurier' bewohnten paralische Meeresgebiete mit einem breiten Spektrum spezifischer Habitate. Plesiomorphe Ahnlichkeiten innerhalb dieser Gruppe können also ebenfalls funktionell bedingt sein.

Eine genaue geologische Analyse des Alcova-Kalks ergänzt das palökologische Bild von *Corosaurus* und beleuchtet die biogeographischen Ausbreitungs-Möglichkeiten der Nothosaurier im alten Sinn (d. h. unter Ausschluss der Plesiosaurier und Placodontier). Paläontologische, sedimentologische und geochemische Daten

lassen, wie im germanischen Muschelkalk, ein teilweise abgeschlossenes, übersalzenes Meeresbecken vermuten.

Chronologisch wird der Alcova-Kalk (als Unterglied der Crow-Mountain-Formation und der Chugwater-Gruppe) in den oberen Teil der Untertrias (Spathium) gestellt.

1. INTRODUCTION

HISTORY OF INVESTIGATION

The 'nothosaurs' are a grade-level grouping of sauropterygian marine reptiles well represented by skeletal remains in the Middle Triassic rocks of Europe. They were apparently well adapted to a littoral, possibly amphibious, existence and are of special interest because of their presumed evolutionary relationships to both the primitive diapsid terrestrial reptiles which were their probable ancestors, and the highly specialized, fully aquatic plesiosaurs of the Jurassic and Cretaceous. The various types of 'nothosaurs' (traditionally grouped as a suborder—seemingly artificially) and the plesiosaurs are obviously closely related and together form part of the Order Sauropterygia. The 'nothosaurs,' particularly, are in need of in-depth study and the general anatomic characteristics of many individual taxa are still very confused, as are their systematics, evolutionary relationships, and paleobiology. Major studies of 'nothosaurs' have been undertaken in the past by such workers as Arthaber (1924), Edinger (1921), v. Huene (1952), Koken (1893), v. Meyer (1847–55), Nopsca (1928b), Peyer (1931, 1932, 1933, 1934, 1939), Seeley (1882), Young (1958, 1959, 1960, 1965a), Zangerl (1935), and others. Recent efforts of note include those of Carroll (1981), Carroll and Gaskill (1985), Kuhn-Schnyder (1987), Mateer (1976), Rieppel (1987, 1989), Sander (1989), Sanz (1976, 1980, 1983a), Schmidt (1986, 1987), Sues (1987), and Tschanz (1989). While plesiosaurs are primarily known from the Jurassic and Cretaceous, 'nothosaurs' are presently restricted to the Triassic.

The primary focus of the present study is the largely neglected occurrence of the single described North American 'nothosaur' species, *Corosaurus alcovensis* Case, 1936, from the Triassic Alcova Limestone of central Wyoming. The type specimen was collected in fragments from a highway quarry spoil heap near Goose Egg Ranch, Natrona County, by a University of Wyoming geology student in 1935 (Case 1936). This material was supplemented in 1948 by several partial skeletons and other specimens collected by a Field Museum of Natural History expedition under the leadership of R. Zangerl from the type and adjacent localities in the vicinity of Casper, Wyoming. Of this additional sample, only a portion of one individual has been preliminarily described (Zangerl 1963). Other than in the works of Case (1936) and Zangerl (1963), *Corosaurus* has been discussed in more than just a cursory way only by E. von Huene (1949) and F. von Huene (1948a) but without the benefit of first-hand examination of the fossils. Additional references to *Corosaurus* have been essentially limited to mention of the taxon's existence and to speculation about its possible systematic position. No further discoveries or examinations of *Corosaurus* were made until 1983 when field work of the present study resulted in the collection of numerous new specimens from the Alcova Limestone in the Casper, Wyoming, area, specifically near Freeland Junction.

Studies of the Alcova Limestone itself have previously been limited largely to superficial descriptions of the unit and to attempts at stratigraphic correlation. A famous and easily recognizable stratum, the Alcova has usually been discussed in the context of descriptions and interpretations of its enclosing formations within the Chugwater Group (e.g., Bower 1964; Branson and Branson 1941; Burk 1953; High and Picard 1967a, 1969; Hubbell 1956; Love 1948, 1957; Picard 1967, 1978; Picard et al. 1969; Pipiringos 1953, 1968; Tohill and Picard 1966; etc.). Only Carini (1964) has concentrated specifically on the Alcova in a detailed manner. In many such studies, unsupported interpretations of the geologic age

and paleoecology of *Corosaurus alcovensis* have been used to make claims concerning the geology of the Alcova.

PURPOSE AND SCOPE

E. von Huene (1949) believed *Corosaurus* to represent a very primitive stage in the transition of terrestrial reptiles to a secondarily aquatic format, while Zangerl (1963), because of certain apparently derived features of *Corosaurus*, considered it the most aquatically advanced nothosaur known. F. von Huene (1948a, b, c, 1952, 1956) went still further by placing *Corosaurus* in the Plesiosauria. These conflicting interpretations were the result of an incomplete knowledge of the anatomy of this animal, especially the anatomy of its limb girdles. A characterization of the morphology of *Corosaurus* and the completion of an adequate diagnosis of the taxon are clearly needed. Furthermore, peculiarities of the environment of *Corosaurus* may indicate that its paleobiology differed radically from that of sauropterygians as a whole. This may bear upon possible habitat and behavioral variations within the Sauropterygia.

The apparent geographic isolation of *Corosaurus* is also a reason for interest. Most traditional 'nothosaurs' are known from the Old World, particularly Europe and China, where hundreds of specimens have been assigned to several dozen taxa. The paleobiogeography of early sauropterygians, the paleogeography of the Earth during the Triassic, the distribution of 'nothosaurs' in time, and the exact age of *Corosaurus* are correlative questions. Is a place of origin and route of dispersal of sauropterygians suggested by the spatial and temporal evidence or is the problem merely a function of the distribution of marine Triassic exposures?

The systematics of the 'Nothosauria' are little understood, due in part to problems of preservation, and there is not yet a consensus as to which skeletal characters are significant in establishing detailed relationships for these animals. Rigorous study of *Corosaurus* may provide insights not only into the systematics of 'nothosaurs,' but also into their relationships with plesiosaurs, and into the origins of sauropterygians in general. What are the structural/functional constraints that may have led to the evolution of the Sauropterygia and to its differentiation into separate clades? Can intermediate stages be envisioned? Bearing such questions in mind, *Corosaurus* is a fossil which is particularly well suited to analysis for several reasons. Firstly, the preservation of *Corosaurus* material is generally good. Contained within a carbonate precipitate matrix, many of the specimens are uncrushed and three-dimensional; on occasion it has been possible to totally extract bones from the surrounding rock. This presents an unusual opportunity for description and functional study. Additionally, a good combination of articulated partial skeletons and isolated bones provides an excellent basis for comparison with other taxa. Finally, the relatively large size of the animal facilitates its examination and descriptions, and by being fairly abundant in a localized area, insight into the individual and ontogenetic variation of the species is gained.

Corosaurus and 'nothosaurs' in general are thus of interest, but so is the geologic aspect of their occurrence. This, naturally, bears directly on the question of sauropterygian paleoecology and biostratigraphy. In specific, the stratigraphic and environmental interpretations of the Alcova Limestone have been a matter of debate for some time. It is therefore necessary to characterize the geology of this unit. This is the secondary thrust of this paper. Although it is a widespread stratum, the Alcova is not easily correlated with nearby Triassic rocks of known

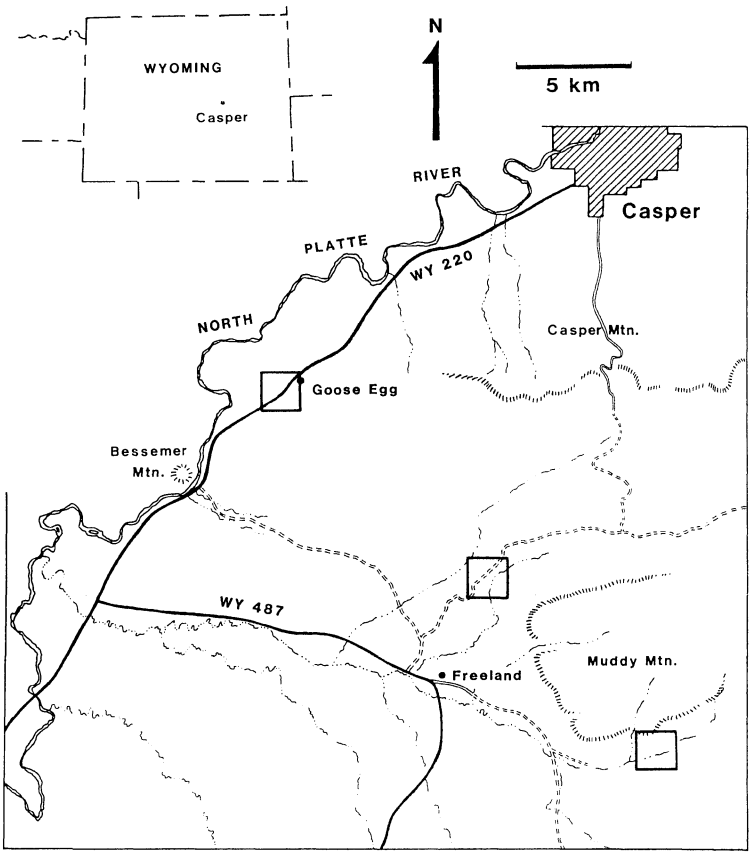

FIG. 1. Locality map of Casper–Goose Egg–Freeland Junction area, Natrona County, Wyoming. Known occurrences of *Corosaurus alcovensis* located within regions marked by squares (approximate).

age. The entire Chugwater sequence is poorly fossiliferous and is in part difficult to date. Most workers have assumed a normal marine setting for the Alcova, but Carini (1964) has proposed a desalted lake-sea as the environment of deposition. These problems deserve additional consideration.

PROCEDURE

The initial descriptive phase of the project required preparation and study of the existing *Corosaurus* material. Each of the known specimens, the holotype in the collection of the University of Wyoming and a large amount of primarily unprepared material in the Field Museum of Natural History collection, was examined. Beyond this, as only a partial composite skeleton could yet be reconstructed, field work was conducted in the summer of 1983 in an attempt to acquire additional and complementary fossil specimens. Exposed examples of *Corosaurus* were found to be not uncommon in the general Casper, Natrona County, Wyoming area (Figs. 1 and 2).

The holotype was originally found near Goose Egg in Jackson's Canyon, approximately 14 km southwest of Casper, along Wyoming State Highway 220, W½, NE¼, Sec 12, T32N, R81W. Other partial specimens were collected by the Field Museum party in the quarry at this locality, and also from steeply dipping outcrops of the Alcova Limestone approximately 5 km northeast of Free-

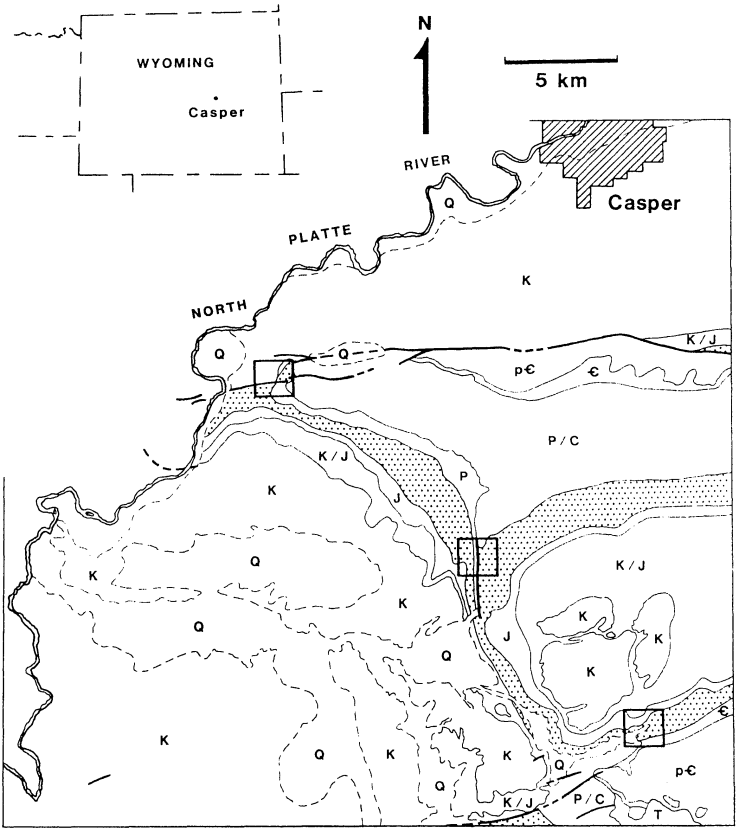

FIG. 2. Simplified geologic map of Casper–Goose Egg–Freeland Junction area, Natrona County, Wyoming, after Fig. 1. Triassic and undifferentiated Permo-Triassic sediments stippled. Areas of Quaternary surficial deposits marked by dashed outlines. Faults indicated by heavy lines. C= Cambrian; J = Jurassic; K = Cretaceous; K/J = undifferentiated Cretaceous and Jurassic; P = Permian; pC = Precambrian; P/C = undifferentiated Permo-Carboniferous; Q = Quaternary; T = Tertiary.

land Junction, Sec 2, T31N, R80W. Most of the Yale Peabody Museum specimens were discovered in talus blocks beneath cliffs of the horizontal Alcova Limestone southwest of Muddy Mountain, along Corral Creek, Milne Ranch, sections 27 and 33, T31N, R79W. It is not possible to prospect directly the resistant, cliff-forming ledge of the Alcova here. Examination of talus blocks yielded occasional *Corosaurus* bones along exposed bedding plane surfaces.

It was originally hoped that the carbonate nature of the Alcova would allow ready acid dissolution of the fossil matrix. However, while the limestone is easily dissolved, the bones themselves have been completely permineralized with calcite and are equally subject to destruction by acid. Due to the relatively dense nature of the bones, no satisfactory method of protective impregnation was found by which the fossils could be easily extracted from the matrix through chemical means. Mechanical preparation with hand and power tools was therefore utilized and, although slow and tedious as noted by both Case (1936) and Zangerl (1963), had the advantage of supplying an intimate knowledge of each fossil. Unfortunately, earlier crude mechanical preparation had already damaged some specimens. Attempts to determine the nature and extent of imbedded examples through X-radiography failed, as they did for Case (1936), because the approximately equal densities of bone and matrix furnishes little detectable contrast. At times, weathered bones were represented partially or only by matrix impressions. In

such instances, latex or epoxy casts were fashioned directly from these molds. Casts and plasticine models were useful in functional reconstructions when it was impossible to completely extricate a fossil from its matrix.

Field work for this study also allowed first-hand knowledge of the Alcova Limestone and of its stratigraphic relationships. Examination of the Alcova's geology in the field was supplemented by collection of matrix samples, sedimentary and stromatolitic structures, and fossil invertebrates. Laboratory techniques employed in their study are discussed below (Chapters 5 and 6).

2. OSTEOLOGY

MATERIAL

The holotype of *Corosaurus alcovensis* Case, 1936 (originally specimen No. 51000 in the geology collection of the University of Wyoming, now catalogued as UW 5485) remains the best and most complete specimen of this animal known. It consists of a semiarticulated, partial skeleton comprising the greater part of the skull, the vertebral column through the proximal caudals, half of the pectoral girdle (pectrum), most of the forelimbs, and various ribs and gastralia. The fossil was collected from a quarry spoil heap (Case 1936) and is contained in numerous limestone blocks, the majority of which can still be pieced together to show the disposition of the type skeleton. The vertebrae lie in a loop, but the other bones are scattered, often overlapping each other or lying partially imbedded in the matrix. Different sections of the blocks have been prepared from different sides, and the relative position of each bone is therefore not initially obvious. A composite drawing has been prepared to indicate the positions of the more important elements of the skeleton (Fig. 3).

A number of bone-containing blocks that were collected and catalogued with

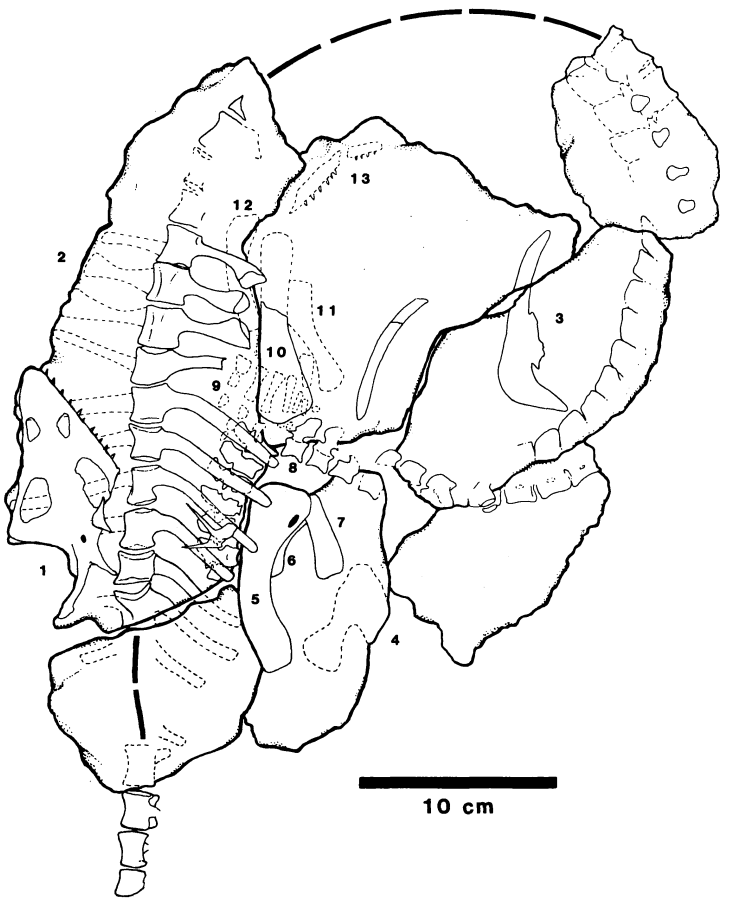

FIG. 3. Composite drawing of holotype of *Corosaurus alcovensis*, UW 5485. 1 = skull; 2 = sacrum; 3 = right clavicle; 4 = left scapula; 5 = left humerus; 6 = left ulna; 7 = left radius; 8 = cervical vertebrae; 9 = right manus; 10 = right humerus; 11 = right ulna; 12 = right radius; 13 = mandible. Coracoids and interclavicle overlie cervicals but are here removed for clarity.

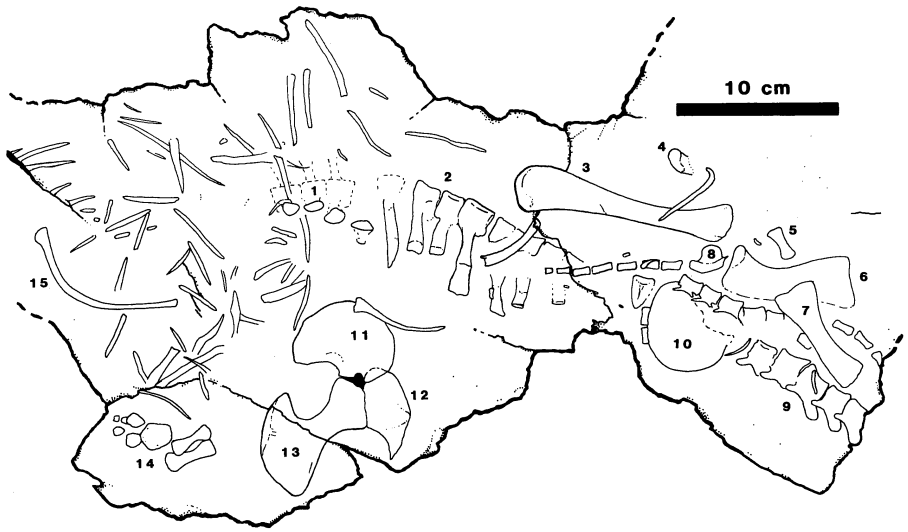

FIG. 4. Partial skeleton of *Corosaurus alcovensis*; map plan of FMNH PR480. 1 = sacrum; 2 = anterior caudal vertebrae; 3 = left femur; 4 = tip of ?left fibula; 5 = metatarsal; 6 = left ischium; 7 = ?left tibia; 8 = left ilium?; 9 = midseries caudals; 10 = left pubis; 11 = right pubis; 12 = right ilium; 13 = right ischium; 14 = associated metatarsals and pes; 15 = dorsal rib.

the type do not fit into the skeletal puzzle. Most, if not all of this scrappy material probably represents one or more additional individuals. This was suggested by Zangerl (1963) and indeed, a second sacrum is included in the isolated blocks. A large, isolated block of gastralia may or may not pertain to the true type. Even so, all of the additional material is apparently assignable to *Corosaurus*. Zangerl (1963) was not, however, correct in assuming that parts of the type have been lost since Case's study. It has been possible to reassemble the type specimen and to relocate and identify all of the elements referred to in the original description,

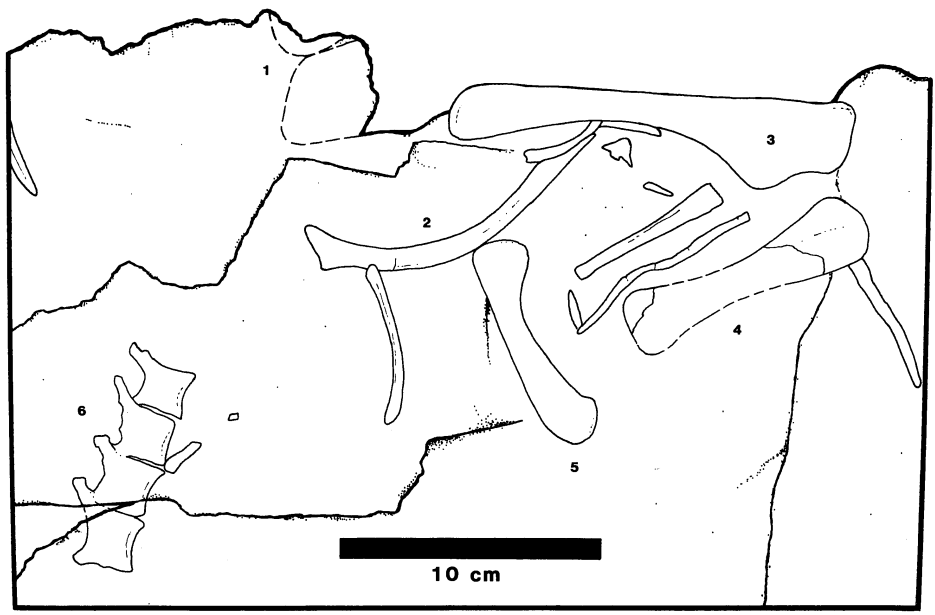

FIG. 5. Partial skeleton of *Corosaurus alcovensis*, schematic diagram of portion of FMNH PR1369. 1 = pubes; 2 = dorsal rib; 3 = right femur; 4 = right tibia; 5 = right fibula; 6 = caudal vertebrae. Hatched lines denote impressions.

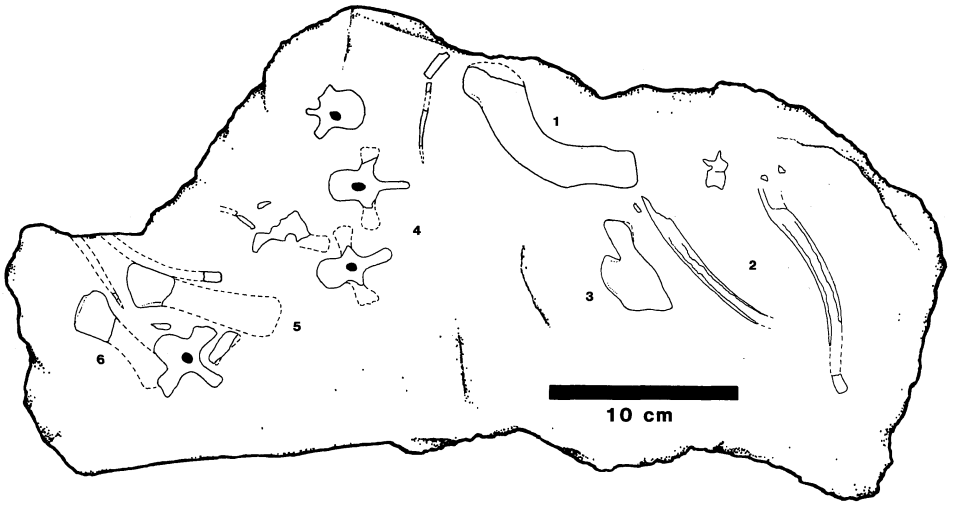

FIG. 6. Partial skeleton of *Corosaurus alcovensis*, map plan of YPM 41031. 1 = left humerus; 2 = dorsal ribs; 3 = left scapula; 4 = dorsal vertebrae; 5 = left ulna; 6 = left radius. Hatched lines denote impressions.

although the interpretation of some of these bones has changed. Only those portions which were never collected, such as the block of six middorsal vertebrae (Case 1936, p. 4), are missing.

The bulk of the known *Corosaurus* material is in the collection of the Field Museum of Natural History, Chicago. Zangerl (1963) preliminarily described the largely disarticulated posterior half of a skeleton making up one of these specimens (FMNH PR480). In the undescribed material are the remains of over a dozen additional individuals. Unfortunately, most are preserved only as isolated or associated vertebrae, ribs, and gastralia, and many such specimens, collected from a single locality near Freeland, Wyoming, have been lumped together under one catalogue number (FMNH PR135). Aside from FMNH PR480, the Chicago collection contains four other *Corosaurus* fossils, of varying quality, which represent significant portions of single individuals and which are very useful in a study of the whole animal. Some of these specimens have, like the holotype, been collected as groups of bone-bearing limestone blocks and have required reassembly prior to study. Map plans of the two most useful Chicago skeletons are given in Figures 4 and 5.

The *Corosaurus* fossils collected for the present study are now housed in the Yale Peabody Museum of Natural History. Two of these specimens [YPM 41030 and 41031 (Fig. 6)] are partial skeletons; each is contained in a single block. The remainder of the Yale collection consists of isolated bones.

From a combination of the existing specimens, most of the bones in the skeleton of *Corosaurus alcovensis* are now known. Only the phalanges of the pes and the interclavicle are poorly represented. It has also not been possible to directly observe the form of the palate. The known 'nothosaur' (i.e., plesiomorphic sauropterygian) palates, however, follow a stereotyped pattern and it is reasonable to assume that the present specimen is structurally similar.

The conditions of the bones in each of the three collections ranges from very poor to excellent. Some are crushed and fractured, and others are preserved only as matrix impressions or outlines (see, e.g., Figs. 5 and 6). Certain bones are visible only as cross sections exposed along fracture surfaces through the matrix. On the other hand, many specimens are undistorted and exhibit extremely fine anatomical details.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
NEODIAPSIDA Benton, 1985
LEPIDOSAUROMORPHA Benton, 1985
SAUROPTERYGIA Owen, 1860
NOTHOSAURIFORMES, new taxon
COROSAURUS Case, 1936

Type species. *Corosaurus alcovensis* (the genus is presently monotypic).

Holotype. Skull and partial skeleton, UW 5485.

Referred material. Numerous specimens in the Field and Yale Peabody museums of natural history (see Appendix A).

Horizon and distribution. Alcova (Limestone) Member, Crow Mountain Formation, Chugwater Group, Triassic System; various localities in general vicinity of Casper, Natrona County, east-central Wyoming, U.S.A.

Etymology. Literally, "northwest-quarter reptile of Alcova."

Diagnosis. A plesiomorphic, intermediately-sized 'nothosaurid' ('nothosauriform') (following systematics of Chapter 4), averaging perhaps 2 m in length, possessing a generally conservative axial skeleton and limbs with rather derived limb girdles. Supratemporal fenestrae of skull larger than orbits. Antorbital region slightly longer than postorbital area. Nasals, frontals, and postfrontals large. Posterolateral process of frontal present. No observed quadratojugal. Postorbital bar and temporal arch narrow. Skull table high and broad; pineal foramen located at center of parietals. Moderately sized posttemporal fenestrae relative to other 'nothosaurs'; opisthotics long and pillar-shaped. Rostrum low and unconstricted. Dermal cranial bones pitted. Upper dentition rather uniform; lower teeth distinctly anisodont with procumbent anterior caniniforms. Mandibular symphysis stout, tip of jaw spatulate. Prominent retroarticular process. Forty-one presacral vertebrae; three sacral vertebrae with distally expanded sacral ribs. Neck of intermediate length relative to other sauropterygians, approximately 50% of thorax. Neural arches broad, transverse processes long in extending laterally beyond arches; zygosphene/zygantrum articulations present throughout thoracic series. Neural spines rectangular and of medium, uniform height relative to other sauropterygians. V-shaped caudal chevrons fully ossified and without distal expansion. Gastralia composed of a median element and two pairs of laterals. Medial and posterior processes of clavicle form 90° angle and distinct anterolateral corner; posteromedial shelf present at angle. Interclavicle possibly barlike. No horizontal ventral plate on scapula. Coracoids large and subrectangular; no supracoracoid foramen. Anterior border of pubis convex; obturator foramen distinct. Ischia long and distally expanded. Ilium with well-formed acetabulum and blade; anterior and posterior projections on sacral process. Humerus strongly curved with prominent entepicondylar foramen and ectepicondylar notch. Femur sigmoidal, approximately 40% longer than humerus; large internal trochanter. Epipodials dorsoventrally compressed; large spatium interosseum. Ulna and radius short; small 'olecranon process.' Tibia and fibula long and narrow. Carpus and tarsus poorly ossified; astragalus twice as large as calcaneum. No evidence of hyperphalangy.

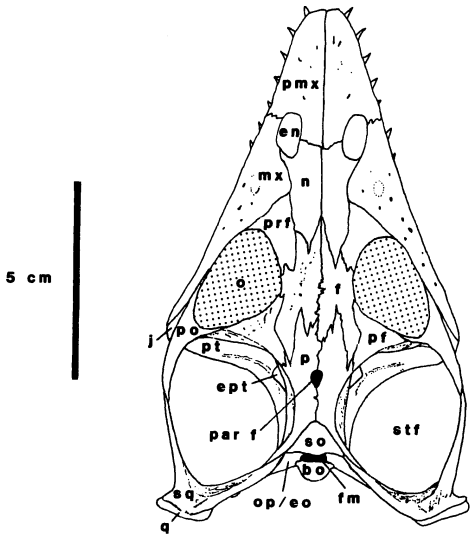

FIG. 7. Reconstructed skull of *Corosaurus alcovensis*, dorsal aspect, based upon UW 5485. bo = basioccipital; en = external naris; eo = exoccipital; ept = epipterygoid; f = frontal; fm = foramen magnum; j = jugal; mx = maxilla; n = nasal; o = orbit; op = opisthotic; p = parietal; par f = parietal foramen; pf = postfrontal; pmx = premaxilla; po = postorbital; pfr = prefrontal; pt = pterygoid; q = quadrate; so = supraoccipital; sq = squamosal; stf = supratemporal fenestra.

DESCRIPTIVE ANATOMY

AXIAL SKELETON

Much of the new material assigned to *Corosaurus* represents parts of the axial skeleton. Aside from the type specimen, several additional strings of vertebrae and associated partial skeletons have now been discovered. The vast majority of new specimens consists, however, of disarticulated and often isolated vertebrae, ribs, and gastralia.

Skull

Only a single skull of *Corosaurus* is known, that of the holotype (UW 5485). This was generally well described by Case (1936). Nevertheless, careful restudy in light of our presently greater understanding of sauropterygian anatomy has permitted the clarification of certain aspects of the cranial morphology of *Corosaurus*. A new description and reconstruction are thus necessitated.

As noted by Case (1936), the skull, while largely complete, has been subjected to a certain amount of distortion due to its position of preservation across the ventral faces of the fourth, fifth, and sixth caudal vertebrae of the type skeleton (Fig. 3). Sedimentary compaction has caused the offset of the right posterolateral corner of the cranium with the resulting disarticulation of some of the component elements and distortion of the margin of the right orbit. The skull roof and braincase are not crushed, however, and seem to present the true appearance of this region. Dissection of the skull along the fractures reported by Case (1936, p. 5) permitted a three-dimensional examination of the posterior cranial region, which is largely imbedded in supporting matrix. Most of Case's findings here are confirmed. While high, however, the posterior margin of the skull is not so

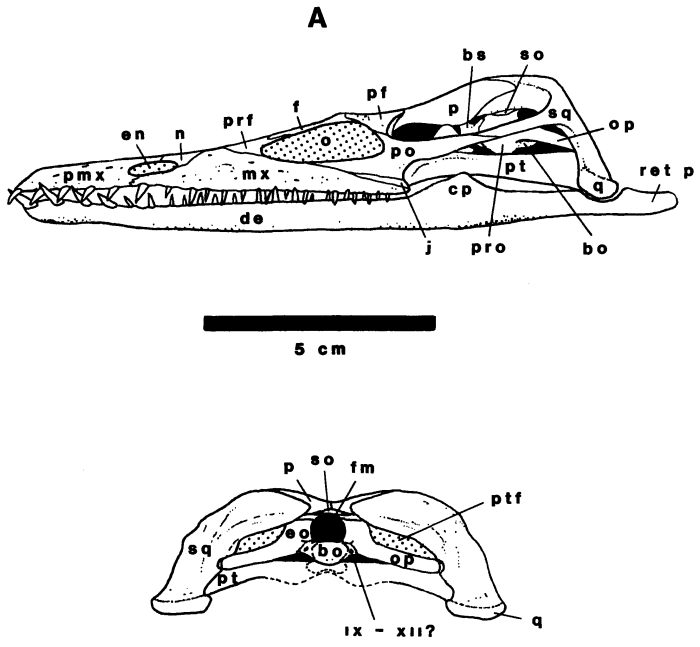

FIG. 8. Reconstructed skull of *Corosaurus alcovensis*, based upon UW 5485 (mandibular suture patterns unknown). A—left lateral aspect; B—posterior aspect. bo = basioccipital; bs = basisphenoid; cp = coronoid process; de = dentary; en = external naris; eo = exoccipital; ept = epipterygoid; f = frontal; fm = foramen magnum; j = jugal; mx = maxilla; n = nasal; o = orbit; op = opisthotic; p = parietal; pf = postfrontal; pmx = premaxilla; po = postorbital; pfr = prefrontal; pro = prootic; pt = pterygoid; ptf = posttemporal fenestra; q = quadrate; ret p = retroarticular process; so = supraoccipital; sq = squamosal.

tall as has been reconstructed by Case (1936, fig. 3). The left squamoso-postorbital bar is not preserved, and both quadrate regions are crushed.

As for the preorbital surfaces, compression and concomitant fracturing of the rostrum has obscured the bone relationships and nowhere are the sutures as clear as those of the skull table. The size and shape of the external nares are nonetheless obvious and little broadening of the rostrum has occurred. The left side of the skull is generally well preserved throughout its length and allows an accurate reconstruction of the skull's gross morphology (Figs. 7 and 8). Both the nostril and the eye faced laterally to a slight degree. The nares are relatively smaller and the orbits larger than in Case's (1936, figs. 2 and 3) reconstruction.

The oblique position of the teeth as noted by Case is undoubtedly true for the anterior rostrum, but the left maxilla has certainly been displaced horizontally and the maxillary dentition should be more correctly regarded as vertical in position. This conclusion is borne out by comparison with the largely undisturbed right maxilla and the configuration of the lower jaw of *Corosaurus*.

The skull of the type specimen is nearly 13 cm long, with a low, broad facial region and a narrow, although short (approximately 2.5 cm) prenarial rostrum. The greatest width of the skull, apparently at the squamoso-postorbital suture, is estimated to have been approximately 7.5 cm. The external nares are retracted posteriorly as is typical for many aquatic reptiles, but remain in a position only midway along the snout. There is no premaxillary/maxillary constriction of the rostrum. The supratemporal fenestrae are large (i.e., larger than the orbits). All

elements of the skull were tightly sutured and the cranium was, as in most, if not all, sauropterygians, virtually akinetic. No sclerotic plates, if originally present, have been preserved.

Premaxillae. The description provided by Case (1936) for these bones is accurate except that only five, rather than six right premaxillary teeth are present. No alveolus exists to accommodate a sixth tooth. In addition, I find little justification for Case's suggestion that the anterior teeth are significantly larger than the others. Any indication of variable length seems to be largely a result of the roots of some teeth breaking through their alveolar walls as the bone was pressed down upon them. The premaxillary–maxillary suture is digitate and lies near the anterior margin of the external naris, which is longitudinally ovate, whereas the premaxillary–nasal suture meets the nares near their midline. Microscopic examination of this region suggests, however, that the suture forms not a straight line between the nares, but actually a posteriorly directed chevron, as shown in Figure 7. Even so, the premaxillae do not extend beyond the posterior margins of the nares as they do in many sauropterygians. The median suture is straight.

Maxillae. The presumed extent of these large, roughly triangular bones can be discerned from a comparison of the two sides of the skull. The lateral margin of the maxilla is long and straight, extending beyond the orbit to the excavated cheek where it meets the posteromedial margin in a relatively sharp spur. The marginal dentition is thus continuous to at least the posterior edge of the orbit. The first maxillary tooth is perhaps slightly more robust than its neighbors, but its apparently greater length is again largely the result of a broken alveolar wall. The medial edges of the right maxilla can be clearly seen due to the preservational depression of the nasals and the disarticulation and loss of the right prefrontal. The left maxilla is similarly raised relative to the nasals. The maxillary–nasal and the maxillary–prefrontal sutures are now seen to be the rather straight limbs of an obtuse triangle. The maxilla correspondingly forms the lateral margin of the naris, but only the anterolateral border of the orbit.

A distinct, pitted sculpturing can be seen on the surface of the right maxilla. There is also the suggestion of a small, circular depression at the center of each maxilla. It is difficult to determine whether or not these depressions are the product of the crushing of the rostrum. If natural, they may represent pits for housing specialized facial glands, although such glands have not been previously reported in sauropterygians.

Nasals. The median cranial suture continues in a straight line between these two elements. Although crushed and fractured, the configuration of the nasal can now be deduced from the shapes of the surrounding bones. Basically wedge-shaped, the nasals are rather large for a sauropterygian and extend from between the nares to between the orbits where they intertongue with the paired frontals. The posterior terminus of each bone is a sharp point defined by clear sutures. The right nasal is slightly longer than the left, complementing the asymmetrical borders of the frontals. There is no great extension of the premaxillae between the nasals.

Prefrontals. While Case (1936) was unable to delimit the nature of the prefrontals, like the nasals their form can be inferred from the adjoining bones. The left prefrontal, while crushed, is present and forms the anteromedial margin of the orbit. Its serrate suture with the frontal is also evident. The right prefrontal has broken away from the rim of the orbit and was not preserved, separating cleanly along its sutures. The free edges of the frontal, nasal, and maxilla are

now apparent, revealing also the shape of the missing prefrontal. It had a sharp anterior point and a concave posterior edge. There is no indication of a lachrymal bone.

Frontals. These bones, lying directly between and entering into the rims of the orbits, were accurately described by Case (1936, p. 7). All of the frontal sutures are irregularly serrate, including the median one as shown in Figure 7. The left frontal is larger than the right and displays a prominent congenital surface rugosity. Throughout the skull, none of the elements of the paired dorsal series are fused. This is a character, however, which may have varied ontogenetically, and fusion may have been exhibited in older individuals of *Corosaurus*. Variously fused frontals are present among the many known specimens of Alpine pachypleurosaurs (Carroll and Gaskill 1985; Rieppel 1989). While both fused frontals and parietals are characteristic of *Nothosaurus* (see, e.g., Schroeder 1914, Schultze 1970) and *Paranothosaurus* (Kuhn-Schnyder 1966), there has been no ontogenetic study of these genera, and juveniles may have possessed unfused skull table elements. Rieppel (1989), however, suggests that mere individual variation may control this trait. Phylogenetic analysis (Chapter 4), on the other hand, indicates that some evolutionary significance is possible for this character.

Parietals. These flat components of the skull table are relatively wider than those of most 'nothosaurs' possessing so-called large supratemporal fenestrae, and the openings are rather well separated. The conspicuous parietal foramen is centrally placed along the serrate median suture. The jagged anterior end of each parietal is bounded by the frontal and postfrontal, and the posterior end by the supraoccipital and squamosal. The long, narrow posterior parietal process overlaps the squamosal and forms most of the medial wall of the supratemporal fenestra. Case's (1936) so-called postparietal suture to the rear left of the parietal foramen is nothing more than a hairline fracture. Postparietal bones are unknown in traditional sauropterygians, although they have been mistakenly reported (along with tabulars) in *Simosaurus* (Kuhn-Schnyder 1961, 1962; see Schultze 1970).

Postfrontals. Only the left postfrontal is in place. This stout, ridged, rugose bone forms the posteromedial rim of the orbit and much of the anterior wall of the supratemporal fenestra as described by Case (1936). It is triangular in dorsal aspect and meets the postorbital in a squamous articulation. This relationship can be seen on both sides of the skull, although on the right side both bones have been displaced. The postfrontal meets the parietal in the anteromedial wall of the supratemporal fenestra.

Postorbitals. Case (1936) could find no postorbitals but small portions of both are actually preserved, and together with the shape of the squamosal, they can be fairly accurately reconstructed. The posterolateral corner of the left orbit exhibits the impression and fragments of the inner surface of the broken postorbital. This was a pronged element that clearly formed part of the bony spur at the front of the lower temporal emargination, the anterior portion of the lateral wall of the supratemporal fenestra, and the posterior half of the lateral orbital margin. The vertical "flange" referred to by Case (1936, p. 8) which meets the postfrontal in the wall of the supratemporal fenestra, is also undoubtedly part of the postorbital. The thin anterolateral process of the squamosal presumably lay superficial to the posterior projection of the postorbital, a portion of which is apparently preserved on the right side of the skull.

Jugals. No jugal can be observed on the distorted right side of the skull, but its position on the left can be estimated from the divergent bone fibers in the cross-

sectional fracture of the "spur" adjoining the anterior edge of the lateral temporal emargination. A line running through this section may represent the suture between the postorbital and the jugal. From this evidence, it appears that the jugal was a sliver of bone between the postorbital and the maxilla, thinning anteriorly, and not reaching the margin of the orbit. This is the same condition observed in *Nothosaurus* (Schroeder 1914; Schultze 1970).

Squamosals. The position of these bones can be seen in Figure 7 and in Case (1936, plate 1, fig. 1), the right squamosal offset to the right, the medial half of the left still articulated with the parietal. Case's (1936) account of the form of these bones is correct. The right squamosal is particularly useful in displaying the narrow postorbital process, whereas the left squamosal clearly shows the squamous articulations with both the parietal and the quadrate, and the peg-and-socket joint with the paroccipital process of the opisthotic. The parietal process of the squamosal forms the topographically highest part of the skull.

Quadrates. The form of the quadrates is greatly disturbed but it appears that most of the posterior surface of each bone was overlain by the squamosal, leaving only the transverse articular surface exposed. This is rather typical of nothosauriform (following Chapter 4) suspensoria. Anteriorly, the bone forms an expanded plate that lies deep to the squamosal, and to which it is broadly sutured. The pterygoids abut against this sutural line, forming a tight brace with the quadrate and the squamosal.

I have been unable to locate quadratojugals in the type specimen, in spite of the suggestion by Case (1936) that they may exist. The squamosoquadrate region of each side of the skull is sufficiently broken to preclude a definite conclusion. Although pachypleurosaurs and possibly *Simosaurus* apparently retain a vestigial quadratojugal (Carroll and Gaskill 1985; Kuhn-Schnyder 1961; Rieppel 1989; Schultze 1970), this bone is lost in most advanced sauropterygians, perhaps as a consequence of the presumed loss of the diapsid lower temporal arch in the transition to the euryapsid condition (Carroll 1981; Kuhn-Schnyder 1962, 1963a, 1967, 1980) and continued phyletic reduction of the temporal arcade. It is therefore quite likely, and I believe probable, that quadratojugals were lacking in *Corosaurus*. This question must be considered unresolved, however.

Braincase. This region of the skull has been primarily reconstructed from examination of numerous fractures through the posterior portion of the skull. These fractures extend through the braincase and the bones of the occiput and have necessitated a reliance on the use of bone fragments and impressions. As a result, few of the sutural relationships between bones can be accurately determined. Nevertheless, a generalized picture of the posterior neurocranium can be constructed (Fig. 8).

On the occiput, the basioccipital is prominent and exclusively forms the bulbous occipital condyle and the floor of the large, subcircular foramen magnum. The foramen magnum is situated high on the occipital face. Contrary to Case (1936), the occipital condyle is not constricted at its base. The basioccipital is bounded laterally by the opisthotics and separated from them by the only obvious sutures of the occiput. Just medial to the left of these sutures, and within the basioccipital, a fracture has exposed a small cranial nerve passage originating at the posterior end of the braincase and exiting the occiput as a foramen at the side of the occipital condyle. From such foramina any or all of cranial nerves IX through XII left the skull. The opisthotics form long, cylindrical paroccipital processes quite unlike those of other 'nothosaurs' in which these bones are known. Each is directed

posteroventrally from its position adjacent to the basioccipital towards the posteromedial edge of the squamosal. Here the braincase is buttressed against the suspensorium in a single peg-and-socket joint. The proximal extremity of the opisthotics cannot be differentiated in the specimen from the highly fractured exoccipitals that are assumed to flank the foramen magnum. The opisthotic and exoccipital are generally fused in sauropterygians (Romer 1956). The supraoccipital roofs the foramen magnum and is apparently a triangular shelf of bone set just below and between the posterior fork of the paired parietals. The posttemporal fenestrae are bounded by the squamosal dorsally and laterally, and the opisthotic/exoccipital ventrally and medially. The left fenestra is preserved and appears, largely from its internal aspect, to be not only rather rhomboidal in cross section, but also unusually large for a 'nothosaur.'

Like the occiput, the anterior portion of the braincase is very poorly preserved, being heavily fractured. Portions of the left side of the braincase have been lost while the right side is unobservable. However, it is known that the proximal end of the opisthotic approaches a spherical, matrix-filled cavity identified as the otic capsule and the position of the prootic bone. Anterior to this, and lying along the sagittal plane of the skull, a small exposed section of the basisphenoid can be seen. It is situated at a point midway between the pterygoids below and the vertical walls of the parietals above, and is anterolaterally bounded by the epipterygoids. The epipterygoid and the basisphenoid are joined at the basipterygoid process which is just visible. Similar processes appear to buttress the basisphenoid against the prootic and the parietal. No stapes is preserved.

Palate. The delicate nature of the skull prohibits the removal of matrix from its undersurface, thus the palatal complex remains largely unknown. Only the pterygoid and the epipterygoid can be partially reconstructed. The posterior edge of the palatal ramus of the left pterygoid is clearly exposed and reveals a typical, smoothly concave anterior margin to the subtemporal fossa. However, while anteriorly the palatal ramus of the pterygoid is a broad, flat, horizontal plate of normal configuration, the posterior edge is ventrally deflected in an apparent pterygoid flange. Additionally, from the position of the epipterygoid caudad, the quadrate ramus of the pterygoid is seemingly not horizontally, but rather vertically expanded, an unusual and possibly primitive condition among nothosauriforms. This is evident from the displaced right temporal region of the skull, where the pterygoid is tightly sutured to both the squamosal and the quadrate, effectively closing the posterior end of the subtemporal fossa.

Much of the left pterygoid's quadrate ramus is broken and missing, but its partial impression indicates a divergence of the rami beneath the basisphenoid and otic capsule, a good deal farther forward than is typical for traditional 'nothosaurs.' The presence or absence of a true interpterygoid vacuity cannot, however, be established. As *Corosaurus* is certainly a primitive nothosauriform in its overall morphology as is later to be discussed in this work and as all known 'nothosaurids' have a solid palate, such a vacuity is more than likely absent. The data are, however, inconclusive. Case's (1936, p. 13) "hook-like projection" on the quadrate ramus of the right pterygoid is difficult to interpret and, if not an artifact, may have functioned in connection with the basisphenoid, as he suggested.

The left epipterygoid clearly has a broad footplate that rests on the palatal ramus of the pterygoid. The dorsal process of the epipterygoid is tall, narrow, and rounded; the right one showing these characteristics most effectively. Most nothosauriforms have a narrow dorsal process, although that of *Nothosaurus* is hourglass-shaped (Romer 1956).

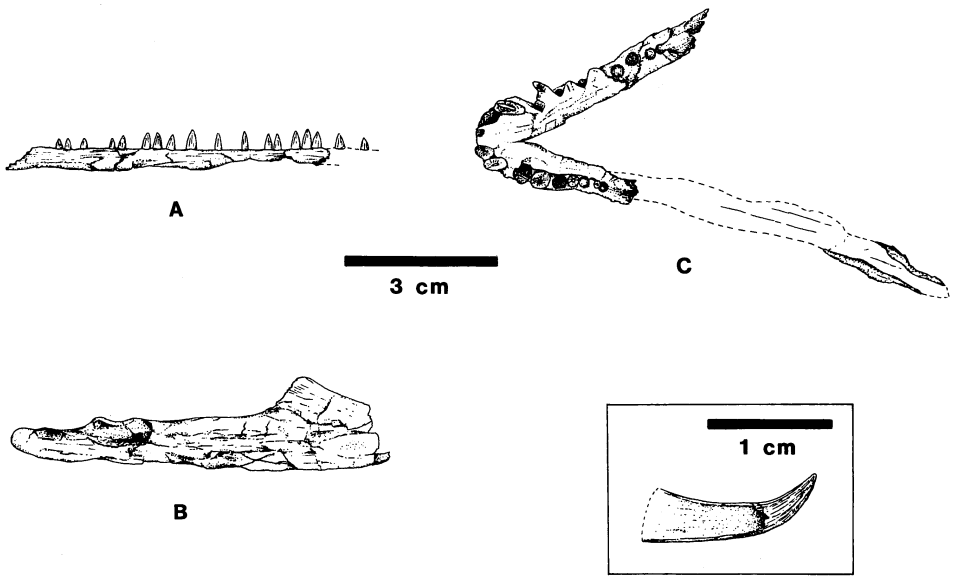

FIG. 9. Mandible of *Corosaurus alcovensis*. A, partial right dentary of FMNH PR1382, anterior to right; B, proximal end of left mandibular ramus, FMNH PR246; C, dentary symphysis, YPM 41043; Inset, isolated tooth from FMNH PR135.

MANDIBLE

In addition to the partial lower jaw of the type specimen that was described by Case (1936), four new examples of the mandible of *Corosaurus* have been recovered (FMNH: PR1368, PR246, PR1382; and YPM 41043). From this material, a more exact knowledge of the form of the mandible may be gleaned. FMNH PR1382 consists of portions of the dorsal edges of both rami, the right exhibiting eighteen teeth in place (Fig. 9A), the left only eleven. Specimen No. PR246 shows the internal aspect of the left ramus from the coronoid process to the retroarticular process (Fig. 9B). The remaining two jaws consist primarily of the symphysial region, but only the Yale specimen (Fig. 9C) is well preserved. The jaws were long, slender, and shallow, with the two rami meeting at an average angle of approximately 40°. The type specimen shows an angle of approximately 35° that matches the angle formed by the rostrum. All known jaw specimens are approximately equivalent in size and differences between them probably reflect simple individual variation.

The articular region of the mandible is elongate. Specimen No. PR246 displays a long (1.5 cm), straight, retroarticular process, a well-formed, transverse articular cotylus corresponding to the articular process of the quadrate, and a distinct coronoid process. The cotylus and retroarticular process lie along the plane of the straight tooth row. Unfortunately, due to the highly fractured nature of the specimen, no bone sutures are evident. The adductor fossa appears troughlike and relatively deep, but an undetermined amount of preservational distortion may have exaggerated this condition.

Anteriorly, the lingual surfaces of the mandibular rami of *Corosaurus* each bear a single, raised, longitudinal ridge, which is easily seen on the type mandible. The labial surface is smoothly rounded and displays a series of longitudinal striae corresponding to the fibers of the bone.

Case's (1936) report of large, anterior mandibular teeth is obviously correct and is reinforced by examination of YPM 41043. The anteriormost teeth are

exceptionally large, far larger than the premaxillary teeth, and are directed anterolaterally. In the region where the mandibular teeth oppose the maxilla, however, the teeth rapidly decline in size and point vertically. In YPM 41043, the observed teeth clearly alternate with adjacent vacant alveoli, whereas in FMNH PR1382 the condition of seemingly less predictable positions for unerupted, young, and mature teeth resulting from the *zahnreihe* replacement mechanism of reptiles, is evident. With the noted exceptions of size and position, all upper and lower teeth of *Corosaurus* are alike. They are sharp, conical, and bear fine longitudinal striae, but no carinae. The rami of FMNH PR1382 show particularly well how most teeth are medially recurved, as does a fine example of an isolated tooth from FMNH Lot No. PR135 (Fig. 9). The isolate also displays a wide root that is at least equal in length to the crown. Tooth implantation is thecodont.

The symphysial region of the mandible of *Corosaurus* is more robust than the remainder of the jaw. It is slightly spatulate and was strengthened by an internal thickening of the bone. The symphysis itself, however, while strong is not exceptionally long. A similar symphysial expansion or "scoop" is known in *Nothosaurus* (see, e.g., Geissler 1895; v. Meyer 1847–55; and Schuster and Bloch 1925). A small lower jaw with an even more exaggerated scoop was described by von Huene (1958) as belonging to *Anarosaurus,* although this assignment is questionable.

Vertebral Column

Essentially the entire spinal column of *Corosaurus* is now represented in the collected fossils as several articulated partial series and numerous isolated vertebrae. Only the very distalmost caudals are unknown. Although the preparation resistant nature of the microsparite matrix has allowed few of the vertebrae to be examined in their entirety, examples of each vertebral type are exposed from several different perspectives (e.g., Figs. 3, 4, 5, 6, 10). The form of the complete column is therefore clearly shown. The total vertebral count of *Corosaurus* approaches 85 or more. The presacral number is 41. The vertebral centra are generally elongate and nearly cylindrical, ranging from deeply amphicoelous to nearly platycoelous, while the neural spines of *Corosaurus* are of medium height and relatively uniform design throughout the column.

Cervical Vertebrae and Ribs

Although badly broken, the vertebrae from the neck of the *Corosaurus* type specimen are all at least partially present. They form a twisted, articulated series, the disposition of which was described by Case (1936). Fragments of an additional series and the cross section of an isolated vertebra (both specimens from FMNH Lot No. PR135) augment our knowledge of the neck. The cervical series is here considered to consist of eighteen vertebrae, making the length of the neck in the type specimen approximately 25 cm. The centra are small (averaging 1 cm in length for the type), but gradually increase in size caudad, as do the narrow, subrectangular, neural spines. The length of each centrum is approximately equal to its height, and no dorsal transverse thickening of the neural spines exists. The smooth neural canal is tubular and unconstricted.

The cervical ribs are dichocephalous, articulating exclusively with, and in each specimen examined fused to, the centrum (e.g., Fig. 10A and B). The articular

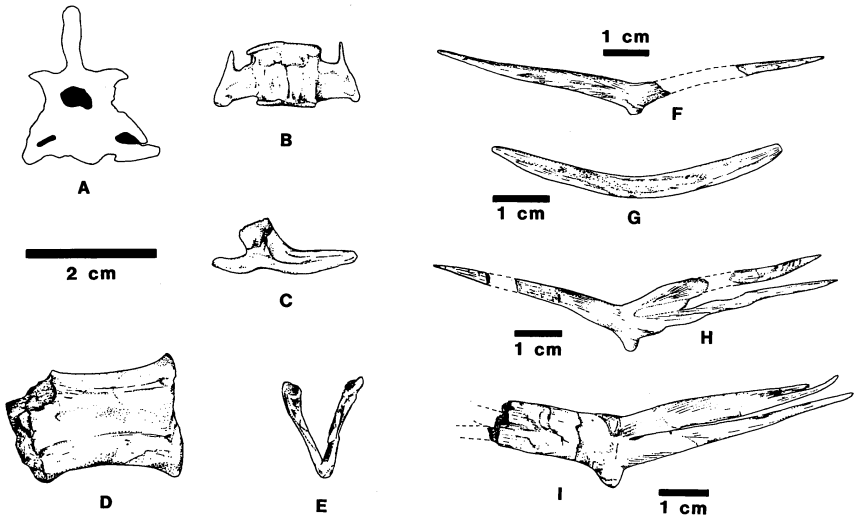

FIG. 10. Axial skeletal components of *Corosaurus alcovensis*. A, oblique transverse section of midseries cervical vertebra from FMNH PR135 showing bicipital ribs; B, ventral view of midseries cervical vertebra with ribs, UW 5485, anterior to top; C, posterior cervical rib from FMNH PR135, anterior to left; D, midseries caudal vertebra, ventral aspect, YPM 41047; E, caudal chevron, YPM 41045; F, typical median gastralium from FMNH PR135; G, typical lateral gastralium from FMNH PR135; H, asymmetrically pronged median gastralium from FMNH PR135; I, doubly pronged median gastralium from FMNH PR135.

facets for these ribs are set upon two short parapophyses lying low on the centrum. The facets are longitudinally oriented and set one above the other. The ribs are distinctly pronged, with both an anterior and a posterior projection lying parallel to the body axis (Fig. 10C). The anterior prong is the largest in the anteriormost ribs; the posterior prong dominates caudally.

The atlas/axis complex is poorly known in 'nothosaurs' but is partly preserved in the type of *Corosaurus*. The spine of the axis differs from those of the other cervicals in being broad and roughly triangular. Its anterior edge overlaps the posterior zygapophysis of the atlas. Pronged, bicipital ribs are present on the axis. The spine of the atlas is very low. Only the neuropophysis of the atlas seems to be preserved, although the nondescript "preatlas" elements of Case (1936, p. 16) may be fragments of the atlas. In any case, the so-called "preatlas" is difficult to evaluate.

Dorsal Vertebrae and Ribs

The dorsal series is well known through the collection of several strings of vertebrae, groups of associated vertebrae, and isolated dorsals which complement the type specimen. I am inclined to accept Case's (1936, p. 15) estimate of six missing dorsal vertebrae from the type for a total of 41 presacrals. If then, 18 vertebrae can be counted as cervicals, and ignoring the sometimes nebulous category of transitional "pectorals" often used in describing the Plesiosauria, we are left with 23 dorsal vertebrae for *Corosaurus*. [It should be noted that the distinction between cervical and trunk vertebrae is relatively clear in pachypleurosaurs (Carroll, personal communication, 1988).] The dorsal series of the type of *Corosaurus* then, including an estimate for those missing vertebrae, measures approximately 50 cm in length. The 17 preserved dorsals of FMNH PR1383 total 36 cm. The thoracic region of the skeleton was thus about twice the length of the neck.

The dorsal vertebrae are the largest of the column, and average nearly 2 cm in length in the holotype. Despite their increasingly greater size, the dorsal

vertebrae are little different from the cervicals except in possessing relatively long (approximately 1 cm), stout, transverse processes. These processes are fully developed on the neural arch by the twentieth vertebra of the column. Vertebra number 19 exhibits a transitional or "pectoral" position of the process. The single-headed processes are as long in the anterior dorsals as the spines are tall, and are approximately equal in length to the height of the vertebral centra. They are directed slightly upwards, are thickest distally, and have ovate cross sections. While the neural arch and zygapophyses are broad as in all 'nothosaurs,' the transverse processes extend well beyond their lateral margins. This is a seemingly advanced condition in the Sauropterygia. The transverse processes become somewhat more robust, but shorter, caudad. The neural spines average 1.5 cm in height from the level of the transverse process, 1.5 cm long, and are subrectangular in outline. They are thickened dorsoposteriorly.

Accessory articulations are present on the neural spines of the dorsals as zygosphene and zygantrum. These are particularly well shown on vertebrae 29 and 30 of the type specimen where the basal anterior edge of each spine has a projection (zygosphene) which fits into a wedge-shaped cavity (zygantrum) at the base of the preceding spine. As a consequence, the leading and trailing edges of adjacent spines are in close contact. This condition persists throughout the dorsal series. Accessory articulations have been reported in several 'nothosaurs' [e.g., *Dactylosaurus* (Sues and Carroll 1985), *Nothosaurus* (Schmidt 1986), *Neusticosaurus* (*Pachypleurosaurus*) (Carroll and Gaskill 1985; Zangerl 1935), *Serpianosaurus* (Rieppel 1989), *Simosaurus* (v. Huene 1952)] but are unknown in all plesiosaurs save the primitive genus *Pistosaurus* (Sanz 1983b; Sues 1987). Most, if not all, nonplesiosaur sauropterygians probably possessed such articulations (placodonts exhibit hyposphene/hypantrum articulations (Rieppel 1989)).

The large, dorsal zygapophyses of *Corosaurus* are set close together with flat, essentially horizontal articular faces. The neural canal remains circular in section but is constricted near the origin of the transverse processes. As in all 'nothosaurs,' (i.e., plesiomorphic sauropterygians) no nutritive foramina exist in the floor of the canal or on the undersurface of the centrum as they do in plesiosaurs. The dorsal ribs are of normal appearance; curved, long, and slender with a single, expanded head (see Figs. 4 and 5). None are fused to the transverse processes. The longest complete thoracic rib of FMNH PR480, an animal of approximately equal size to the holotype, is 11.5 cm long. Others were no doubt longer. The posteriormost ribs extend almost horizontally, but most were directed laterally and ventrally. As opposed to such forms as *Ceresiosaurus, Neusticosaurus* and *Lariosaurus* (Carroll and Gaskill 1985; Mazin 1985; Peyer 1931; Sanz 1976, 1983a; Seeley 1882; Zangerl 1935), there is no outwardly observable sclerotic thickening ("pachyostosis") of the dorsal ribs.

Sacral Vertebrae and Ribs

The sacrum of *Corosaurus* consists of only three vertebrae. This is the apparently primitive condition for sauropterygians. Three examples of the sacrum, each complete, are known; that of the type, one from a skeleton (FMNH PR480) preliminarily described by Zangerl (1963), and another specimen numbered as part of the type but obviously belonging to a second individual. Each sacrum is approximately 6 cm long and at a maximum, 9.5 cm across. The vertebrae are very similar to the preceding dorsals. They are not coossified in the type but are tightly articulated; the neural spines closely contact each other. The zygapophyses are smaller than those craniad and have medially inclined articular surfaces. The long (3.5 cm) sacral ribs are tightly sutured to short, stout, transverse processes

arising from both the neural arch and the centrum. These ribs are directed ventrolaterally, with great expansion of their distal ends. The iliac articular surfaces are roughly triangular in section and are deeply excavated.

The second specimen of UW 5485 is an isolated, yet articulated, sacrum. The vertebrae are tightly joined to each other and to their ribs. In this case, there is a possibility of some fusion of the elements. Nevertheless, the sutures remain obvious.

Caudal Vertebrae and Ribs

The primary source of information on these vertebrae is Zangerl's (1963) specimen, FMNH PR480 (Fig. 4), although several other caudal specimens are known (see, e.g., Fig. 5). The anterior caudals are present in both the holotype and FMNH PR480; the latter also retains most of the rest of the tail. At least 33 caudals are preserved in FMNH PR480, possibly as many as 36. The actual number is obscured by the overlap of the distorted column and by covering matrix. The distalmost caudals have not been found but it is estimated that a total of about 40 vertebrae formed the long, tapering, unspecialized tail. The tail was perhaps 1.25 times as long as the thorax, possibly 70 cm long in the type.

The anterior caudal centra are short and robust, much like those of the sacrum, but posteriorly they lengthen relative to their diameters. As throughout the column, the centra are cylindrical although constricted at their midsection. The undersurfaces of the anterior caudal centra are smoothly concave. The median and posterior caudal vertebrae each bear twin, longitudinal, ventral ridges which stretch from the chevron facets to the anterior edge of the centrum (Fig. 10D).

Stout, horizontally oriented ribs are borne by the anterior caudals upon short parapophyses on the centra, to which they are tightly sutured, possibly fused. These ribs are of similar character to the sacral ribs, but are flatter, generally longer, and without the distal expansion. The first caudal rib is directed towards the sacrum, although not involved in the sacroiliac articulation, whereas the remainder point posterolaterally. The third and fourth caudal ribs are the longest; successive ribs gradually decrease in size through about the fourteenth caudal vertebra (see Fig. 3). Several vertebrae posterior to the fourteenth caudal maintain vestigial parapophyses but these probably held no ribs.

The subrectangular neural spines of the anterior vertebrae rapidly shorten and give way to low, rounded, swept-back spines that extend well past the posterior margins of the centra (e.g., Figs. 4 and 5). Eventually these are lost, as are the gradually narrowing zygapophyses. Contrary to Case (1936, p. 20), well-developed chevron facets are visible on the posteroventral ends of the caudals of the type specimen, beginning with the fifth caudal vertebra. The fifth and sixth caudals of FMNH PR480 are damaged but the chevrons appear to have begun on vertebra number seven. If so, this individual difference might be ascribed to a sexual variance in the region of the cloaca. The chevrons themselves are poorly known in most 'nothosaurs,' but several good examples are now known for *Corosaurus*. These are slender, delicate chevrons, the two arms of which are joined in a solid V at their distal ends (Fig. 10E). Proximally, the two arms are free and bear prominent, posteromedially inclined, articular heads for their attachment to the centra. The chevrons were not fused to the vertebrae.

Gastralia

Very many isolated gastral ribs occur with the *Corosaurus* specimens, along with rock slabs displaying groups of associated gastralia. Zangerl (1963) has suggested that the block of gastralia associated with the type specimen of *Corosaurus* (Case

1936, fig. 14) belonged to a separate individual. This is quite possible in light of the aforementioned second sacrum catalogued with the holotype. Sauropterygian ventral baskets are often found as isolated, coherent units, presumably owing to the interlocking nature of their gastralia and their associated sheets of muscle. YPM 41030 also consists primarily of a cluster of gastralia although these are rather randomly oriented. It is therefore impossible to assign Case's (1936) gastralia specimen to his type skeleton with any degree of certainty. In spite of this problem, the block of gastralia indicate well the pattern of arrangement of the ventral armour of *Corosaurus*.

Each gastral segment is composed of a primitive, V-shaped median element which is closely flanked on each side by two imbricating lateral rods (Fig. 10F and G). The lateral elements are straight and doubly pointed; each lies craniad to its medial neighbor. From the size and concentration of the gastralia it is assumed that two rows of these ribs were associated with each vertebral segment between the pectrum and the pelvis.

A solitary median gastral element found in the blocks unarguably containing the type skeleton is approximately 13 cm long. This suggests a rather broad body region for the animal. Other isolated gastralia in the Field Museum and Yale collections show that occasionally, the median elements can be pronged on one or both ends (Fig. 10H and I). This is a congenital deformity of no phylogenetic consequence and has been previously reported in *Nothosaurus* (Koken 1893). One partial median rib amid the Yale material is very large and stout (approximately 1.5 cm thick at its center), giving the first indication that *Corosaurus* grew much larger than is suggested by the type. All the gastralia are formed of rather dense, heavy bone.

Appendicular Skeleton

The appendicular skeleton of sauropterygians is highly modified in response to their use in an aqueous medium. The specialized limbs are broad and flattened and often exhibit hyperphalangy. These limbs usually conform to several similar patterns of little taxonomic value. On the other hand, aside from the skull, the limb girdles are perhaps the most taxonomically useful skeletal elements in the Sauropterygia, as long as ontogenetic variations are taken into account. They form massive, platelike assemblies, often possessing significant intergeneric differences.

The appendages and girdles of *Corosaurus* have, to date, been poorly understood and inadequately discussed. Now, however, new material in conjunction with the old presents us with the opportunity for a nearly complete description of its appendicular skeleton. Included in the specimens of *Corosaurus* are the probable remains of an interclavicle, three clavicles, two scapulae, four coracoids, three pubes, two ischia, three ilia, at least seven humeri, three radii, five ulnae, six femora, four or five tibiae, two fibulae, and substantial portions of both a fore and a hind "foot."

Pectrum

The pectoral girdle of *Corosaurus* is unique among the 'nothosaurs' but has, due to inadequate material, been incorrectly reconstructed in previous studies (Case 1936; E. von Huene 1949; F. von Huene 1948a; and Zangerl 1963). Only the disarticulated pectrum of the type specimen was previously available for study and while its components were correctly identified, they were often misinterpreted.

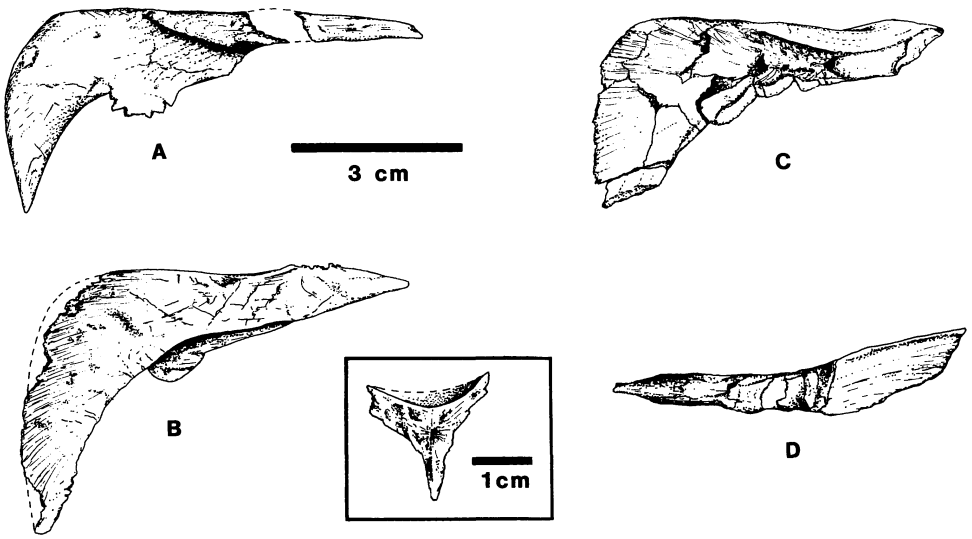

FIG. 11. Pectoral elements of *Corosaurus alcovensis*. A, right clavicle, ventral aspect, UW 5485; B, left clavicle, internal aspect, YPM 41037; C, right clavicle, ventral aspect, from FMNH PR135, interclavicular facet at right; D, posterior view of C, lateral edge to right. Inset, probable interclavicle of UW 5485, oblique section, anterodorsal? surface to top.

Elements of the shoulder girdle to be found in the holotype are the major portion and impressions of the right coracoid as exposed from the dorsal (or internal) and medial sides, a partial impression of the left coracoid (dorsal surface), the exposed lateral surface of the left scapula, the ventral surface of the right clavicle, and what appear to be two fragments of the interclavicle. New specimens are a virtually complete, matrix-free, right coracoid (YPM 41034), a large cross-sectional fragment from an indeterminate coracoid (YPM 41064), a left scapula exposed from its medial side (YPM 41031), the completely exposed dorsal (internal) surface of a left clavicle (YPM 41037), and a nearly complete, matrix-free, right clavicle (from FMNH Lot No. PR135). These additional fossils leave little doubt about the structure of the pectrum.

Clavicle. The dermal girdle comprises the clavicles and the interclavicle. The clavicle is an L-shaped bone with a stout, barlike, pointed, medial process and a thin, spatulate, posterolateral process which meet at an angle of nearly 90° to form a sharp anterolateral corner (Fig. 11). In this regard the clavicle is similar to those of most other 'nothosaurs,' i.e., plesiomorphic sauropterygians. The concave medial edge of the posterolateral process is smoothly rounded and decidedly thickened (tapering caudad). The lateral and anterior edges, toward which the structural fibers of the bone are directed, are rough and unfinished. The lateral edge is thin, the anterior thickened, and the entire posterolateral process is dorsally deflected. The medial bar of the clavicle is thick and dense. It bears an anterodorsal ridge or tuberosity and a posteroventral, interclavicular facet or attachment scar. The interclavicular facet forms a rugose trough oriented along the axis of the medial process. At the juncture of the two clavicular processes a thin, rounded, tablike shelf projects posteromedially. This shelf is broken in the type specimen and in FMNH PR135, but is complete in YPM 41037. The transverse dimension of the type clavicle is 8 cm.

The clavicle of *Corosaurus* is unusual among those of many 'nothosaurs' in not being tightly sutured to either the scapula or the opposite clavicle. Rather than

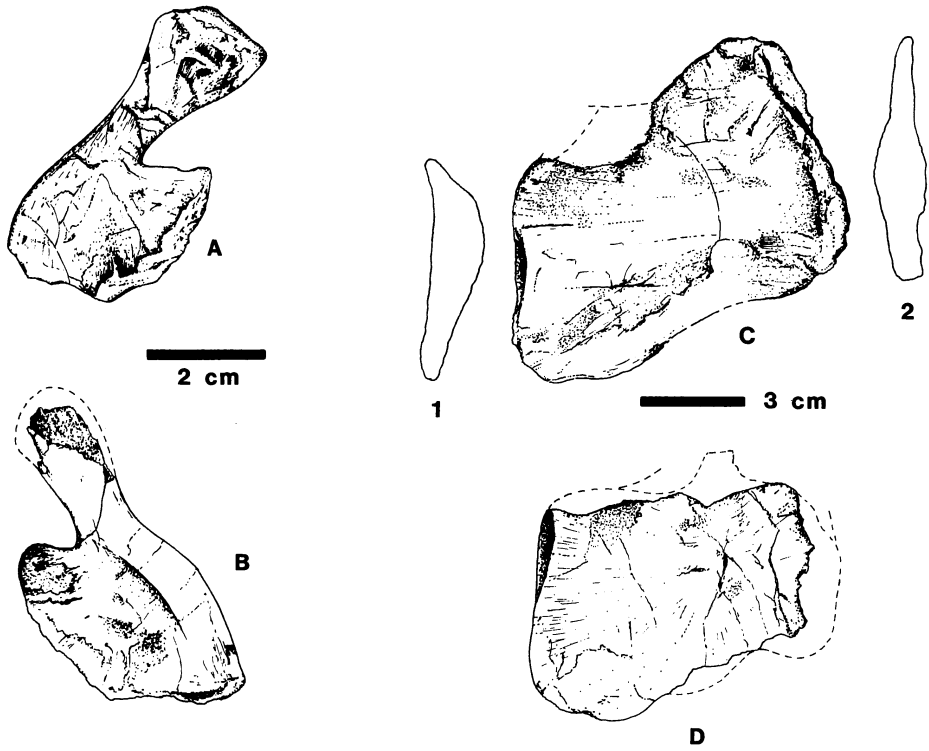

FIG. 12. Pectoral elements of *Corosaurus alcovensis*. A, left scapula of UW 5485, lateral aspect; B, left scapula of YPM 41031, internal aspect; C, right coracoid, internal aspect, YPM 41034; C1, silhouette of symphysis, dorsal side to right, C2, silhouette of glenoid, dorsal side to left; D, right coracoid, internal aspect, UW 5485. Impressions denoted by hatched lines.

being joined at a broad contact of their medial processes, the clavicles merely met at their tips and were strongly braced by the interclavicle.

Interclavicle. The presumed interclavicle is exposed next to the right coracoid along a fracture in the matrix of the type specimen. This bone is partially obscured by matrix, and while it cannot be considered a fragment of any other element, it is the only pectoral component which is incompletely known. It appears that the interclavicle is a small, triangular bone with a sharp posterior projection (Fig. 11) as it is in certain forms such as *Keichousaurus, Neusticosaurus,* and *Simosaurus* (see Chapter 4). What is probably the anterodorsal surface is smoothly concave. However, the interclavicular attachment scars of the clavicles, as noted by Zangerl (1963, p. 118), seemingly indicate the presence of lateral, barlike projections from the interclavicle, but nothing of the sort is visible in the present specimen. Such projections are possibly broken off or hidden by matrix.

Scapula. The endochondral portions of the shoulder girdle, the scapula and coracoid, are dense, robust bones. In a general manner, these elements follow the typical 'nothosaurian' pattern, yet also present characters peculiar to the genus. The scapula (Fig. 12A and B) is an independent bone which is sutured to neither the clavicle nor the coracoid. It features a prominent, though relatively narrow, dorsal blade which projected posterodorsally to a point above the glenoid. A somewhat similar scapula is illustrated by Young (1965a, fig. 5) for *Chinchenia.* The anterior edge of the scapula of *Corosaurus* is smooth and slopes craniad in a sinuous curve. The distal extremity of the blade is anteroposteriorly widened,

although this is exaggerated in the somewhat crushed blade of the type specimen. The glenoid area of the scapula is thickened and rugose, with a slight lateral bulge. Its posterior slope parallels that of the dorsal blade. A distinct notch separates the glenoid from the blade. There is no ventral, horizontal expansion of the scapula as is sometimes observed in 'nothosaurs' and is ubiquitously present in the plesiosaurs. The anterior corner or expansion of the bone ("acromion" of Romer 1956) is smoothly rounded in profile and slightly concave on its lateral surface. The anterior edge of this expansion is greatly thickened to form a barlike border opposite the glenoid and acts as the attachment surface for the clavicle. The medial surface is smooth and flat and is demarcated from the thick anterior bar by a sharp ridge or escarpment. The ridge is most pronounced at its center, is reduced at its extremities, and joins the anterior edge of the scapular blade near its base. The medial surface of the "acromion" merges with the inner face of the scapular blade, which is slightly offset in relation to the body of the scapula. The type scapula is approximately 6 cm long from anterior tip to the top of the blade.

Coracoid. The coracoid is a large, flat, roughly rectangular bone (Fig. 12C and D). It is unique among known 'nothosaurs' in that its anteroposterior dimensions are rather uniform, whereas typical 'nothosaurs' exhibit a very pronounced central narrowing of the coracoid between expanded lateral and medial ends. The anterior and posterior edges of the coracoid of *Corosaurus* are only shallowly concave. These edges are smooth and are the thinnest parts of the bone. They can also display a certain amount of individual variation as witnessed by the wavy posterior edge of the type specimen versus the straighter border of the only slightly larger YPM 41034. This variation is not unexpected in light of the latently cartilaginous nature of sauropterygian limb girdles. The limb girdles of all sauropterygians display a striking amount of ontogenetic variation because of the large amounts of cartilage persistently present in juvenile and subadult specimens. Secondarily adapted aquatic tetrapods often have little need to replace cartilage with bone, at a high metabolic cost, when the extra weight of cartilage can be easily neutralized and supported through natural hydrostatic buoyancy. The resulting ontogenetic variation is especially noticeable in the more aquatically specialized plesiosaurs, whose skeletons are often never fully ossified, but should be expected in 'nothosaurs' as well.

The ventral surface of the coracoid is essentially flat with only a slight concavity of the medial half, whereas the dorsal or internal surface is marked by a thick, rounded, transverse strut. This strut, formed by a thickening of the coracoid midline, particularly in the glenoid and symphysial regions, is characteristic of most sauropterygians and presumably braced the glenoid against internally directed forces generated during forelimb movement. The glenoid edge of the bone is rather straight and deeply pitted where it was capped by cartilage. The large, crescent-shaped symphysial surface was also finished in cartilage and forms the thickest part of the coracoid. Its upper surface is convex, its lower concave. The articular surface of the glenoid is not parallel with the symphysis but is directed slightly craniad as in other 'nothosaurs.'

There is no supracoracoid foramen or notch in the anterolateral corner of the coracoid. Such a notch, sometimes closed by the adjacent scapula, is known in many other primitive sauropterygians ('nothosaurs') in which the pectrum has been described. A possible small notch is indicated in the partial impression of the left coracoid in the type specimen, but may be only an individual imperfection as the other preserved coracoids obviously lack a notch. The right coracoid of the

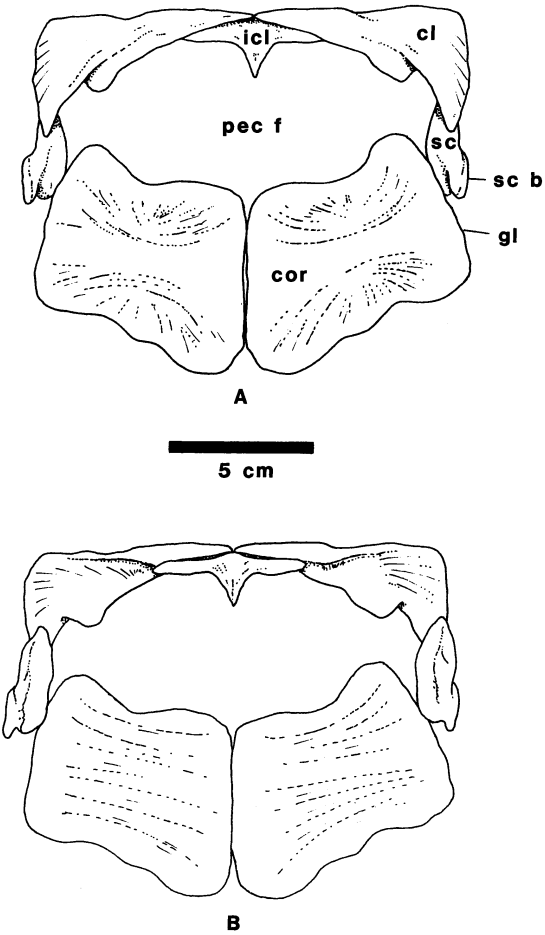

FIG. 13. Reconstructed pectrum of *Corosaurus alcovensis* (interclavicle hypothetical). A, dorsal (internal) aspect, anterior to top; B, ventral aspect. cl = clavicle; cor = coracoid; gl = glenoid; icl = interclavicle; pec f = pectoral fenestra; sc = scapula; sc b = scapular blade.

type is estimated to have been approximately 7.5 cm in breadth along the transverse strut. A cross section through YPM 41064 indicates that the coracoid was a heavy, "pachyostotic" bone with dense, thickened compacta layers.

Restoration. The complete pectrum of *Corosaurus* is reconstructed in Figures 13 and 14. The gross morphology of this girdle is unquestionably 'nothosaurian'—that is, plesiomorphic for sauropterygians, albeit unusual. As in other sauropterygians, and in contrast to the usual reptilian condition, both the scapula and the interclavicle are positioned superficially to the clavicles. The posterolateral portion of each clavicle meets and overlies the corresponding scapula's anteromedial ridge as in *Nothosaurus*. The clavicle and scapula were not tightly sutured as was typical for many sauropterygians. Rather, the scapuloclavicular assembly is assumed to have been held together by attendant musculature, cartilage, and ligaments. The clavicles and interclavicle formed a stout transverse bar across the front of the trunk, bracing the anterior part of the pectrum in a manner similar to the coracoid strut. Behind this bar lay a wide opening that was bounded posteriorly by the large coracoids. This pectoral fenestra was relatively shorter (anteroposteriorly) than in other 'nothosaurs' due to the great size and unusual shape of the coracoids of *Corosaurus*. These coracoids, the dominant structures of

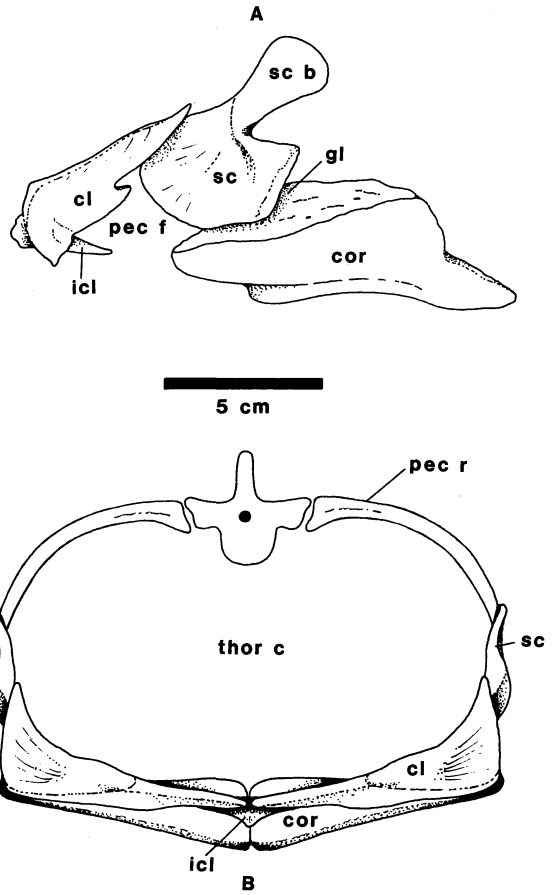

FIG. 14. Reconstructed pectrum of *Corosaurus alcovensis* (interclavicle hypothetical). A, left lateral aspect; B, anterior aspect. cl = clavicle; cor = coracoid; gl = glenoid; icl = interclavicle; pec f = pectoral fenestra; pec r = pectoral rib; sc = scapula; sc b = scapular blade; thor c = thoracic cavity.

the pectrum, met in a strong symphysis to counteract the thrust from the forelimbs. As in all sauropterygians, there was little dorsal development of the pectrum. The scapular blades probably held the large ventral basket only loosely against the ribs of the thorax. The glenoids were, of course, largely formed in cartilage and were positioned between the posterior edges of the scapulae and the lateral faces of the coracoids. This same cartilage held the scapulae to the anterolateral corners of the coracoids.

Pelvis

As noted by Zangerl (1963), the posterior portion of a skeleton of *Corosaurus* represented by FMNH PR480 contains the articulated right half of a pelvis (Fig. 15A). The left half is also present, although disarticulated, somewhat distorted, and largely buried beneath matrix and other bones. What Zangerl (1963, p. 120) has interpreted as a fibula is probably the crushed left ischium; his possible left ilium (1963, plate 5) is a caudal vertebra. Two additional specimens are what is probably the left pubis as exposed from the ventral side (YPM 41040) and a well-preserved right ilium (FMNH PR243) with exposed lateral and ventral surfaces (Fig. 15B and C).

Pubis. The ventral elements of the pelvis are, like the pectrum's coracoid, large and platelike. Zangerl (1963, p. 118) has noted that the convex anterior border

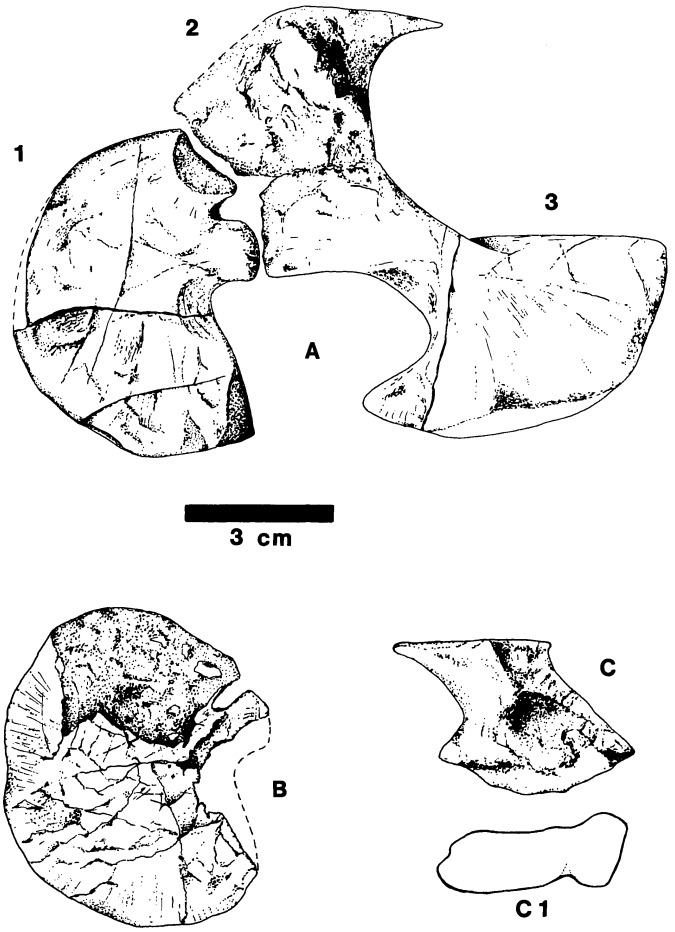

FIG. 15. Pelvic elements of *Corosaurus alcovensis*. A, right side of pelvis of FMNH PR480, internal aspect: 1, pubis, 2, ilium, 3, ischium; B, ?left pubis, YPM 41040, ?ventral aspect, anterior to left; C, right ilium, FMNH PR243, lateral aspect: C1, silhouette of articular facets.

of the pubis of *Corosaurus* is in sharp contrast to the concave front ends of the pubes of all other described 'nothosaur' genera. This border is partially obscured in the pubes of FMNH PR480 but is completely visible on YPM 41040 (Fig. 15B). The posterior border of the pubis is concave in normal fashion. The ventral side of the pubis is flat; dorsally it is contoured to accommodate a transverse strut or thickening as was earlier seen in the coracoid. The iliac and ischial facets are located on stout posterolateral prongs, between which is a large obturator notch. The iliac prong and its semicircular facet are directed dorsad. The thin anterior and thickened lateral and medial edges of the pubis were finished in cartilage; thus a certain amount of ontogenetic or individual variation or both can be expected to have existed in its overall shape. The transverse dimension of the right pubis of FMNH PR480 is approximately 6 cm.

Ischium. The ischium of *Corosaurus* is typical of sauropterygians in having a long shaft, an expanded foot, and a greatly thickened symphysial edge (see Fig. 15A). There are few significant differences from the ischia of other 'nothosaurs.' Its posteromedial edge is convex and unfinished; the anteromedial margin is broadly concave. The head of the ischium is stout and bears an ovate iliac facet on its dorsolateral surface. As in the pubis, a thickened transverse strut runs from

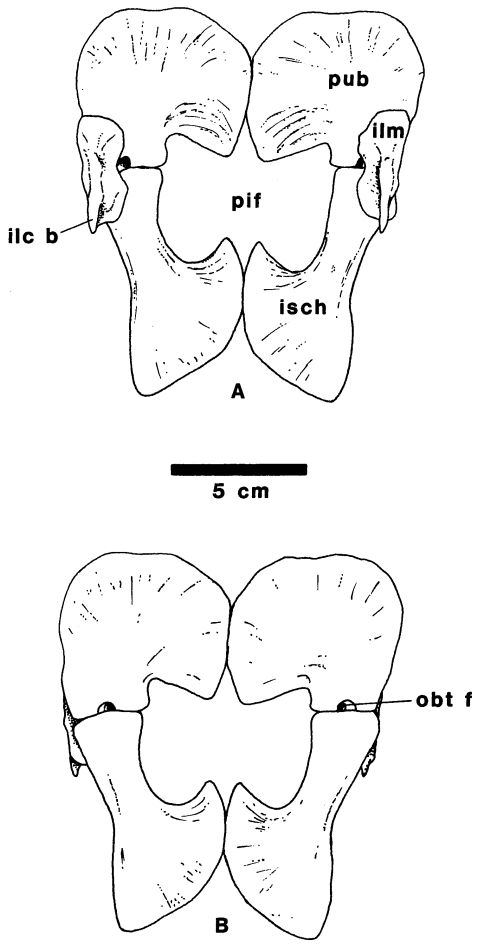

FIG. 16. Reconstructed pelvis of *Corosaurus alcovensis*. A, dorsal (internal) aspect, anterior to top; B, ventral aspect. ilc b = iliac blade; ilm = ilium; isch = ischium; obt f = obturator foramen; pif = puboischiadic fenestra; pub = pubis.

the glenoid region to the symphysis. The greatest length of the right ischium of FMNH PR480 is approximately 8 cm.

Ilium. As in the pectrum, the dorsal component of the pelvis of *Corosaurus* is reduced as in all sauropterygians. The ilium is the smallest element of the pelvis and is of typical 'nothosaurian' appearance, although more robust than most (Fig. 15C). It is a low, stout, laterally curving bone retaining a prominent dorsal blade. The blade is flat across its top, with a very small anterior point and a somewhat larger posterior projection or ramus. These projections, particularly the anterior one, are not present in all 'nothosaurs.' The distinct pubic and ischial facets of the ventral surface of the ilium correspond in size and shape to the iliac facets of the ventral bones; the ilium sits nearly vertically upon the ventral elements. The anterior surface of the ilium slopes gently forward; the posterior is smoothly concave. The large acetabulum is subcircular and shallowly concave. A low external ridge runs from the top of the acetabulum to the posterior point of the iliac blade. The right ilium of FMNH PR480 is 4 cm long and 3 cm high.

Restoration. The pelvis of *Corosaurus* is restored in Figures 16 and 17. The broad ventral plates meet in a strong, cartilage supported, symphysis. In anterior

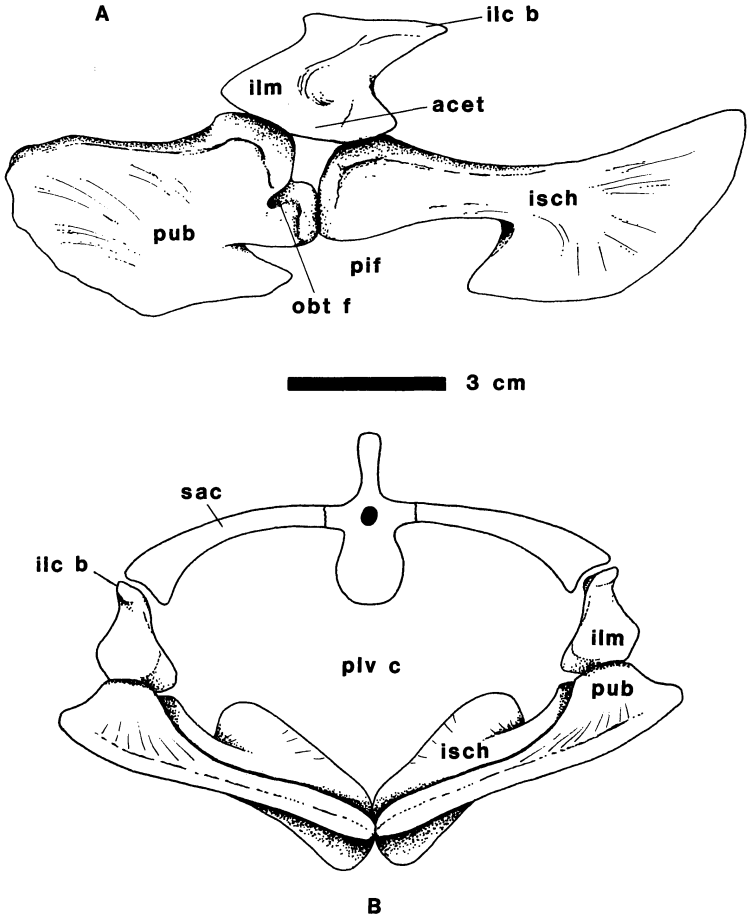

FIG. 17. Reconstructed pelvis of *Corosaurus alcovensis*. A, left lateral aspect; B, anterior aspect. acet = acetabulum; ilc b = iliac blade; ilm = ilium; isch = ischium; obt f = obturator foramen; pif = puboischiadic fenestra; pelv c = pelvic canal; pub = pubis; sac = sacrum.

or posterior aspect, the symphysis presented something of a V-shape, rather than the largely horizontal union seen in plesiosaurs. Between the ventral plates of *Corosaurus* was a rather typical, large, puboischiadic (thyroid) fenestra. The ilia sat upon the laterodorsal corners of the ventral elements and were joined to them by the cartilage of the acetabula. Only small portions of the pubis and the ischium contributed to the rather well-formed acetabulum, however. At the junction of the three pubic bones, a large obturator foramen was formed by closure of the obturator notch of the pubis. The ilia were apparently tightly joined to the ribs of the three sacral vertebrae.

Forelimb

The type specimen of *Corosaurus* (UW 5485) preserves both humeri, the left one being free of matrix, both radii, both ulnae, and portions of the right carpus and manus. Supplementing the information available on the forelimb are three left humeri and the distal end of a right humerus in the Yale collection (YPM 41031, 41032, 41033, and 41035, respectively), a crushed right humerus (from FMNH Lot No. PR135), the impressions of both a left radius and ulna (YPM 41031), an indeterminate ulna impression (FMNH PR135), and the proximal end of a right ulna (YPM 41036) which is free of matrix.

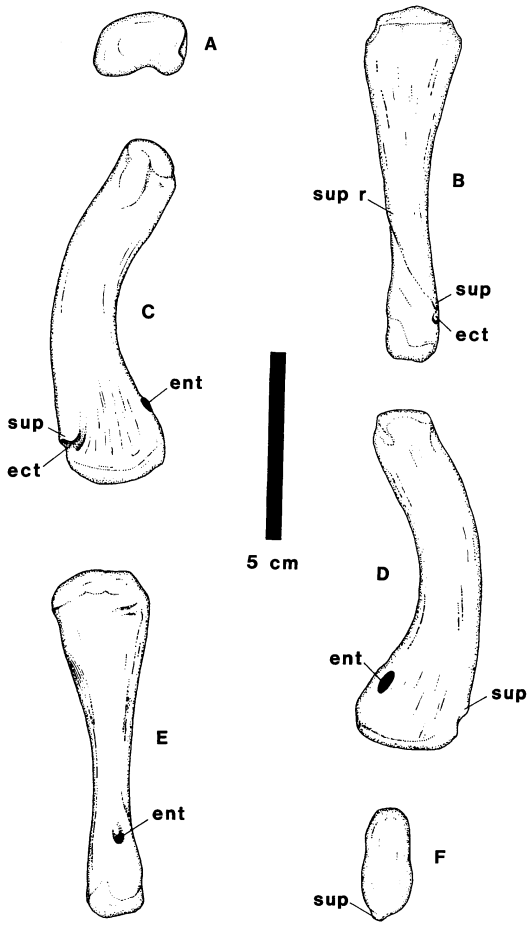

FIG. 18. Left humerus of *Corosaurus alcovensis,* based primarily upon UW 5485 and YPM 41033. A, proximal aspect, anterior to top; B, anterior aspect, proximal end up; C, extensor aspect; D, flexor aspect; E, posterior aspect; F, distal aspect, anterior to bottom. ect = ectepicondylar notch; ent = entepicondylar foramen; sup = supinator process; sup r = supinator ridge.

Humerus. The humerus is strongly curved caudad and is generally similar to those of other nonplesiosaurian nothosauriforms (Fig. 18). The shaft is relatively short and stout. The proximal head of the humerus is expanded dorsoventrally and is somewhat rectangular in cross section; the distal end is lateromedially expanded with an ovate cross section. Both ends of the bone are unfinished, being originally capped by cartilage. There is a prominent ectepicondylar notch for the passage of the radial nerve and blood vessels and a large entepicondylar foramen allowing supply of the flexor surface of the antebrachium. Just distal to the foramen, the entepicondylar corner of the humerus bears a small process which enlarged the surface area available for the origins of the flexor musculature. There is no demarcation between the ulnar and radial facets. A small, though distinct, supinator process for the origin of the M. supinator longus is situated immediately proximal to the ectepicondylar groove. A sharp, sinuous supinator ridge runs along the anterior edge of the shaft from this process to the anteroventral corner of the proximal articular head. There is essentially no deltopectoral crest, merely a sharp anteroventral edge to the proximal part of the shaft for apparent insertion of the M. pectoralis. A roughened convexity on the dorsoproximal end of the bone probably served as the attachment site for the M. deltoideus. The dorsal surface

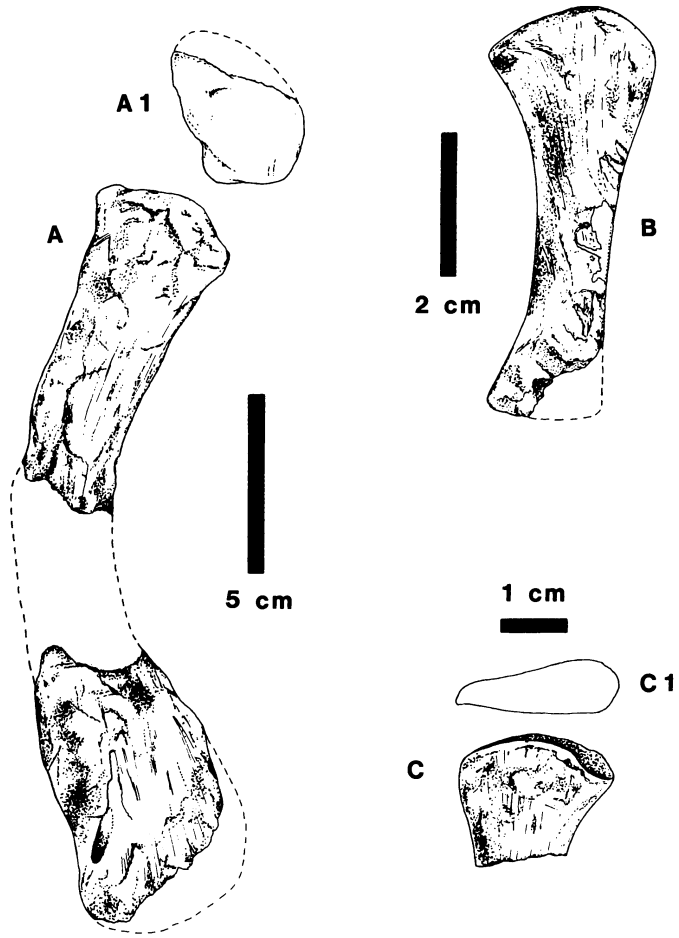

FIG. 19. Forelimb elements of *Corosaurus alcovensis*. A, left humerus, YPM 41032, shaft preserved by matrix impression, A1, proximal aspect; B, left ulna of UW 5485, extensor aspect; C, proximal end of right ulna, YPM 41036, extensor aspect, C1, silhouette of articular head.

of the bone is convex; the ventral surface is largely flat. The proximal head of the humerus bears both shallowly concave scars and low, ridged processes for the insertions of a number of additional shoulder muscles, notably the M. scapulohumeralis cranialis, the M. subcoracoscapularis, the M. coracobrachialis, and the M. latissimus dorsi (Fig. 18). The attachment particulars of the limb musculature are discussed below in the section on functional morphology.

The left humerus of the holotype of *Corosaurus* is approximately 9 cm long, and while from an individual that was certainly a young adult, it and its right counterpart are the smallest humeri represented in the collection. The largest humerus (YPM 41032) is approximately 21 cm long. The ontogenetic implications of this situation are more fully discussed below, although several morphological changes in the largest humerus are obvious (Fig. 19A). The proximal muscle attachment sites have become more pronounced. The proximal head is much more flattened and expanded, and the subscapular process enlarged and distally deflected. The site of insertion of the M. latissimus dorsi has become an elongate ridge lying just distal to and behind the much enlarged insertion scar of the M. deltoideus. Distally, the supinator process has been lost, but the supinator ridge is more pronounced and is directed ventrally, forming the lower face of the

humerus into a concave scoop. The ectepicondylar notch has been closed laterally and, along with the entepicondylar foramen, lies relatively farther from the distal end of the bone. Intermediate stages to these changes can be seen in the intermediately-sized humerus YPM 41033.

Ulna. Contrary to Case (1936, p. 23), the left ulna of the type specimen is not crushed, but provides a good indication of the overall shape of this epipodial (Fig. 19B). It is a short, flat bone with expanded proximal and distal ends. The leading or anterior (internal) edge of the ulna is broadly concave, the posterior (external) edge more nearly straight. As opposed to the condition of the humerus, the dorsal surface of the ulna is, at least proximally, flatter than the ventral. The articular extremities of the bone are, as in all the limb elements, unfinished. The rounded, proximal articular surface is tear-shaped (Fig. 19C). The point of the tear drop forms the slight external expansion of the blunt "olecranon process." The left ulna of UW 5485 is approximately 5.5 cm long.

Radius. The radius of *Corosaurus* is a curved, narrow bone of approximately equal length to (or somewhat shorter than) the ulna (see Fig. 6). The proximal end is slightly enlarged, whereas the distal end is unexpanded in the type. However, the radius impression of the slightly larger individual in YPM 41031 shows both articular ends as possibly expanded. The radius is not much flattened and has a subcircular cross section. The curvature of both epipodial elements resulted in a large spatium interosseum, as noted by Case (1936, p. 23). The right radius of the type specimen is approximately 5.5 cm long.

Carpus. Only four carpal bones of the type right forelimb are known. Case (1936) recognized only three of these. The largest element of the four, that which was partially lost during the original preparation (Case 1936, p. 23), is probably either the intermedium or ulnare. The smaller disks, averaging about 3 mm in diameter, are distal carpals. From the small size of the bones, it is apparent that the carpus of *Corosaurus* was poorly ossified and consisted largely of cartilage (even if one allows for some progressive ossification in older individuals). A conservative but reasonable restoration might place three small distal carpals and two larger (8 mm–1 cm diameter?) proximal carpals (intermedium and ulnare) in the wrist as in *Lariosaurus.*

Manus. The manus of *Corosaurus* is known only from the right forelimb of the type specimen (see Fig. 3). Fortunately, this foot remains largely articulated in a natural position. The typical, rod-shaped metacarpals are only slightly flattened, mostly as a result of diagenetic compression. Metacarpal III is the longest at 2 cm, metacarpal I the shortest at 9 mm. The first digit possesses two phalanges, the second, three. The terminal ungual phalanx of each of these digits is a blunt claw. Only a single phalanx remains articulated to metacarpal III. The remaining phalanges of the foot are not properly articulated, but fragments or impressions of nine of these are exposed beneath the manus along a fracture in the matrix. From the total number and position of the phalanges it is probable that no hyperphalangy was present in the manus, and a nearly primitive phalangeal formula is estimated. A reasonable reconstruction has a formula of 2-3-4-5-3.

Hindlimb

No hindlimb components are preserved with the holotype but numerous specimens have been found more recently. These include the left femur, tibia, and fibula, and a left metatarsal and a partial foot of FMNH PR480; what are presumably the right femur, fibula and the right tibia impression of FMNH PR1369; a femur

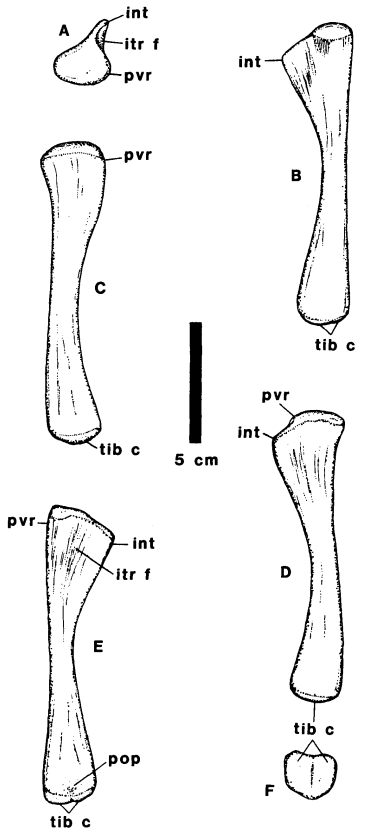

FIG. 20. Right femur of *Corosaurus alcovensis,* based primarily upon YPM 41038 and YPM 41039. A, proximal aspect, anterior to top; B, extensor aspect, proximal end up; C, posterior aspect; D, anterior aspect; E, flexor aspect; F, distal aspect, anterior to bottom. int = internal trochanter; itr f = intertrochanteric fossa; pop = popliteal space; pvr = posteroventral ridge; tib c = tibial condyle.

and one or possibly two tibiae from an individual in FMNH Lot No. PR135, a crushed tibia belonging to FMNH PR1368, and the proximal end of a left (?) femur (YPM 41055). All of this material is imbedded in matrix, but two undistorted femora in the Yale collection, a left and a right (YPM 41038 and 41039, respectively), have been freed and are especially useful for descriptive purposes.

Femur. The femur of *Corosaurus,* as pointed out by Zangerl (1963, p. 120), was relatively longer than the humerus. This is evident from a comparison of specimens UW 5485 and FMNH PR480 which represent individuals of approximately equal size. The femur of FMNH PR480 is approximately 13.5 cm long. Unlike the humerus, the femur is little modified from the primitive reptilian condition. It is a slender, sigmoid bone with a long, cylindrical shaft (Fig. 20). The bone is expanded at both ends but is nowhere flattened. The extremities have rough, unfinished, articular surfaces. The proximal articular surface is irregularly triangular in outline. There is a very large, crestlike, internal trochanter and an only slightly smaller posteroventral ridge. Between these two ridges lies a broad, concave, triangular, intertrochanteric fossa in which lay the powerful M. puboischiofemoralis externus. There is no fourth trochanter. The distal articular face of the femur is roughly semicircular. The two equisized tibial condyles are reduced relative to the primitive condition but remain distinct (Fig. 20F). There is, how-

ever, no intercondylar fossa, although ventrally a shallowly depressed popliteal space exists. No clear fibular facet is present.

Tibia and fibula. The tibia of *Corosaurus* is a straight, thick bone of unremarkable appearance and apparently nearly circular cross section. The ends are rounded and a little expanded, both ends being as wide as the distal head of the femur (see Figs. 4 and 5). The tibia of FMNH PR480 is approximately 7 cm long. The fibula, on the other hand, is relatively thin and narrow, with a deeply concave internal edge indicating that a large spatium interosseum was present in the hind epipodium as well as in the fore (Fig. 5). The lateral or posterior edge of the bone is largely straight. The proposed fibula (FMNH PR480) of Zangerl (1963, p. 120) is probably the partly crushed and distorted left ischium. The proximal (?) end of the true fibula of FMNH PR480 projects from the matrix next to the femur. This end of the fibula is only 5 mm thick; it is concave on one side, convex on the other (Fig. 4). The rounded proximal head of the fibula is expanded and directed proxomediad. The distal end of the fibula is also flat and expanded, but has a rather squared-off articular face. The fibula was slightly shorter than the tibia.

Tarsus and pes. A partial tarsus and pes (FMNH PR480) gives us an idea of the form of the hindfoot in *Corosaurus* (Fig. 4). The two large, disk-shaped elements (approximately 1.8 and 1 cm in diameter, respectively) are undoubtedly homologous with the fibulare and intermedium of the primitive reptilian tarsus. They have unfinished rims and depressed centers. A third circular bone (5 mm in diameter) is a distal tarsal. Up to five of these distal tarsalia may have been present in the living animal, but two to three is more likely. Like the carpus, the tarsus was obviously poorly ossified. Three metatarsals are preserved, the longest being 3 cm in length; in general they are much longer and stouter than the metacarpals. A fourth metatarsal is exposed near the distal end of the left femur, along with what are possibly several poorly preserved tarsals. The partial pes contains only one small phalanx (1.3 cm long). In keeping with the forelimb, however, a primitive phalangeal formula is assumed (2-3-4-5-4).

RESTORATION

Reconstructions of the skull and the limb girdles have been presented above. Now the complete description of *Corosaurus alcovensis* can be summarized and followed with a restoration of the entire skeleton of the animal (Figs. 21 and 22). Although the limb girdles and the skull display features that are unique to this genus, the gross morphology of *Corosaurus* is generally similar to that of other known nothosauriforms. The body was narrow and elongate, and from the known lengths of ribs and gastralia, likely to have been broader than high. The tail was long and tapering, at least as long as the trunk, but was relatively shorter than the tails of the much smaller pachypleurosaurs and was not greatly compressed laterally. In fact, although caudal chevrons were present throughout much of the tail of *Corosaurus,* the neural spines were rather low from the midtail region caudad. Throughout the vertebral column, the spines were somewhat rectangular and never high. There was, for example, no elongation of the spines in the shoulder region as is seen in some examples of *Nothosaurus* (Schmidt 1984).

As the transitional "pectoral" rib position suggests placement of the anterior edge of the pectrum beneath the nineteenth vertebra of the column, the probable length of the neck has been established. It was long, thin, and serpentine, as in

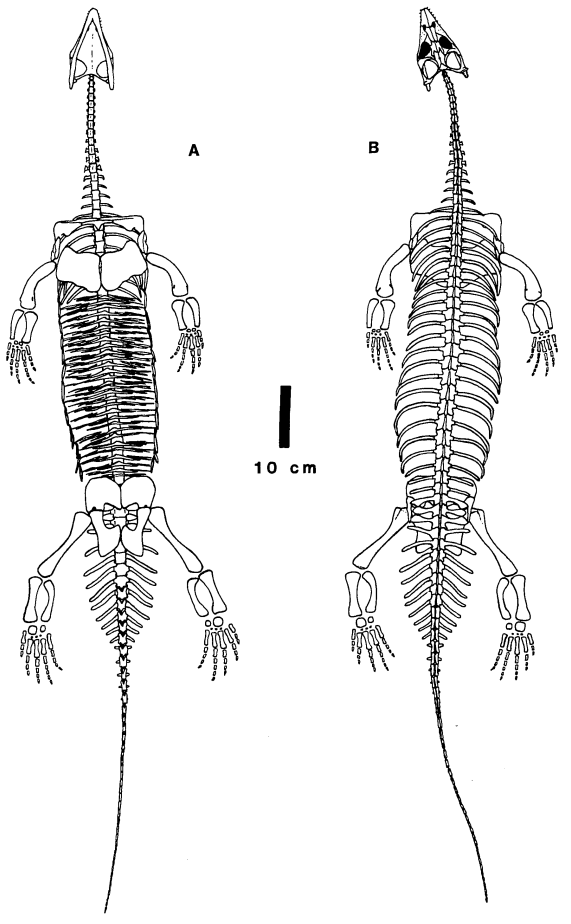

FIG. 21. Skeletal reconstruction of *Corosaurus alcovensis*. A, ventral aspect; B, dorsal aspect.

all primitive sauropterygians, but was only about half as long as the body. Many 'nothosaurs' had longer necks and at least one (*Ceresiosaurus*) possessed a neck that equaled the trunk in length. The head of *Corosaurus* was rather small and brevirostrine; it was also generally broader than high. The total estimated length of the type individual, from the tip of the snout to the end of the tail, was approximately 165 cm. It must be emphasized, however, that individuals of *Corosaurus* could, and did, grow to much larger sizes, as evidenced by isolated elements.

The limbs were long and specialized, but without well-formed osseous joints. The robust forelimb was strongly curved. The "feet" were small and flat, presumably with little or no hyperphalangy. The metapodials were relatively short by 'nothosaur' standards, and were unexpanded. The hindlimbs of *Corosaurus* were at least 40% longer than the forelimbs in the type specimen, although this

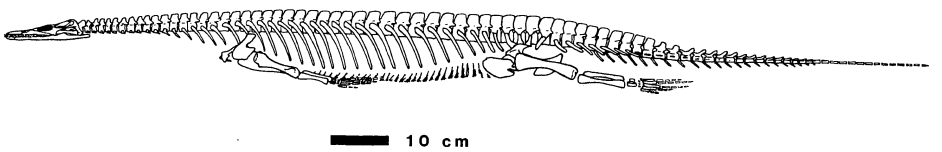

FIG. 22. Skeletal reconstruction of *Corosaurus alcovensis*, left lateral aspect.

is a proportion which may have changed during ontogeny (Zangerl 1963). The crus of *Corosaurus* was similarly longer than the antebrachium, and the pes longer than the manus. The ventral side of the body of *Corosaurus* was fitted with both a dense framework of interlocking gastralia, and expanded, platelike girdle assemblies.

DISCUSSION

Through comparison of the skeleton of *Corosaurus* with those of other sauropterygians, it appears that many of its morphologic features display the presumably "primitive" character state (see Chapter 4), while certain others can be considered as "advanced" or derived. Some of the latter serve as autapomorphies that define the taxon. Relative to other nothosauriforms, its axial skeleton has in general retained many apparently conservative traits. The appendages of *Corosaurus* are rather unspecialized (although certainly adapted for aquatic use); yet the limb girdles are notably derived.

Among the characters of the skull and vertebral column of *Corosaurus* that are perhaps primitive with respect to other nothosauriforms, are the short brevirostrine skull; large nasals, prefrontals, and postfrontals; relatively wide skull table with unfused skull table elements; posterolateral process of the frontal; intermediately-sized postorbital region; rather small, equisized upper teeth; generally conservative vertebrae; and existence of only three true sacral vertebrae. On the other hand, the slight elongation of the transverse processes of *Corosaurus* is unlike that of most 'nothosaurs,' but is reminiscent of the larger processes of plesiosaurs. Another plesiosaur-like and possibly derived trait is the presence of relatively large posttemporal fenestrae, creating an "open" occipital face. All other 'nothosaurids' in which the occiput is known have a "closed" occiput, that is, very small posttemporal fenestrae. The relatively high temporal region of *Corosaurus* is also characteristic of plesiosaurs but can be observed in nothosauriforms such as *Cymatosaurus* and *Lariosaurus* as well.

Although of general 'nothosaur' configuration, the limb girdles of *Corosaurus* are nevertheless uniquely derived relative to those of all other known nonplesiosaurian sauropterygians. The greatly expanded coracoids are, as detailed above, relatively larger and more rectangular in outline than any others known, and are without both the supracoracoid foramen and extreme median constriction of those of other genera. The result of these changes is a very massive, platelike pectrum. Even so, it does not greatly resemble those of plesiosaurs. There is no great posterior elaboration of the coracoids as is found in plesiosaurs (including *Pistosaurus*), no medial expansion of the ventral process of the scapula, no longitudinal division of the pectoral fenestra by a scapulocoracoid midline bar, and the dermal elements are well developed to form the anterior strut of the pectrum, whereas such anterior support is accomplished in plesiosaurs (in which the dermal elements of the shoulder girdle are vestigial or even lost) by the large ventral plates of the scapulae.

The large pelvis of *Corosaurus* superficially resembles those of plesiosaurs, especially in the convex anterior border of the pubis. *Corosaurus,* however, primitively retains an obturator foramen that is lacking in plesiosaurs. The ilium of *Corosaurus* is also plesiomorphic, larger and better formed than that of any plesiosaur and indeed, that of most nothosauriforms. The plesiosaur ilium articulates only with the ischium; *Corosaurus* and other 'nothosaur' ilia contact both the ischium and the pubis.

The classification and relationships of the 'nothosaurs' are more fully discussed in Chapter 4. However, as the supratemporal fenestrae of the skull of *Corosaurus* are larger than its orbits, the animal clearly falls into the nothosauriform clade (Chapter 4) as opposed to that containing the much smaller pachypleurosaurs in which the fenestrae are far smaller than the orbits. Additional comparisons between *Corosaurus* and other sauropterygians can also be found in Chapter 4.

3. PALEOBIOLOGY

INTRODUCTION

The study and discussion of a fossil taxon should not be limited to the physical description of specimens but should include, where possible, interpretive analysis of its paleobiology. In the case of fossil vertebrates, preserved bones are only partially indicative of the whole-animal biology of the once living organisms. Among topics that may be addressed in a general study are the theoretical reconstruction of unpreserved soft tissues, the functional morphology and behavior of the animal during life, the observed natural (biological) variation among individuals, and the paleoecologic interaction of the animal with its environment. To the extent possible, these areas are here examined with respect to the skeletal anatomy of *Corosaurus*. Many of the following observations and speculations are also applicable to the Sauropterygia as a whole.

ONTOGENETIC AND INDIVIDUAL VARIATION

It was hoped at the outset of this study that a sufficient amount of new *Corosaurus* material could be collected to enable a detailed characterization of ontogenetic changes in the 'nothosaur' skeleton. While the growth patterns of the Alpine pachypleurosaurs, *Neusticosaurus*, "*Pachypleurosaurus*," and *Serpianosaurus* have been discussed by Carroll and Gaskill (1985), Rieppel (1989), Sander (1988, 1989), and by Zangerl (1935), a *Corosaurus* growth series would be particularly valuable because of its closer relationship to advanced sauropterygians. An understanding of nothosauriform ontogeny and variability could lead to a more critical evaluation of the taxonomic validity of certain characters within the group. A discussion of our current understanding of some of these characters follows in Chapter 4. Unfortunately, while many new *Corosaurus* specimens have been obtained, all those collected are of adult individuals, most represent only small portions of the entire animal or are isolated bones, and there is little correspondence between the elements represented in the sample. Even so, some variation is evident.

The type specimen of *Corosaurus alcovensis* is presumed to represent a young adult individual. The skeleton is relatively large, all bones are well formed, and the sutures are tight though not fused. The texture of the cranial bones is rough in places and the orbits are not disproportionately large. Orbital size exhibits negative allometry in the Vertebrata (Dodson 1975). Juvenile specimens might be expected to be less well ossified, have a relatively larger head to body size ratio, and perhaps have a more abbreviated rostrum. The very young individual of the pachypleurosaur *Keichousaurus* in Figure 23 illustrates this point, as do the juvenile pachypleurosaurs illustrated by Peyer (1932, plate 29; 1944, fig. 39) and the *Neusticosaurus* embryo shown in Sander (1988, fig. 1; 1989, fig. 33). However, numerous examples of *Corosaurus* are comparatively larger, and probably ontogenetically older, than the holotype. Neither does the type display any evidence of age related pathology. Thus it apparently was not fully grown (although it must be admitted that absolute size is not always an accurate indication of relative age). Of course, the attainment of osteologic and sexual maturity are rarely coincident (Johnson 1977). Therefore, no presupposition of sexual maturity or immaturity may be made for specimens of *Corosaurus* as unequivocal size independent criteria for such determinations are unknown.

The most obvious example of size (as the only available indicator of age), and

FIG. 23. Immature specimen of *Keichousaurus* in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, exhibiting juvenile body proportions. Scale in one-sixteenths of an inch (1.6 mm). Photo courtesy of N. Mateer.

probable ontogenetic, variation in *Corosaurus* is associated with the humeri of six separate individuals. These range from approximately 9 to 21 cm in length (Fig. 24). Volumetrically, the largest known humerus of *Corosaurus* (YPM 41032) is approximately 2.5 times larger than the humeri of the holotype. Progressive allometric changes occur most notably in the proximal and distal ends of each humerus in the sample and have been described above for the largest example (Chapter 3). Progressively thinner articular cartilages are assumed as described by Haines (1969) for recent reptiles, principally crocodilians and chelonians. The curvature and relative thickness of the humeral shaft remain constant throughout the sample but the ventral surface becomes increasingly "scooped." As the type individual of *Corosaurus* is estimated to have been approximately 165 cm in total length, and assuming a crude 1:1 humerus length/total length scaling ratio, the large *Corosaurus* humerus may have belonged to an animal approaching 3.8 m long. This is the size reported by Peyer (1939) for the type of *Paranothosaurus* and is in the range of some *Nothosaurus* specimens. At least in crocodilians, however, relative limb size does not remain constant throughout ontogeny but is negatively allometric (Kälin 1955), although relative propodial size increases

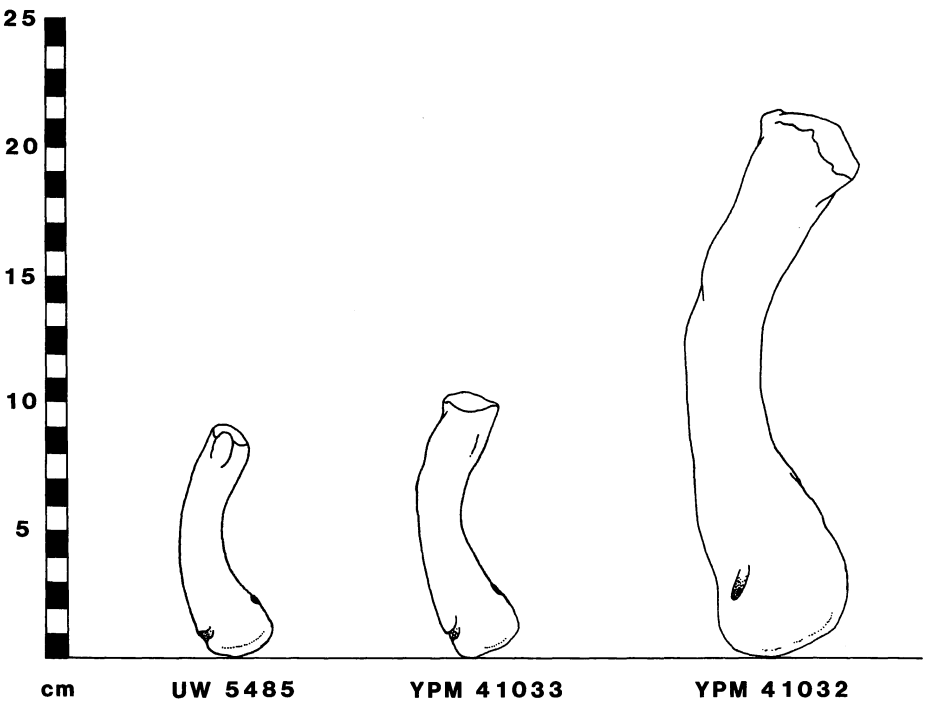

FIG. 24. Partial ontogenetic series of left humerus of *Corosaurus alcovensis,* based upon UW 5485, YPM 41032, and YPM 41033.

(Dodson 1975). Still, it is evident that individuals of *Corosaurus* occasionally grew to great size. The indeterminate, yet decelerating rate of growth of reptiles in general suggests that YPM 41032 represents a long-lived individual.

Few other elements of *Corosaurus* can be directly compared or exhibit as large a size range. Most known vertebrae and ribs from corresponding areas of the axial skeleton are of similar size. Only one isolated, partial, median gastralium (YPM 41067) is significantly larger than any other. It is approximately 1.5 cm in maximum anteroposterior breadth versus about 8 mm for average specimens.

The five relatively complete femora in the present *Corosaurus* sample are not greatly divergent in size. They range only from approximately 12.5 cm in length in YPM 41038 to approximately 15 cm in YPM 41039. Therefore, little morphologic variation is present among them. Distally, the tibial condyles are only slightly more pronounced in the larger specimen, whereas proximally the articular head is somewhat larger and joins the internal trochanter at a greater slope. If a femur specimen relatively as large as the aforementioned humerus were known, greater variation, perhaps extending these trends, might be seen.

The known girdle elements of *Corosaurus* are all from animals of approximately equal size and ontogenetic variations cannot be shown. In light of the persistent cartilage of sauropterygian limb girdles, as discussed in Chapter 2, age variation may have been considerable, at least between juvenile stages. Some slight individual variability, however, is seen in the edges of the ventral plates of the girdles, particularly in the coracoid (Fig. 12C and D).

Size may have been correlated with gender as it is in modern crocodilians where the male is generally larger than a female of equal age, environmental conditions being equal. Perhaps the position of the first haemal arch behind the cloaca (see Chapter 3) was a variable sexual trait. However, gender cannot be determined in any *Corosaurus* fossil. No pathologic variations are known in *Corosaurus.*

FUNCTIONAL MORPHOLOGY

The nearly complete skeletal reconstruction of *Corosaurus* allows consideration of the potential movement and behavior of the animal as it may have operated while alive. The perfect, matrix-free nature and large size of some of the bones is a fortuitous circumstance allowing the three-dimensional study of numerous skeletal relationships. Of particular interest are the articulation and movement of the limbs and the presumed manner of *Corosaurus* locomotion. The swimming behavior of sauropterygians has been a matter of conjecture for some time. Plesiosaurs, for example, with a locomotor construction radically different from that of most vertebrates, have been claimed both as "rowers" utilizing fore-aft paddle strokes (Newman and Tarlo 1967; Tarlo 1957, 1959a; Watson 1924, 1951) and "underwater flyers" with vertical "wing" movement (Frey and Riess 1982; Robinson 1975, 1977; Tarsitano and Riess 1982; Taylor 1981). "Flying" is characteristic of modern penguins (Clark and Bemis 1979) and sea turtles (Walker 1971, 1974; Zangerl 1953). "Rowing" is seen in seals (phocids) and sirenians (Webb and Blake 1985). It now seems probable that the power stroke of plesiosaurs combined elements of the two styles, with both a vertical and a fore-and-aft (drag-based) component, more in the manner of present-day sea lions (otariids). Here the recovery stroke is primarily horizontal yet also provides thrust through lift because of the hydrofoil action of the limb (English 1976; Godfrey 1984).

Although the morphology of *Corosaurus,* and of 'nothosaurs' in general, is far less removed from that of their terrestrial ancestors than is that of plesiosaurs, it may shed light on the functional evolution of the latter. *Corosaurus* is apparently not ancestral to plesiosaurs (see Chapter 4) but its derived appendicular skeleton may be partially analogous to that of the structural predecessor of plesiosaurs, thus perhaps indicative of the particular functional constraints and precursors which led to the successful invasion of a new functional niche. Carroll and Gaskill (1985) have discussed the question of possible functional relationships between 'nothosaurs' and plesiosaurs, particularly as they relate to pachypleurosaurs. At the very least, consideration of the functional morphology of *Corosaurus* will emphasize the differences in locomotion which obviously existed between the various sauropterygian types. Just as plesiosaurs maintained a single locomotor morphology and style throughout their known history (Robinson 1975), the plesiomorphic 'nothosaur' pattern, appears to have remained relatively constant for nonplesiosaurian sauropterygians (the placodonts are excluded from the present discussion).

Corosaurus was certainly an aquatic reptile as evidenced by its occurrence in the Alcova Limestone. Beyond this, its orbits and external nares are dorsal in position, the orbits are large, and the nares retracted. These are all adaptations common in secondary swimmers. The limbs, especially the forelimbs, are greatly modified from those of terrestrial vertebrates, as are the limb girdles, and there is a large percentage of persistent cartilage in the appendicular skeleton. Peyer (1934) and Zangerl (1935) list similar suites of aquatic adaptations observed in *Lariosaurus* and pachypleurosaurs. What is the functional role of these adaptations and can they be related to the adaptations of plesiosaurs?

Aquatic Locomotion

As with plesiosaurs, little agreement has been reached concerning the swimming style of the various forms of 'nothosaur.' Carroll and Gaskill (1985) have proposed

an axial propulsion mechanism: that they swam without the use of their limbs by lateral undulations of the tail. Sues (1987) and Sues and Carroll (1985) have accepted this interpretation. Kuhn-Schnyder (1987) gives credit to the forelimbs and tail for aqueous locomotion in *Lariosaurus*. Sanz (1976, 1980) and Schmidt (1984, 1986) have sided in favor of paraxial, limb-dominated propulsion ("subaqueous flight" and "rowing," respectively) as has Storrs (1988a). It seems very likely that the tails of 'nothosaurs' were at times employed in swimming, especially in the forms with the longest tails such as the pachypleurosaurs. Long, powerful tails are characteristic of secondarily aquatic undulatory swimmers. The tail functionally extends and amplifies the undulations of the body. Crocodilians, for example, are noted for propulsive lateral undulations of the tail (Manter 1940). A strongly developed epaxial and hypaxial proximal caudal musculature is attested to in both pachypleurosaurs and plesiomorphic nothosauriforms by the broad shelf of their anterior caudal ribs and by the relatively tall proximal caudal neural spines. Medially and distally, the tails of *Corosaurus* and similar forms are deeper than broad by virtue of the neural arch and chevron configurations. This may be considered a sculling adaptation, but is plesiomorphic and often the case with terrestrial reptiles as well. The tail of *Corosaurus* is not exceptionally long, deep, or bilaterally compressed relative to those of reptiles in general.

Another suggestive structural feature of *Corosaurus* is its stiffened trunk. The vertebral column craniad of the tail tends to be relatively stiff in caudal propulsors (Hildebrand 1974). The amphicoelous/platycoelous centra, zygosphene/zygantrum articulations, broad neural arches, and closely spaced, rectangular neural spines of *Corosaurus* may all have served to limit flexibility between the precaudal vertebrae. This was probably also true of the densely packed gastralia of the ventral basket. However, because of such traits, the 'nothosaur' trunk was perhaps stiffer to a degree greater than in typical undulatory swimmers. The base of the tail in caudal propulsors must also be flexible when used for locomotion. The long proximal caudal ribs of 'nothosaurs' may have actually reduced flexibility here as well.

On the other hand, the limbs of both pachypleurosaurs and traditional 'nothosaurids' must have played a major role in aquatic locomotion. The specializations exhibited by the limbs do not involve general reduction of hydrostatic drag as would be expected in animals using primarily their tails for thrust. Neither are they adapted for efficient terrestrial locomotion. Moreover, the specializations observed, especially in the forelimbs, act to increase the functional surfaces (whether drag- or lift-based) of the limbs as is typical of paraxial swimmers. The humeri of 'nothosaurs' are always distally expanded and flattened. Ventrally, they are flat or even "scooped." The epipodials are universally shortened as well as expanded and flattened, and wide spatia interossea are present. The ulnae are particularly broad, especially in *Keichousaurus* (see Chapter 4). The manus and pes are always broad and flat, as in *Keichousaurus* (Young 1958) and *Lariosaurus* (see Boulenger 1896; Peyer 1933, 1934; Sanz 1976), or even, as in *Ceresiosaurus*, display slight hyperphalangy (see Kuhn-Schnyder 1964; Peyer 1931, 1944). Finally, the cartilaginous nature of all 'nothosaur' limb joints indicates limited intralimb flexibility.

Hypothetical Myology

What was the specific locomotor pattern of 'nothosaur' limbs? The limits of movement and the character of the associated musculature must first be determined. As in plesiosaurs, the appendicular girdles of pachypleurosaurs and 'nothosaurids' are largely platelike, with little elaboration outside the horizontal

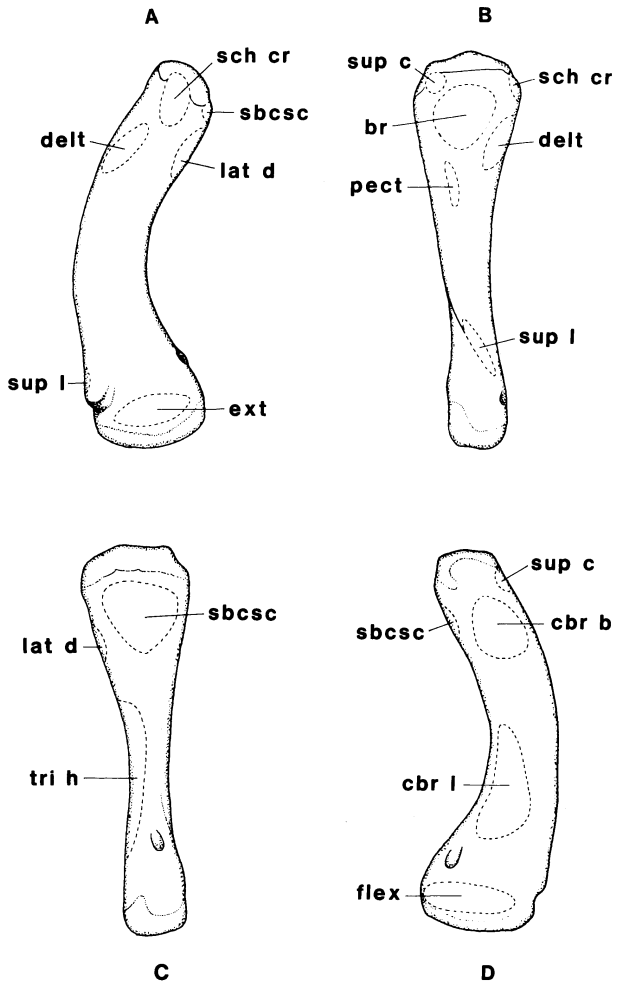

FIG. 25. Left humerus of *Corosaurus,* based primarily upon UW 5485 and YPM 41033, with inferred points of muscle attachment. A, dorsal (extensor) aspect; B, anterior aspect; C, posterior aspect; D, ventral (flexor) aspect. br = M. brachialis; cbr b = M. coracobrachialis brevis; cbr l = M. coracobrachialis longus; delt = M. deltoideus (undivided); ext = extensors; flex = flexors; lat d = M. latissimus dorsi; pect = M. pectoralis; sbcsc = M. subcoracoscapularis; sch cr = M. scapulohumeralis cranialis; sup c = M. supracoracoideus; sup l = M. supinator longus; tri h = M. triceps humeralis.

plane. The scapulae and ilia are the smallest components of their respective assemblies and the only elements with a significant vertical orientation. The ventral plates and stout median symphyses obviously acted to brace the body cavity against transverse compressive forces generated by the limbs, particularly in the pectrum in those forms with tightly sutured scapuloclavicular assemblies, as discussed by Watson (1924). They were also apparently the points of origin of major locomotor muscles, the positions of which can be crudely estimated.

Watson (1924) discussed the possible disposition and function of the pectoral musculature of 'nothosaurs' based primarily upon the pectrum of *Nothosaurus* and a humerus of "?*Conchiosaurus*" (BMNH R. 1409) (probably also *Nothosaurus*). The muscle insertion scars of the humerus as interpreted by Watson (1924) were duly figured. Other interpretations of 'nothosaur' humeral musculature position can be seen in studies by F. von Huene (1944, 1956) and Mazin (1985) [and Sues (1987) for *Pistosaurus*]. As noted in Chapter 2, the known humeri of *Corosaurus,* complete with muscle scars, also allow a hypothetical, yet reasonable,

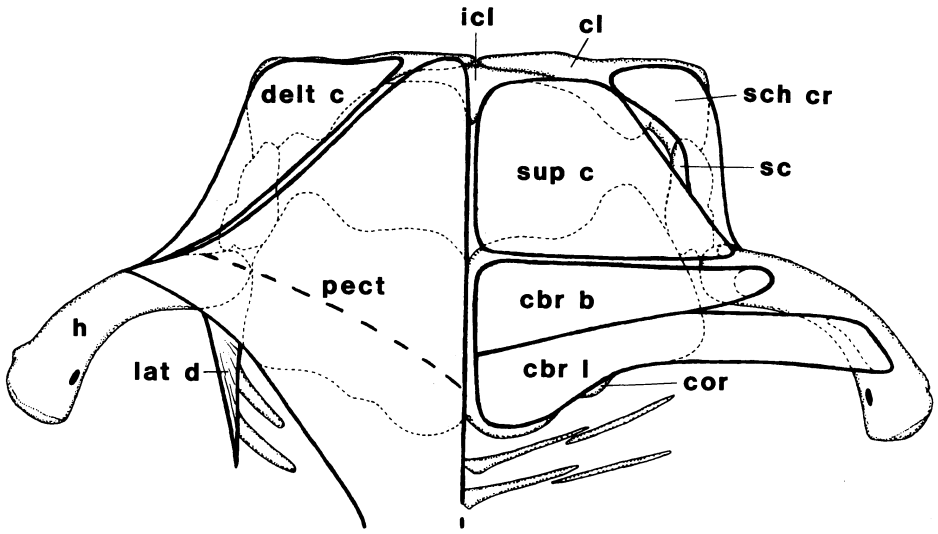

FIG. 26. Reconstructed pectrum and humeri of *Corosaurus* with hypothetical musculature (ventral aspect). Right half of figure, deep musculature; left half, superficial musculature. cbr b = M. coracobrachialis brevis; cbr l = M. coracobrachialis longus; cl = clavicle; cor = coracoid; delt c = M. deltoideus clavicularis; h = humerus; icl = interclavicle; lat d = M. latissimus dorsi; pect = M. pectoralis; sc = scapula; sch cr = M. scapulohumeralis cranialis; sup c = M. supracoracoideus.

reconstruction of pectoral muscle insertions (Fig. 25). The positions of presumably homologous muscles are drawn from comparison with modern reptiles and birds (e.g., Howell 1936; Jenkins and Goslow 1983; Romer 1944; Romer and Parsons 1977; Schreiweis 1982). Muscle relationships are relatively standardized in these groups. Nomenclature is largely that of Romer (1922, 1944).

For the most part, the present humeral reconstruction differs little from that of Watson (1924). However, the M. latissimus dorsi seems to have been positioned far more dorsally in *Corosaurus*; more as shown by Watson (1924) for *Plesiosaurus dolichodeirus*. The M. scapulohumeralis cranialis of *Corosaurus* also lies in a position similar to that of *P. dolichodeirus*. The large scar assumed by Watson (1924) to represent the insertion of this muscle in "?*Conchiosaurus*" probably marks the site of origin of the M. brachialis. The insertion of the M. coracobrachialis brevis appears to be located somewhat more proximally in *Corosaurus* than in "?*Conchiosaurus*." No obvious scar exists for the M. coracobrachialis longus in *Corosaurus*, but this is presumed to have inserted along the mediodistal ventral face of the humerus. Watson (1924) has shown the M. coracobrachialis longus to have been present in "?*Conchiosaurus*" and a distinct scar for this muscle occupies a similar position in *Lariosaurus* (Mazin 1985). The insertions of the M. pectoralis and M. deltoideus are located far more distally in *Lariosaurus* than in *Corosaurus*.

Watson (1924), Tarlo (1957), and Robinson (1975) have further presented hypothetical reconstructions of plesiosaur pectoral musculature with respect to its origins on the shoulder girdle. Based upon the above humeral insertion reconstruction, the form of its girdle elements, and the comparative myology of homologous structures in modern reptiles, a similar reconstruction is here attempted for the pectrum of *Corosaurus* (Figs. 26 and 27). A large M. coracobrachialis, presumably with short and long branches inserting on the ventral face of the humerus, obviously arose deeply from the ventral surface of the coracoid. The expanded nature of this bone relative to that of other known 'nothosaurs' provided space for a possibly larger muscle. The anterior portion of the coracoid

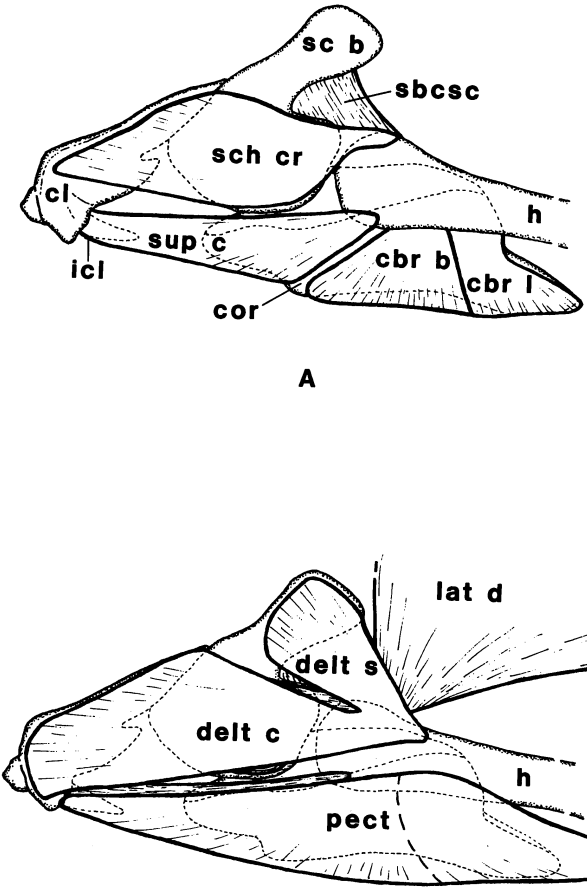

FIG. 27. Reconstructed pectrum and humerus of *Corosaurus* with hypothetical musculature (lateral aspect, anterior to left). Compare with Fig. 14 A. A, deep musculature; B, superficial musculature. cbr b = M. coracobrachialis brevis; cbr l = M. coracobrachialis longus; cl = clavicle; delt c = M. deltoideus clavicularis; delt s = M. deltoideus scapularis; h = humerus; icl = interclavicle; lat d = M. latissimus dorsi; pect = M. pectoralis; sbcsc = M. subcoracoscapularis; sc b = scapular blade; sch cr = M. scapulohumeralis cranialis; sup c = M. supracoracoideus.

was no doubt also the site of origin of part of the M. supracoracoideus. Inserting on the anteroproximal end of the humerus, this muscle also spread over the ventral surface of the scapula and probably the posterior margins of the ventral sides of the clavicle and interclavicle. Depending on the amount of cartilaginous and ligamentary support present, the M. supracoracoideus may have covered much or all of the pectoral fenestra. A prominent M. scapulohumeralis cranialis inserted on the dorsoproximal end of the humerus. Its origin apparently lay along the lower lateral half of the scapula, which is noticeably dished for its reception, and probably reached across part of the ventral surface of the clavicular shelf. The size of this muscle may be reflected in the sharpness of the anterolateral corner of the clavicle. The medial face of the scapula of *Corosaurus*, except for the anterior part of its dorsal blade, is also cupped, presumably as the origin for the last major deep pectoral muscle, the M. subcoracoscapularis. Its insertion was on the posterior proximal end of the humerus. Part of the anterolateral edge of the visceral surface of the coracoid of *Corosaurus* probably also contributed to the origin of

the M. subcoracoscapularis. Whether or not this muscle was subdivided into two distinct rami (i.e., M. subscapularis and M. subcoracoideus) cannot be determined.

The M. deltoideus and the M. pectoralis of *Corosaurus* presumably lay superficial to the deep ventral muscle masses of the pectrum. The M. deltoideus certainly formed two separate branches, the M. deltoideus scapularis and the M. deltoideus clavicularis. The first probably spread from the pronounced deltoid scar of the humerus to the spoon-shaped lateral side of the scapular blade. The second, from the scar to the lateral and anterior edges of the clavicle. The M. pectoralis scar on the humerus is weak; so this muscle may not have been strong. It originates on much or all of the ventral surface of the pectrum in modern reptiles and this configuration was tentatively adopted for plesiosaurs by Robinson (1975, 1977). Watson (1924), however, limited the M. pectoralis origin to the posteriormost section of the coracoid and extended it onto the anterior gastralia, suggestions followed by Tarlo (1957). Neither of these positions can be directly confirmed in *Corosaurus*. Two alternatives are presented in Figures 26 and 27. Finally, the M. latissimus dorsi of *Corosaurus* evidently led from the proximodorsal end of the humerus to the anterior thoracic ribs.

While the above reconstruction remains hypothetical, it suggests that the major part of forelimb movement in *Corosaurus,* and probably in most 'nothosaurs,' occurred in the horizontal plane. Apart from the seeming predominance of pectoral muscles occupying this plane and the force vectors they would have generated within it, the configuration of the glenoid and proximal head of the humerus of *Corosaurus* obviously favored horizontal movement. The glenoid articulation suggests possible adduction of the limb in the horizontal plane through an arc of perhaps 80°, from approximately 80° to 160° with respect to the longitudinal axis of the body (0° craniad). The strongly ovoid articular head of the humerus was vertically oriented and probably prevented vertical movement through an arc greater than 40° (approximately 20° of movement possible both above and below the horizontal). However, the proximal cartilaginous cap may have affected this figure to a certain extent. The articular configuration also indicates that the forelimb of *Corosaurus* could not be held in the rotated position suggested for "*Pachypleurosaurus*" by Carroll and Gaskill (1985) in their reconstruction of that animal. Additionally, propulsion through a primarily up-and-down limb stroke does not appear to have been possible because of the lack of significant skeletal support between the vertebral column and vertical elements of the pectrum (scapulae) as discussed by Godfrey (1984) for plesiosaurs.

It is suggested that, in *Corosaurus* at least, forelimb "rowing" was possible whereby the horizontally held limb, beginning essentially perpendicular to the body, was adducted backward against the body together with a small downward component. This power stroke was accompanied by partial downward rotation of the anterior edge of the limb, especially along its distal half, thus providing a blade surface by which drag-based thrust could be created. Because the limb was not completely (perpendicularly) rotated, lift was also generated in the manner of a hydrofoil or "wing." Rotational feathering occurred at the end of the power stroke so that the limb was abducted in a horizontal attitude, perhaps still providing lift. Both forelimbs probably acted simultaneously because of the stiffened nature of the thorax. This model is analogous to that suggested for plesiosaurs by Godfrey (1984) but because of their structural differences was probably less efficiently applied by 'nothosaurs.' It also approaches that of Tarlo (1957) (for pliosaurs). The greater structural and mechanical efficiency of plesiosaur subaqueous propulsion was probably a result of their likely abandonment of terrestrial locomotion, possibly rudimentarily retained in 'nothosaurs.' Godfrey (1984) has shown that

the model of Watson (1924) overemphasizes the importance of a horizontal power stroke in sauropterygian swimming and ignores the possibility of a vertical element, just as that of Robinson (1975) exaggerates the role of vertical limb motion while suggesting that "rowing" is inefficient. The relationships of drag as a function of surface area, and momentum of mass, as discussed by Godfrey (1984) apply as equally to pachypleurosaurs and 'nothosaurids' as to plesiosaurs and otariids. Thrust that is produced in periodic pulses as this model suggests is therefore also presumed to be not inefficient in at least the large 'nothosaurian' nothosauriforms.

The muscle assumed to have been primarily responsible for limb adduction in *Corosaurus* and other sauropterygians is the M. coracobrachialis. Its apparently large origin on the posterior expansion of the coracoid, and its relatively distal insertions on the humerus evidently produced a high degree of leverage and a powerful backwards stroke. Resultant stress vectors were directed predominantly towards the coracoid strut. More precise resolutions of forces cannot be calculated from a hypothetical muscle reconstruction. Also likely contributing to adduction were the M. pectoralis, M. subcoracoscapularis, and M. latissimus dorsi, although Sanz (1980) appears to have overstated the importance of the latter. The M. pectoralis also provided the downward movement, or depression, of the humerus as well as the downward rotation of its leading edge. Abduction was accomplished through the M. supracoracoideus, the M. scapulohumeralis cranialis, and the M. deltoideus. The M. deltoideus scapularis appears to have been primarily responsible for the elevation and feathering of the humerus. The muscles presumably originating on the humerus and inserting on the antebrachium, rather than facilitating intralimb flexion and extension, may have helped to stiffen the forelimb and adjust the trim of the "wing" as suggested by Robinson (1975) for plesiosaurs. These muscles include the M. brachialis, M. triceps humeralis, M. supinator longus, and the flexor and extensor groups.

The hindlimbs of *Corosaurus* are far less specialized for aquatic locomotion than are the forelimbs. Indeed, in the plesiomorphic 'nothosaurs' in general, flexure of the femoral/epipodial joint is indicated in many articulated skeletons, whereas the forelimb is always essentially straight. The plesiosaur analogy in which both sets of limbs and their girdles are virtually identical, and thus assumed to have operated in a similar manner, does not strictly apply. As in the forelimb, however, the distal elements of the hindlimb (epipodials, metatarsals, and pes) are somewhat flattened and expanded. The large ventral plates of the pelvis anchored powerful musculature operating primarily in the horizontal plane. Did these muscles produce a "rowing" action of the hindlimbs similar to that of the forelimbs? The rather featureless femora of *Corosaurus* (all of young adults) display few muscle scars, making a reconstruction of muscle origins and insertions extremely difficult. Only the positions of the M. puboischiofemorales internus and externus are well known, although examination of living reptiles suggests the approximate positions of several other muscles. The hypothetical positions of these major thigh muscles are indicated in Figure 28. Terminology is that of Romer (1923).

Because the femoral muscle positions are so poorly known, and because of the complexity and variability of reptilian pelvic muscles, a complete reconstruction of the pelvic musculature of *Corosaurus* has not been attempted. However, certain of its features are known. As the internal trochanter of the femur is quite pronounced and the intertrochanteric fossa very large, it is obvious that a powerful M. puboischiofemoralis externus inserted at these points. Its origin would have covered a large part of the broad ventral surfaces of the pubis and ischium. A

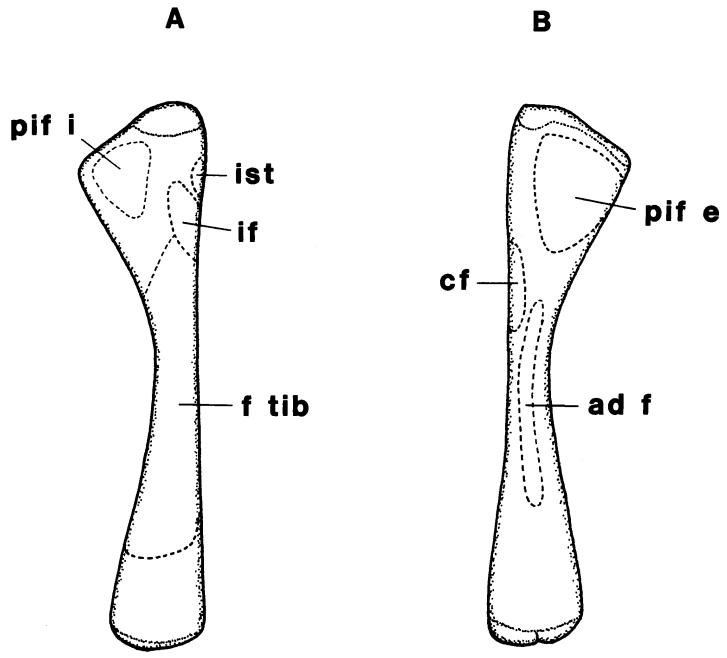

FIG. 28. Right femur of *Corosaurus*, based primarily upon YPM 41038 and YPM 41039, with inferred points of muscle attachment. A, dorsal (extensor) aspect; B, ventral (flexor) aspect. ad f = M. adductor femoris; cf = M. caudofemoralis; f tib = M. femorotibialis; if = M. iliofemoralis; ist = M. ischiotrochantericus; pif e = M. puboischiofemoralis externus; pif i = M. puboischiofemoralis internus.

shallow, slightly rugose, depression on the anterodorsal surface of the internal trochanter probably marks the insertion of a somewhat smaller M. puboischiofemoralis internus, originating from the internal sides of the ventral girdle plates. The expanded anterior edge of the pubis of *Corosaurus* relative to those of other 'nothosaurs' may indicate increased leverage for larger M. puboischiofemorales. Although no fourth trochanter is present, the long ribs of the proximal caudal vertebrae indicate the presence of a large and powerful M. caudofemoralis, which probably inserted on the proximal posteroventral surface of the femoral shaft. It is likely that the M. adductor femoris, originating on the ventral face of the ischium, also inserted along much of this surface of the shaft.

The wide inner face of the ischium of *Corosaurus* may have accommodated a well developed M. ischiotrochantericus. This muscle primitively inserts on the dorsoposterior surface of the femoral head in reptiles. The remnant blade of the ilium suggests retention of workable extensors of the thigh and lower leg, such as the M. iliofemoralis and M. quadriceps femoris of typical reptiles. The M. iliofemoralis usually inserts near the M. ischiotrochantericus. Only one branch of the complex M. quadriceps femoris contacts the femur, the M. femorotibialis, which typically has a fleshy origin along much of the dorsal and lateral surfaces of the femur.

It seems clear that powerful fore and aft strokes of the hindlimb of *Corosaurus* were possible as in the forelimb. The M. adductor femoris, M. ischiotrochantericus, and particularly the M. caudofemoralis provided adduction and presumably rotation; the large M. puboischiofemorales abduction and feathering of the limb. However, because of the bowllike nature of the acetabulum and the rather convex head of the femur, a large amount of rotation and polydirectional limb movement is postulated. This, together with the inferred presence of functioning dorsal

muscles on the limb, indicate that the hindlimb was probably not as restricted in its movements as was apparently the forelimb. These differences may have resulted from a greater role for the hindlimb in either rudimentary terrestrial locomotion or subaqueous directional control. It seems likely that steering was largely controlled by the attitude of the hindlimbs as in *Alligator* (Manter 1940).

Discussion

To summarize, the major propulsive force for aquatic locomotion in *Corosaurus,* and probably in most primitive nothosauriforms, was apparently paraxial "rowing." The drag-based thrust of limb adduction was quite likely augmented to some extent by hydrostatic lift as the limbs were concurrently depressed, and perhaps also by the hydrofoil action of their feathered return stroke, much as in otariid sea lions. All four limbs may have operated simultaneously with each stroke followed by a short gliding phase. Plesiosaurs are believed by Godfrey (1984) to have swum in a similar manner. On the other hand, the 'nothosaur' hindlimb may have been particularly important in steering. The still long tail of many 'nothosaurs' may have acted as a counterbalancing rudder, and possibly as an accessory thrust producing organ, initiating quick starts and rapid changes of direction, for example. Increased neck length and flexibility, disadvantageous in undulatory swimmers, were made possible. With reduction of the tail and continued elaboration of the limbs, 'nothosaur'-like animals would have made ideal functional precursors of plesiosaurs in which there was apparently no undulatory propulsion. Such a change probably coincided with complete abandonment of the land or paralic environments or both.

It remains to consider why elongate, secondarily aquatic reptiles should have developed a limb dominated style of subaqueous locomotion rather than an undulatory style such as seen in lizards and crocodilians. The basic ingredients for undulatory swimming are already in place in the undulatory walking format of plesiomorphic "sprawlers." A sprawling stance was undoubtedly present in the terrestrial forebears of the Sauropterygia. Several possibilities come to mind, each perhaps a contributing factor. Initially, undulatory swimming was probably obligatory for the immediate ancestors of the Sauropterygia. Limb reduction and developmental restructuring of the girdles as discussed by Carroll and Gaskill (1985), particularly with regard to pachypleurosaurs, may have followed. They have suggested a need for occasional terrestrial forays as a cause for limb reelaboration, although an amphibious capability is far from certain. If, however, a bottom dwelling or feeding mode of life was adopted by these animals, increased limb propulsion may have been advantageous in moving the body along, and/or pushing it off from, the substrate. Perhaps this form of behavior would have "preadapted" [exapted of Gould and Vrba (1982)] the limbs for aquatic propulsion.

More interestingly, the requirement of neutral buoyancy in habitually aquatic animals may have played an important part in the transition to paraxial swimming. Organisms that can maintain a static position in the water column without expenditure of energy are at a decided advantange over those which cannot. The tetrapod lung imparts secondarily aquatic vertebrates with a natural positive buoyancy that tends to float these animals to the surface unless counteracted. Darby and Ojakangas (1980) have shown that crocodiles voluntarily ingest stones as a probable hydrostatic compensation mechanism perhaps as, by analogy, did plesiosaurs. The pachyostotic nature of sirenian ribs is a well known buoyancy compensator. While no 'nothosaur' has been discovered with gastroliths, their ribs and gastralia are dense and often "pachyostotic." Their limb girdles too are constructed of dense, heavy bone. It may be assumed that the development of a

thick ventral basket of closely-packed gastralia in 'nothosaurs' was a hydrostatic adaptation to their aquatic existence as suggested by Nopsca (1923a). This basket is far denser and more solid than that of crocodilians. As suggested above, the numerous gastralia of 'nothosaurs' probably severely limited the undulatory capability of the trunk. In fact, in every known specimen of articulated pachypleurosaur or nothosauriform skeleton in which the ventral basket is intact, little flexion is exhibited by the largely straight abdomen. With flexibility reduced by such buoyancy compensation, paraxial propulsion would have added importance; would be developed, perhaps, by necessity. Sanz (1980) has suggested the presence of a ventral keel developed from the gastralia for aid in swimming, but this seems unlikely.

Terrestrial Locomotion

A few words may be said about the ability of *Corosaurus* to navigate on land. 'Nothosaurs' are often assumed to have been amphibious (e.g., Colbert 1955, 1969; Romer 1933, 1945, 1966). Case (1936) pictured *Corosaurus* as emerging from the water to bask and lay eggs. Peyer (1931) did the same for *Ceresiosaurus*. While a habitually aquatic existence for all 'nothosaurs' is obvious, they are perhaps not specialized to the point of having lost their ability to come ashore. In *Corosaurus,* the feet do not seem to have been greatly hyperphalangic, if at all. However, sharp terminal claws, useful on land, are unknown in any sauropterygian. While reduced intralimb flexibility existed, especially in the forelimbs, some small movement was probably possible. The femur of *Corosaurus* retains obvious tibial condyles and the hindlimb was probably flexible to a relatively large degree. The strong caudofemoral musculature might have propelled the animal forward on land while the pelvis was elevated by the dorsal extensors of the ilium and femur. The stout sacral ribs and remnant iliac blade indicate a strong sacroiliac articulation that may have supported the posterior half of the body against the downward-acting force of gravity. The scapular blade was not as strongly supported but was securely anchored by soft tissues.

Schmidt (1984) has stated that the presence of elongate anterior dorsal neural spines in upper Muschelkalk specimens of *Nothosaurus* is evidence for terrestrial locomotion in this genus. Exposure to terrestrial gravity conditions might have necessitated such supporting structures for the head and neck. However, other explanations might exist, such as need for supporting, and facilitating rapid movement of, the neck when hunting. *Corosaurus* has uniformly short neural spines but may not have required as well developed a nuchal ligature because of its smaller head. Large amounts of leverage and increased structural support would have been even less necessary in the smaller pachypleurosaurs.

If 'nothosaurs' maneuvered on land, their limited limb and thoracic flexibility would have mandated an awkward progression. The sinuous body and alternate limb movements of sprawlers probably were not possible. Carroll and Gaskill (1985) have suggested a crawling or dragging posture based upon symmetrical movements of the forelimbs. The forelimbs of some 'nothosaurs,' such as *Neusticosaurus,* are often stronger than the hindlimbs. The forelimbs of *Ceresiosaurus* are especially robust. The relatively long hindlimbs of *Corosaurus,* however, may have pushed the body forwards, whether the forelimbs pulled or not. Here too, the elaborate ventral armor might have been useful, along with the expanded ventral girdle plates, in protecting the underbelly as proposed by Carroll and Gaskill (1985), although no analogous armor is present in pinnipeds. In any

event, if either pachypleurosaurs or 'nothosaurids' were amphibious, they were far less at home on land than in the water, and terrestrial forays, if at all possible, were probably quite rare.

Two isolated footprints have been interpreted as those of 'nothosaurs' and as providing direct evidence of terrestrial locomotion. The first is the ichnogenus *Pontopus* Nopsca, 1923b. This is the impression of an apparently webbed foot from the Upper Triassic of Cheshire, England, but was probably made by a terrestrial lacertiloid (see Appendix B). Secondly, F. von Huene (1935) described as of possible sauropterygian origin a small unwebbed print (*Nothosauripus* Kuhn, 1958a) from the pachypleurosaur-rich Ladinian shales of Besano, Italy. However, this print can not be directly linked with a known sauropterygian genus, and extensive quarrying by Peyer in the 'nothosaur'-rich shales of Tessin failed to produce a single track (Zangerl, personal communication, 1986). The ichnological evidence is thus inconclusive. K. Thiessen (Arizona) reports (personal communication, 1989) possible "swim-tracks" of an undescribed pachypleurosaur-like animal (younginiform?) from the Wupatki Member of the Moenkopi Formation of Arizona (see Chapter 7 for additional information on this occurrence). These are interesting, but rather nebulous "scratch" marks on bedding plane surfaces and do not bear directly on the question of 'nothosaur' terrestrial locomotion. No tracks of *Corosaurus* are known.

The question of webbing in 'nothosaur' feet is also problematic. It may have been present in some forms while lacking in others. Peyer (1931, 1934) reconstructed *Ceresiosaurus* and *Lariosaurus* with webbed feet (actually paddlelike forelimbs in *Lariosaurus*), and Case (1936) followed suit with *Corosaurus*. Webbing would certainly have aided aquatic propulsion but would probably not have hindered movement ashore if 'nothosaurs' had this capability.

PALEOECOLOGY

It is assumed (Chapter 6) that *Corosaurus* was an indigenous element of the Alcova Limestone fauna. As such, the structure of *Corosaurus* and the paleoenvironment of the Alcova (see also Chapter 6) clearly indicate that this animal was a shallow water, largely nearshore marine form. While perhaps spending time basking along the shores of the Alcova "sea" in crocodile or seal fashion, most of its activity no doubt occurred subaqueously where it assumed a predaceous role. The apparent top carnivore of its ecosystem, as evidenced by its large size (perhaps partly due to a freedom from predators) and the absence of associated carnivores, *Corosaurus* is thought to have been primarily, if not exclusively, piscivorous. The long, sharp, recurved, conical teeth, particularly the large caniniforms of the anterior dentary, were especially well suited to piercing and gripping struggling prey. The stout retroarticular and coronoid processes of the mandible indicate high leverage of the depressor and levator musculature, respectively. These are coupled with the large supratemporal fenestrae, possibly accommodating strong adductors, so that a powerful bite is postulated. The strong dentaries were well braced by their relatively stout symphysis against the force of such a bite.

All 'nothosaurs' display an elongate neck that may have made possible sweeping arcs of the head and jaws through which passing fish were intercepted. The longirostrine, anisodont format of certain nothosauriforms, considered ichthyo- and herpetophagous by Sanz (1980), would have increased their ability to seize and hold other vertebrates. Kuhn-Schnyder (1964) has documented the association of the large nothosauriform *Ceresiosaurus* with seven individuals of the much

smaller pachypleurosaur "*Pachypleurosaurus*" (= *Neusticosaurus*). Both he, Peyer (1932), and Sander (1989) also noted the bones of *Neusticosaurus* in coprolites presumed to belong to *Ceresiosaurus*. Remains of the palaeoniscoid fish *Gyrolepis* have been found in a "*Nothosaurus*" coprolite in the German Muschelkalk (Trusheim 1937), while small, juvenile tooth plates of the placodont *Cyamodus* have been found in the body cavity of a *Lariosaurus* specimen from Monte San Giorgio (Kuhn-Schnyder 1987; Tschanz 1989).

In the case of *Corosaurus,* however, in spite of its carnivorous adaptations, fish or other potential vertebrate prey have not yet been discovered in the Alcova. Nor have coprolites of *Corosaurus* been found that might illuminate its diet. Some pelecypods and gastropods were available but *Corosaurus* lacks obvious molluscivorous adaptations, such as a crushing dentition. Sanz (1980) has suggested that *Simosaurus,* with its short rostrum and spatulate teeth, possibly ate cephalopods but this is unsubstantiated. Mateer (1977) has also proposed that "*Pachypleurosaurus*" supplemented its diet with cephalopods. However, cephalopods are not known from the Alcova. I believe it still likely that *Corosaurus* ate fish but, perhaps due to environmental conditions (Chapter 6), their remains and the fecal pellets of *Corosaurus* have not been preserved.

Corosaurus may have lingered underwater, possibly on the shallow bottom, preferring to wait for fish rather than actively pursuing them. The plesiomorphic 'nothosaurs' in general are from shallow paralic environments, whereas plesiosaurs, which may have been faster swimmers and chased their food, were open water forms. Sues (1987) has assumed that the earliest known plesiosaur, *Pistosaurus,* was ecologically isolated from contemporaneous littoral 'nothosaurs' by inhabiting offshore waters, thus accounting for its rare occurrence. He further considers the pachypleurosaurs to have inhabited lagoonal and shallow marine environments and the 'nothosaurids' only shallow marine ones. Nevertheless, the great size of some nothosauriforms, particularly *Nothosaurus,* rivaled that of Early Jurassic plesiosaurs and may have allowed them to parallel the plesiosaur niche in some cases.

The habits of the young of *Corosaurus* are unknown. Tarlo (1967) suggests that juvenile 'nothosaurs' spent more time ashore than did their parents, although numerous immature pachypleurosaurs have been found in association with adults in subtidal marine environments. Tarlo (1967) also believes that the young may have been littoral scavengers, feeding upon the fish remains with which they have sometimes been found (Tarlo 1959c). It's possible, however, that young 'nothosaurs' fed upon insects and other invertebrates as do juvenile crocodilians today (Sanz 1980).

'Nothosaur' reproductive function is equally speculative. Robinson (1977) presumed ovoviviparity in plesiosaurs, but there is no direct evidence either way to suggest that either pachypleurosaurs or 'nothosaurids' bore live young or laid eggs. The "immature individuals" of Tarlo (1967) represent a separate genus from their supposed "mother"; as noted above, these seem to be the prey of *Ceresiosaurus* (Kuhn-Schnyder 1964). Elsewhere, as in China (Fig. 23) and the Alps, very young animals (pachypleurosaurs) are known which may be considered either hatchlings or newborns. Recently, Sander (1988) has described a likely embryonic *Neusticosaurus* specimen from Monte San Giorgio. However, for reasons which he discusses, it remains unclear whether this represents an egg without its shell preserved or is an aborted fetus. No gravid 'nothosaur' female has ever been found and all presently known evidence is ambiguous. The question of egg-laying capability in primitive sauropterygians is in part connected to the still open question of their amphibious ability.

4. PHYLOGENY AND TAXONOMY

INTRODUCTION

Since the description of *Corosaurus* in 1936 (Case), there has been little success in classifying this animal, and much disagreement among the numerous schemes suggested. The primary factors responsible for these problems have been the inadequate knowledge of the anatomy of *Corosaurus* and the lack of a sufficient understanding of sauropterygian relationships. The latter problem is itself a result of inadequate or misinterpreted fossil material and descriptions, of convoluted and unclear synonymies, and of poorly applied evolutionary and hence, phylogenetic, taxonomic, and systematic, theory. These broader difficulties have been addressed to a certain degree in a number of recent works (Carroll 1981; Carroll and Gaskill 1985; Rieppel 1989; Schmidt 1987; Sues 1987; Taylor 1989) and will be further discussed here.

Following Peyer's (1934) classification, Case (1936) was unable to place *Corosaurus* in a more specific category than Nothosauria. The classification as constructed was unable to accommodate the apparently conflicting characters of *Corosaurus* and Case (1936) believed that this placed the genus in a position possibly intermediate between Peyer's (1934) two accepted families, Pachypleurosauridae and Nothosauridae. In 1948a, F. von Huene concluded that *Corosaurus* was closely related to *Simosaurus,* largely on the basis of proportional similarities in their skulls (e.g., their roughly triangular shapes and short snouts). On these rather shaky grounds, he united them in the family Simosauridae and further considered the two genera, largely by virtue of the postcrania of *Corosaurus,* to be primitive plesiosaurs (F. von Huene 1948a, b, c). Maintaining the view that *Corosaurus* was a primitive plesiosaur, he later (von Huene 1952, 1956) assigned it to the family Pistosauridae which he placed in the Plesiosauria, while shifting *Simosaurus* back amongst the 'nothosaurs'. E. von Huene, however, had in 1949 judged *Corosaurus* to be a primitive 'nothosaur.'

Romer originally (1945) classified *Corosaurus* as a 'nothosaurid' but in 1956 (and questionably in 1966), followed F. von Huene's lead, calling the animal a 'simosaurid,' although placing the Simosauridae in the Nothosauria. Tatarinov and Novozhilov (in Orlov 1964) adhered to this scheme, as did Schultze and Wilczewski (1970). Zangerl (1963), who actually studied the available material of *Corosaurus,* interpreted the fossil as being that of an advanced 'nothosaur' but made no familial assignment. Kuhn (1961, 1964a, b) and Young (1965a) both placed *Corosaurus* in a monotypic family of its own (Corosauridae), albeit without any formal diagnoses (and with some hesitation from Young). Carroll and Gaskill (1985) and Storrs (1986a, b) returned *Corosaurus* to the Nothosauridae, although Carroll (1987) merely treats the genus as *incertae sedis.*

As only three examinations of the original material of *Corosaurus* have been made [including within the present study, Storrs (1986a, b, 1990)], such taxonomic confusion as described above is not surprising. Now that our anatomical knowledge of *Corosaurus* is for the first time nearly complete, it has become possible to make a taxonomic assignment of the genus with a more reasonable degree of certainty. Nevertheless, before this can be done, the problem of sauropterygian relationships must be examined.

HISTORICAL CONCEPTS OF THE SAUROPTERYGIA

The term Sauropterygia was coined by Owen (1860) to include both the 'nothosaurs' and the plesiosaurs (as well as the placodonts), two obviously related and important groups of Mesozoic marine reptiles. Romer (1956, 1966) reaffirmed this usage as a clear alternative to more recent and ambiguous designations. That the 'nothosaurs' and plesiosaurs together form a monophyletic group can be clearly seen from their many shared derived characteristics, in both the skull and the postcranial skeleton (Sues 1987). Indeed, this relationship was recognized from the time of the earliest descriptions of these animals in the first half of the nineteenth century.

One of the most obvious of the characters uniting the 'nothosaurs' and plesiosaurs is the configuration of the temporal regions of their skulls. Both groups possess a single supratemporal fenestra on either side of the skull that is bounded medially by the postfrontal and parietal, and laterally by the postorbital and squamosal—a condition that Colbert (1945) described as euryapsid. The upper temporal opening found in the bizarre reptilian order Placodontia has been considered by many to be similarly euryapsid, and most workers have traditionally followed Owen (1860) and allied them with the sauropterygians. With this addition, Williston (1925) placed the Sauropterygia under the resurrected subclass Synaptosauria of Cope (1885), a name reflecting his belief that they were possibly related to synapsids (Romer 1956).

In the search for possible ancestors to the Sauropterygia, the desire to find presumed forebears possessing single supratemporal fenestrae has, understandably, been strong. Thus, in 1933, Romer expanded the Synaptosauria to include a poorly known assemblage of Permian/Triassic, primarily terrestrial, reptiles known as protorosaurs or araeoscelids (at that time including *Araeoscelis, Protorosaurus, Tanystropheus,* and *Trilophosaurus*) whose cranial anatomy seemed to be compatible with this desire. Romer (1933) believed that the construction of the temporal regions of the skulls of these animals was sufficiently close to that of 'nothosaurs' to warrant their consideration as the sauropterygian parent stock. In 1945, Colbert renamed the Synaptosauria as the Euryapsida to reflect the terminology associated with the clearly defined anapsid, synapsid, and diapsid skull conditions, and later (1969) included the Ichthyosauria, whose upper temporal openings had recently been found to be possibly comparable with those of the Sauropterygia (Romer 1968a).

The ichthyosaurs may or may not be true euryapsids but, in any case, as extremely derived reptiles are of no great consequence in the present discussion of sauropterygian origins. If at all related, they likely diverged from an ancestral stock very early in the group's history. Kuhn-Schnyder (1962, 1963a, 1967, 1980), following an early proposal by Jaekel (1910), has hypothesized the descent of sauropterygians from primitive, diapsid, eosuchian grade reptiles through the loss of the lower temporal arch, not the from the presumed solid-cheeked protorosaurs. Romer (1968b) has disputed this view, primarily as a result of his mistaken impression of the nature of the cheek region of the 'Nothosauria.' In fact, the cheeks of 'nothosaurs' are not solid as Romer (1933, 1945, 1966) had believed, but are of a fundamentally different nature from that ascribed to the protorosaurs (themselves problematical and probably representing several structural types). While often secondarily closed in the Plesiosauria (euryapsid is literally "broad arched") (and the placodonts?), the cheek in 'nothosaurs' is deeply emarginated, and the postorbital/squamosal arcade is very narrow (see, e.g., Fig. 8A). Carroll (1981) has reviewed the history of this anatomical misconception and demonstrated

the likelihood of a diapsid ancestry for the Sauropterygia. His description of *Claudiosaurus* provides a reasonable transitional analog to 'nothosaurs' and plesiosaurs from the 'Eosuchia' and he included his new family Claudiosauridae in the Sauropterygia. Whatever their affinities, the protorosaurs are not ancestral to the Sauropterygia and are probably an artificial taxon (Kuhn-Schnyder 1980; Romer 1971). Benton (1985), Rieppel (1989), and Sues (1987) have further discussed the possible relationship of *Claudiosaurus* to the Sauropterygia. Each has expressed certain reservations regarding the exact placement of *Claudiosaurus* within the diapsid hierarchy, but all accept the inclusion of the Sauropterygia within Benton's (1985) Neodiapsida.

HISTORICAL CLASSIFICATIONS OF THE 'NOTHOSAURIA'

The 'nothosaurs' themselves have, from the beginning, been frequently recognized as forming a well-defined group whose constituents largely share a single generalized morphology. This recognition, however, is based on overall similarity rather than demonstrated synapomorphy and the group may actually be paraphyletic (Rieppel 1989; Sues 1987; see also discussion below). This circumstance, along with often incomplete anatomical knowledge of most forms, has resulted in a confused classification history of 'nothosaur' taxa.

Some of the earliest reports of 'nothosaur' remains were produced in the mid-nineteenth century from specimens collected in the Triassic of Bavaria. Of these, the first study which combined thorough descriptions with adequate (in this case excellent) illustrations was provided by von Meyer (1847–55). Included in this work were descriptions of *Nothosaurus, Pistosaurus,* and *Simosaurus.* These fossils were known to be closely related to the plesiosaurs and were identified as such by von Meyer and contemporary workers. At the same time, similar animals were being reported from the Alpine region of southern Europe (e.g., *Lariosaurus* Curioni, 1847 and "*Pachypleura*" Cornalia, 1854). It was not until 1882, however, that the formal designation 'Nothosauria' was established as a taxon of subordinal rank. This was done by Seeley (1882) following his description of *Neusticosaurus,* although students of the 'nothosaurs' were already wrestling with the problem of familial associations.

While Gervais had proposed the Simosauridae in 1859, the first widely recognized family was the Nothosauridae (Baur 1889, in Zittel 1887–90), in which had been placed all the genera then known. This was quickly followed by the creation of the Lariosauridae Lydekker, 1889. Lydekker (1889) suggested that his Lariosauridae (*Lariosaurus* and *Neusticosaurus*) were perhaps transitional between plesiosaurs and the Nothosauridae (then including *Nothosaurus, Pistosaurus, Simosaurus,* and "*Conchiosaurus*"). It was Arthaber (1924), however, who made the first major attempt at an in-depth classification of the 'Nothosauria,' including all of the genera then known. He again distinguished the Lariosauridae from the Nothosauridae, but split the latter into two informal groupings. The Lariosauridae here consisted of *Lariosaurus, Partanosaurus,* and *Proneusticosaurus. Neusticosaurus* was shifted to the Nothosauridae which now additionally included *Anarosaurus, Cymatosaurus, Dactylosaurus,* "*Macromerosaurus,*" "*Pachypleura,*" and *Phygosaurus.* Unfortunately, Arthaber's (1924) classification contains several inconsistencies that reflect the difficulty of making systematic judgments among subjects that are not completely known and the difficulty of merely relying upon degree of overall similarity. Subsequent workers have been similarly hampered and the resultant classifications are confusingly varied. The most important of

these schemes are outlined chronologically in Table 1. Obviously, there has been little agreement on the nature of 'nothosaur' families, and no clear concept of many of the genera. Furthermore, it can also be seen from Table 1 that certain genera (e.g., *Corosaurus, Cymatosaurus, Pistosaurus, Rhaeticonia,* and *Simosaurus*) have at times been considered 'nothosaurs,' while at others, have been labeled plesiosaurs.

THE GENERA OF 'NOTHOSAURS'

In the present study of 'nothosaurs,' the traditionally included genera are first anatomically compared and taxonomically clarified. The phylogenetic relationships of the Sauropterygia as a whole, and of the better known 'nothosaur' genera, are then examined cladistically using presumably valid (homogenetic) taxonomic characters.

Table 1 lists over fifty names of 'nothosaurs' (plesiomorphic sauropterygians) that have previously appeared in the literature. Of these, many are now accepted as junior synonyms of other genera (some are actually misspellings). *Corosaurus* Case, 1936 is undoubtedly a valid genus as per the diagnosis presented in Chapter 2, and a taxon for which no synonyms exist. Other obviously or presumably valid genera (and traditionally accepted as such) include *Anarosaurus* Dames, 1890; *Ceresiosaurus* Peyer, 1929; *Cymatosaurus* Fritsch, 1894; *Dactylosaurus* Gürich, 1884; *Keichousaurus* Young, 1958; *Lariosaurus* Curioni, 1847; *Neusticosaurus* Seeley, 1882; *Nothosaurus* Münster, 1834; *Pachypleurosaurus* Broili, 1927; *Paranothosaurus* Peyer, 1939; *Proneusticosaurus* Volz, 1902; *Psilotrachelosaurus* Nopsca, 1928b; *Serpianosaurus* Rieppel, 1989; and *Simosaurus* v. Meyer, 1842. Each of these can be clearly identified as 'nothosaurs' (sensu lato) and, with the exception of *Pachypleurosaurus,* apparently generically differentiated through largely unambiguous morphologic criteria. For instance, *Anarosaurus* (Figs. 29C, 32A, and 33B) is a small supratemporal fenestra form in which the femur is significantly longer than the humerus in the apparent adult condition (Carroll and Gaskill 1985). This pronounced situation is unique among adult 'nothosaurs' with small temporal openings [juvenile pachypleurosaurs exhibit relatively long femora (Zangerl 1935, 1963)]. *Anarosaurus* may be further distinguished by its relatively robust humerus. Unfortunately, the type specimen was destroyed during World War II, although casts exist. *Ceresiosaurus* (Figs. 30D, 37C, and 39A) has, among other traits, large temporal fenestrae, a relatively long neck, massive clavicles and humeri, and slight hyperphalangy. These form a suite of characters suitable for generic distinction.

While the body [other than the gastralia (Schrammen 1899)] of *Cymatosaurus* is unknown (Volz also assigned some questionable postcrania to *Cymatosaurus* in 1902), the robust, longirostrine skull is obviously distinct from those of all other known 'nothosaurs' (Figs. 31B, 32D, and 34C). It is proportionally similar to the skull of *Pistosaurus* v. Meyer, 1839 (Figs. 31D, 32F, and 33D) but unlike the latter, its small, splintlike nasals remain in contact with the borders of the external nares and it lacks an interpterygoid fenestra. It is therefore a 'nothosaur' in the traditional sense. The poorly known fossil *Eurysaurus* Frech, 1903 has regularly been equated with *Cymatosaurus,* initially as a subgenus of the latter (e.g., Arthaber 1924), and considering the minor proportional differences in their skulls, *Eurysaurus* is here also viewed as a junior synonym of *Cymatosaurus.* The genus *Germanosaurus* Nopcsa, 1928a was proposed in place of the preoccupied name *Eurysaurus* (Nopcsa, 1928b). Schultze (1970) has provisionally equated

TABLE 1. Chronological outline of the major historical classifications of the 'nothosaurs.'

I. ARTHABER (1924)
Suborder Nothosauria
Family Nothosauridae
"Group I"
Anarosaurus, Cymatosaurus (*Eurysaurus*), *Dactylosaurus, Nothosaurus* (*Conchiosaurus*), *Pistosaurus, Simosaurus,* (*Lamprosaurus, Opeosaurus*)
"Group II"
Macromerosaurus, Neusticosaurus, Pachypleura, Phygosaurus
Family Lariosauridae
Lariosaurus, Partanosaurus (*?Microleptosaurus*), *Proneusticosaurus*

II. WILLISTON (1925)
Suborder Nothosauria
Family Nothosauridae
Anarosaurus, Cymatosaurus, Dactylosaurus, Doliovertebra, Lamprosaurus, Lariosaurus, Microleptosaurus, Neusticosaurus, Nothosaurus, Partanosaurus, Pistosaurus, Proneusticosaurus, Simosaurus

III. NOPCSA (1928a & b)
Suborder Nothosauroidea
Family Pachypleuridae (Pachypleurosauridae)
Subfamily Pachypleurinae (Pachypleurosaurinae)
Anarosaurus, Dactylosaurus, Pachypleurosaurus
Subfamily Neusticosaurinae
Neusticosaurus
Subfamily Simosaurinae
Proneusticosaurus, Simosaurus
Family Nothosauridae
Subfamily Lariosaurinae
Lariosaurus, Macromerosaurus, Phygosaurus, Psilotrachelosaurus (*Philotrachelosaurus*), *Rhäticonia*
Subfamily Nothosaurinae
Cymatosaurus, Germanosaurus (*Eurysaurus*), *Nothosaurus, ?Pistosaurus*

IV. ROMER (1933)
Suborder Nothosauria
Family Pachypleurosauridae
Neusticosaurus, Simosaurus
Family Nothosauridae
Ceresiosaurus, Lariosaurus, Nothosaurus

V. PEYER (1934)
Suborder Nothosauroidea
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Neusticosaurus, Pachypleurosaurus, Phygosaurus, Psilotrachelosaurus
Family Nothosauridae
Ceresiosaurus, Cymatosaurus, Germanosaurus, Lariosaurus, ?Microleptosaurus, Nothosaurus, ?Paranothosaurus, Pistosaurus, Proneusticosaurus, ?Rhäticonia, Simosaurus

Continued on next page

TABLE 1 -- *Continued*

VI. KUHN (1934)
Suborder Nothosauria
Family Nothosauridae
Anarosaurus, Ceresiosaurus, Cymatosaurus, Dactylosaurus, Diplovertebra [sic] (*Dolichovertebra*), *Germanosaurus* (*Eurysaurus*), *Lamprosaurus, Lariosaurus* (*Macromerosaurus, Macromirosaurus*), *Microleptosaurus, Neusticosaurus, Nothosaurus* (*Conchiosaurus, Dracosaurus, Phanerosaurus*), *Opeosaurus, Pachypleurosaurus* (*Pachypleura*), *Partanosaurus, Phygosaurus, Pistosaurus, Proneusticosaurus, Psilotrachelosaurus, Rhaeticonia, Simosaurus*

VII. ROMER (1945)
Suborder Nothosauria
Family Nothosauridae
Ceresiosaurus, Corosaurus, Cymatosaurus, Doliovertebra, Germanosaurus, Lamprosaurus, Lariosaurus, Macromirosaurus, Microleptosaurus, Nothosaurus, Opeosaurus, Paranothosaurus, Partanosaurus, Proneusticosaurus, Rhaeticonia, Simosaurus
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Neusticosaurus, Pachypleurosaurus, Phygosaurus, Psilotrachelosaurus
Suborder Plesiosauria
Infraorder Pistosauroidea
Family Pistosauridae
Pistosaurus

VIII. v. HUENE (1948b)
Suborder Pachypleurosauridea [sic]
Family Pachypleurosauridae
Pachypleurosaurus
Family Proneusticosauridae
Proneusticosaurus
Suborder Nothosauridea [sic]
Family Lariosauridae
Lariosaurus
Family Nothosauridae
Nothosaurus
Suborder Plesiosauroidea
Family Cymatosauridae
Cymatosaurus
Family Pistosauridae
Pistosaurus
Family Simosauridae
Corosaurus, Simosaurus

IX. v. HUENE (1952)
Suborder Nothosauroidea
Family Proneusticosauridae
Proneusticosaurus
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Pachypleurosaurus, ?Phygosaurus, ?Psilotrachelosaurus, Simosaurus

Continued on next page

TABLE 1 -- *Continued*

Family Nothosauridae
Ceresiosaurus, Lariosaurus, Metanothosaurus, Neusticosaurus, Nothosaurus, Paranothosaurus, ?Partanosaurus
Suborder Plesiosauroidea
Family Cymatosauridae
Cymatosaurus, Germanosaurus, Rhaeticonia, Sulmosuchus
Family Pistosauridae
Corosaurus, Pistosaurus

X. SAINT-SEINE (1955)
Suborder Nothosauria
Family Nothosauridae
"Type 1"
Cymatosaurus, Eurysaurus (*Germanosaurus*), *Nothosaurus, Paranothosaurus*
"Type 2"
Ceresiosaurus, Lariosaurus, Simosaurus
Indet. "others"
Proneusticosaurus (*Doliovertebra*), *Macromerosaurus, Parthanosaurus*
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Neusticosaurus, Pachypleurosaurus (*Pachypleura*), *Phygosaurus*
Suborder Plesiosauria
Superfamily Pistosauroidea
Family Pistosauridae
Pistosaurus

XI. v. HUENE (1956)
Suborder Pachypleurosauroidea
Family Pachypleurosauridae
Dactylosaurus (*Anomosaurus*), *Pachypleurosaurus, Phygosaurus, Psilotrachelosaurus, Rhaeticonia, Neusticosaurus*
Family Proneusticosauridae
Proneusticosaurus (*Dolichovertebra, Lamprosaurus*)
Suborder Nothosauroidea
Family Lariosauridae
Lariosaurus (*Macromerosaurus*)
Family Nothosauridae
Ceresiosaurus, Metanothosaurus, Microleptosaurus, Nothosaurus, Paranothosaurus, Parthanosaurus
Family Simosauridae
Anarosaurus, Conchiosaurus, Simosaurus (*Opeosaurus*)
Suborder Plesiosauroidea
Family Cymatosauridae
Cymatosaurus (*Germanosaurus*), *?Sulmosaurus* [sic]
Family Pistosauridae
Corosaurus, Pistosaurus

Continued on next page

TABLE 1 -- *Continued*

XII. ROMER (1956)
- Suborder Nothosauria
  - Family Nothosauridae
    - *Ceresiosaurus, Lariosaurus* (*Macromerosaurus, Macromirosaurus*), *?Metanothosaurus, Nothosaurus* (*Conchiosaurus, Condriosaurus*), *Dracontosaurus, Dracosaurus, Kolposaurus, Oligolycus, Opeosaurus*), *Paranothosaurus, ?Parthanosaurus* (*?Microleptosaurus, Partanosaurus*), *?Proneusticosaurus*
  - Family Cymatosauridae
    - *Cymatosaurus* (*Eurysaurus, Germanosaurus*), *Rhaeticonia*
  - Family Pachypleurosauridae
    - *Neusticosaurus* (*?Anarosaurus, ?Dactylosaurus, ?Philotrachelosaurus, ?Phygosaurus, ?Psilotrachelosaurus*), *Pachypleurosaurus* (*Pachypleura*)
  - Family Simosauridae
    - *?Corosaurus, Simosaurus*
  - Nothosauria *incertae sedis*
    - *Deirosaurus, Doliovertebra, Lamprosauroides* (*Lamprosaurus*)
- Suborder Plesiosauria
  - ?Superfamily Pistosauroidea
    - Family Pistosauridae
      - *Pistosaurus*

XIII. KUHN (1964a)
- Suborder Nachangosauria
  - Family Nachangosauridae
    - *Nachangosaurus*
  - Family Nothosauravidae
    - *Nothosauravus*
- Suborder Nothosauria
  - Family Nothosauridae
    - *Ceresiosaurus, Keichousaurus, Kwangsisaurus, Metanothosaurus, Microleptosaurus, Micronothosaurus, Nothosaurus*, (*Dracontosaurus, Dracosaurus, Kolposaurus, Oligolycus*), *Paranothosaurus, Parthanosaurus, Proneusticosaurus* (*Dolichovertebra, Doliovertebra*)
  - Family Lariosauridae
    - *Lariosaurus* (*Macromerosaurus, Macromirosaurus*)
  - Family Cymatosauridae
    - *Cymatosaurus* (*Eurysaurus, Germanosaurus*), *Rhaeticonia*
  - Family Pachypleurosauridae
    - *Anarosaurus, Dactylosaurus, Elmosaurus, Neusticosaurus, Pachypleurosaurus* (*Pachypleura*), *Phygosaurus, Psilotrachelosaurus* (*Philotrachelosaurus*)
  - Family Simosauridae
    - *Simosaurus*
  - Family Corosauridae
    - *Corosaurus*

Continued on next page

TABLE 1 -- *Continued*

Nothosauria *incertae sedis*
?Charitosaurus, Conchiosaurus, Deirosaurus, Eupodosaurus, Lamprosauroides (*Lamprosaurus*), *?Namuncurania, ?Ocoyuntaia, Opeosaurus*
Suborder Plesiosauria
Superfamily Pistosauroidea
Family Pistosauridae
Pistosaurus

XIV. TATARINOV and NOVOZHILOV (in Orlov 1964)
Suborder Nothosauria
Family Lariosauridae
Lariosaurus (*Macromerosaurus, Macromirosaurus*), *Neusticosaurus, Nothosauravus, Parthanosaurus* (*Microcletosaurus* [sic], *Partanosaurus*)
Family Pachypleurosauridae
Subfamily Pachypleurosaurinae
Elmosaurus, Keichousaurus, Pachypleurosaurus (*Pachypleura*), *Phygosaurus, Psilotrachelosaurus, Rhaeticonia*
Subfamily Proneusticosaurinae
?Lamprosauroides (*Lamprosaurus*), *Proneusticosaurus* (*Dolichovertebra*)
Family Simosauridae
Anarosaurus, Conchiosaurus (*Condriosaurus*), *Corosaurus, Dactylosaurus* (*Anomasaurus* [sic]), *Simosaurus* (*?Opeosaurus*)
Family Nothosauridae
Ceresiosaurus, ?Deirosaurus, ?Kwangsisaurus, Metanothosaurus, Nothosaurus (*Dracontosaurus, Dracosaurus, Kolposaurus, Oligolycus*), *Paranothosaurus, Pontopus*
Suborder Plesiosauria
Superfamily Pistosauroidea
Family Cymatosauridae
Cymatosaurus (*Eurysaurus, ?Germanosaurus*), *?Sulmosaurus*
Family Pistosauridae
Pistosaurus

XV. YOUNG (1965a)
Suborder Pachypleurosauroidea
Family Pachypleurosauridae
Pachypleura, Pachypleurosaurus, Rhaeticonia
Family Keichousauridae
Keichousaurus
Family Simosauridae
Anarosaurus, Elmosaurus, Shingyisaurus, Simosaurus
Suborder Nothosauroidea
Family Nothosauridae
Ceresiosaurus, Chinchenia, Kwangsisaurus, Metanothosaurus, Nothosaurus, Paranothosaurus, Sanchiaosaurus.
Family Lariosauridae
Lariosaurus

Continued on next page

TABLE 1 -- *Continued*

Family Cymatosauridae
Cymatosaurus, Germanosaurus
?Family Corosauridae
Corosaurus

XVI. ROMER (1966)
Suborder Nothosauria
Family Nothosauridae
Ceresiosaurus, Deirosaurus, Keichousaurus, ?Kwangsisaurus, Lariosaurus (*Macromerosaurus, Macromirosaurus*), *Metanothosaurus, Micronothosaurus, ?Nachangosaurus, ?Nothosauravus, Nothosaurus* (*Chondriosaurus* [sic], *Conchiosaurus, Dracontosaurus, Dracosaurus, Kolposaurus, Menodon, Oligolycus*), *Paranothosaurus, ?Parthanosaurus* (*?Microcleptosaurus* [sic]), *Pontopus, Proneusticosaurus* (*Dolichovertebra, ?Lamprosaurus, ?Lamprosciuroides* [sic])
Family Pachypleurosauridae
Neusticosaurus (*Anarosaurus, ?Anomosaurus, Dactylosaurus, ?Philotrachelosaurus, ?Phygosaurus, ?Psilotrachelosaurus*), *Pachypleurosaurus* (*Pachypleura*)
Family Simosauridae
?Corosaurus, ?Elmosaurus, Simosaurus (*Opeosaurus*)
Suborder Plesiosauria
?Superfamily Pistosauria
Family Pistosauridae
Pistosaurus
Family Cymatosauridae
Cymatosaurus (*?Eurysaurus, Germanosaurus*), *?Rhaeticonia, ?Sulmosaurus*

XVII. CARROLL AND GASKILL (1985)
Suborder Nothosauria
Family Nothosauridae
Ceresiosaurus, Corosaurus, Lariosaurus, Nothosaurus, Paranothosaurus, Simosaurus
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, ?Elmosaurus, Keichousaurus, Neusticosaurus, Pachypleurosaurus, ?Phygosaurus, ?Psilotrachelosaurus

XVIII. CARROLL (1988)
Order Nothosauria
Family Cymatosauridae
Cymatosaurus (*Germanosaurus, Micronothosaurus*)
Family Nothosauridae
Ceresiosaurus, Lariosaurus (*Macromerosaurus*), *Nothosaurus* (*Conchiosaurus, Dracosaurus, Oligolycus*), *Paranothosaurus, Proneusticosaurus, ?Rhaeticonia*

Continued on next page

TABLE 1 -- *Continued*

Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Keichousaurus, Neusticosaurus, Pachypleurosaurus (Pachypleura), ?Psilotrachelosaurus, Phygosaurus
Family Pistosauridae
Pistosaurus
Family Simosauridae
Simosaurus (?Opeosaurus)
Nothosauria *incertae sedis*
Corosaurus, Elmosaurus, Kwangsisaurus, Metanothosaurus, Parthanosaurus

XIX. TSCHANZ (1989)
Order Sauropterygia
Pachypleurosauroidea
Family Pachypleurosauridae
Anarosaurus, Dactylosaurus, Keichousaurus, Neusticosaurus, Pachypleurosaurus, Serpianosaurus
Eusauropterygia
Family Simosauridae
Simosaurus
Eusauropterygia, Nothosauria
Family Nothosauridae
Nothosaurus, Paranothosaurus
Family Lariosauridae
Ceresiosaurus, Lariosaurus
Sauropterygia *incertae sedis*
Corosaurus, Elmosaurus, Kwangsisaurus, Micronothosaurus, Proneusticosaurus, Psilotrachelosaurus, Rhäticonia [sic]

Micronothosaurus Haas, 1963 with *Cymatosaurus* on the basis of their similar postorbital cranial proportions and centrally located pineal foramen. This is a reasonable proposal, one that is provisionally followed here in the absence of more useful fossil material.

Dactylosaurus (Figs. 30A and 37E), while similar to *Anarosaurus,* lacks the relatively elongate femur of the latter, although Carroll and Gaskill (1985) cite the presumably greater degree of skeletal ossification and possible pisiform bone of *Dactylosaurus* as sufficient distinctions. Sues and Carroll (1985) cite also the relatively gracile nature of *Dactylosaurus.* Its epipodials are particularly slender. *Keichousaurus* (Figs. 23, 29D, and 36F) is undoubtedly a typical pachypleurosaur, but possesses an extremely broad ulna as elsewhere observed only in *Lariosaurus. Lariosaurus,* on the other hand, is a form with large temporal openings (Figs. 31A, 34B, 37B, and 38B). Features comprising the unique character suite of *Lariosaurus* include its relatively small size, thickened ribs, and five sacral vertebrae with costae of uniform diameter. *Macromerosaurus* Curioni, 1847 *emend.* Cornalia, 1854 is a junior synonym of *Lariosaurus,* apparently having been founded on a juvenile specimen of the latter.

The traditional genera *Pachypleurosaurus* and *Neusticosaurus* (Figs. 29A and B, 32B, 33A, 36G and H, and 38A) are obviously closely related and following Carroll and Gaskill (1985), are most notably distinguished from other taxa by their common exclusion of the postorbital from the supratemporal opening. They

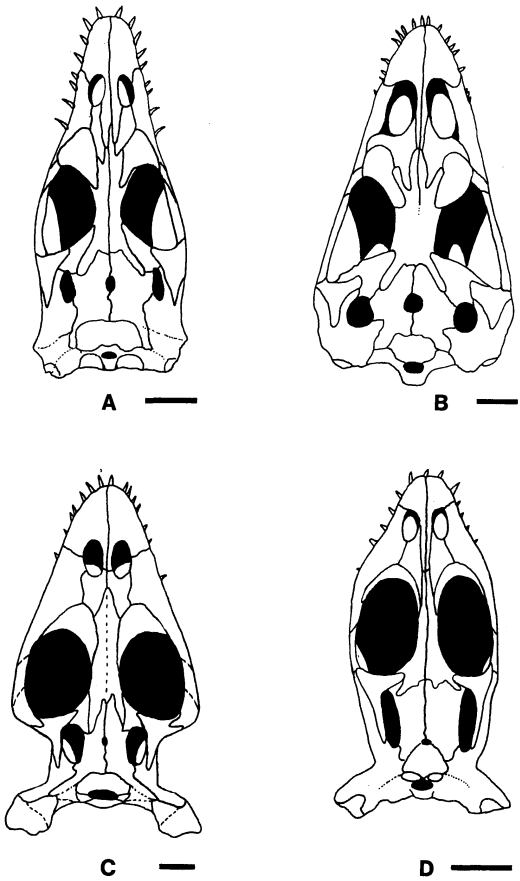

FIG. 29. Reconstructed skulls of pachypleurosaurs in dorsal aspect. A, *Neusticosaurus* modified from Carroll and Gaskill (1985), Mateer (1976) and Sander (1989); B, "*Pachypleurosaurus*" after Carroll and Gaskill (1985); C, *Anarosaurus* modified from Carroll (1981) after Nopsca (1928b); D, *Keichousaurus* modified from Young (1958) after photographs (courtesy of N. Mateer). Compare with Fig. 7. Scale bars = 0.5 cm.

both have small temporal fenestrae, thickened ribs, relatively short femora, and three [variably four (Zangerl 1935)] sacral vertebrae. The sacral ribs are relatively unexpanded at their distal ends. Carroll and Gaskill (1985) distinguished *Neusticosaurus* from *Pachypleurosaurus* by, among other things, the smaller temporal openings, relatively narrow skull table, smaller humerus to femur length ratio, slightly greater phalangeal formula, relatively broader ribs, and generally smaller size of *Neusticosaurus*.The holotype of *Neusticosaurus* (BMNH R53) and numerous small, probably juvenile, fossils described by Fraas (1896), are from the Germanic Province of central Europe. Specimens once identified as *Pachypleurosaurus*, on the other hand, are common in the famous shales of Monte San Giorgio, Switzerland, and adjacent localities of the Alpine Triassic. *Pachypleurosaurus* is the name coined by Broili (1927) and used coincidentally by Nopcsa (1928a) to replace the preoccupied *Pachypleura* Cornalia (1854). Carroll and Gaskill (1985) have attempted to draw an adequate anatomical distinction between these taxa. Their study suggests that many previously described fossils have been erroneously assigned to *Pachypleurosaurus* (e.g., certain specimens discussed by Kuhn-Schnyder 1959; Mateer 1976; Zangerl 1935; and other authors), while actually representing *Neusticosaurus*. Rieppel (1989) has accepted the conclusions

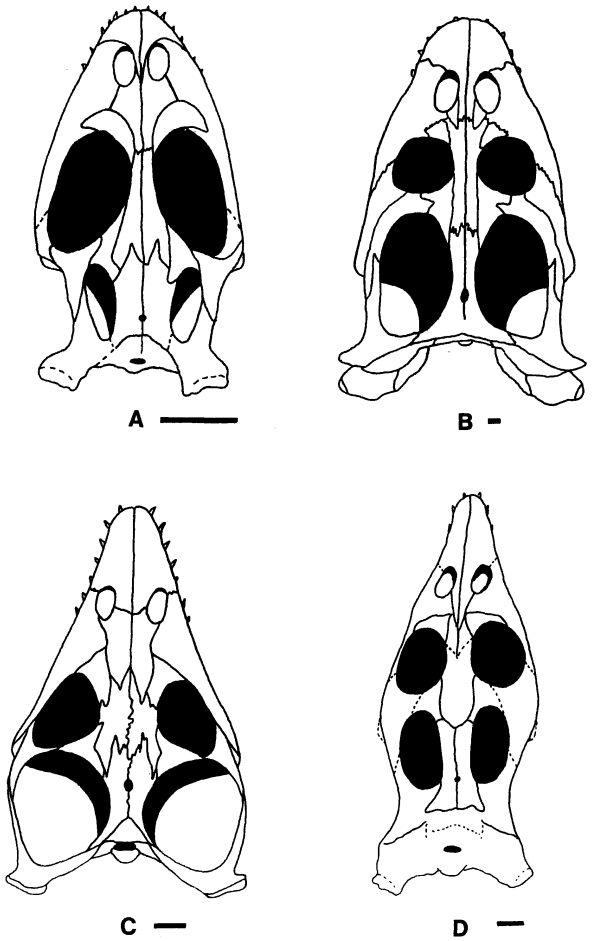

FIG. 30. Reconstructed skulls of various 'nothosaurs' in dorsal aspect. A, *Dactylosaurus* after Nopsca (1928b) and Sues and Carroll (1985); B, *Simosaurus* after Kuhn-Schnyder (1961); C, *Corosaurus*; D, *Ceresiosaurus* after Peyer (1931). Compare with Fig. 7. Scale bars = 1.0 cm.

of Carroll and Gaskill (1985), while most recently Sander (1989) has equated all examples of the two genera as specific variants of *Neusticosaurus,* the name having priority. This interpretation is welcomed and accepted here, although for purposes of clarity, *Neusticosaurus* and "*Pachypleurosaurus*" are retained as distinct in the present phylogenetic analysis. *Serpianosaurus* (Fig. 37D), a relatively plesiomorphic pachypleurosaur from the Grenzbitumen horizon of Monte San Giorgio, has recently been described by Rieppel (1989) as a close relative of *Neusticosaurus. Serpianosaurus* is a small to intermediate-sized pachypleurosaur with a relatively large skull, straight mandible, and often nonthickened ribs. The history of these taxa and other pachypleurosaurs has been reviewed by Rieppel (1987).

A pair of similarly related forms is *Nothosaurus* and *Paranothosaurus* (Figs. 31C; 32E; 34D; 35C; 36A, B and E; and 39B). These are large, derived reptiles that are characterized by long, massive skulls with blunt, constricted premaxillae and extremely elongate supratemporal fenestrae. This unique cranial format is readily identifiable, but the skull of *Nothosaurus* is virtually indistinguishable from that of *Paranothosaurus* [see, e.g., Kuhn-Schnyder (1966) and Schultze (1970)]. Kuhn-Schnyder (1987), however, indicates that the postfrontal is excluded from the margin of the supratemporal fenestra in *Paranothosaurus,* in contrast to the

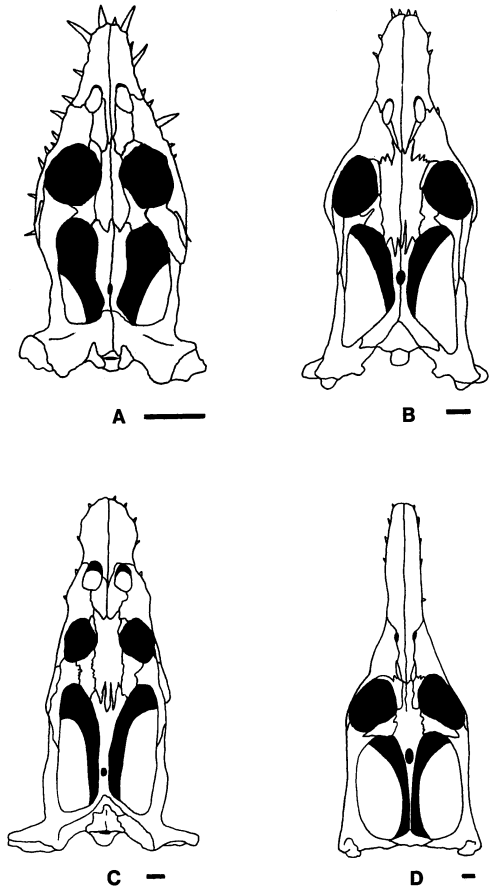

FIG. 31. Reconstructed skulls of nothosauriform 'nothosaurs' and *Pistosaurus* in dorsal aspect. A, *Lariosaurus* after Mazin (1985) with modifications according to Kuhn-Schnyder (1987); B, *Cymatosaurus* after Arthaber (1924), Fritsch (1894), and Schrammen (1899); C, *Nothosaurus* after Schultze (1970); D, *Pistosaurus* after von Meyer (1847–55) and Schrammen (1899). Compare with Fig. 7. Scale bars = 1.0 cm.

apparent condition in other known 'nothosaurids.' The pectra of the two genera (Figs. 36A, B and E; and 39B), however, are radically different. While the type and only specimen of *Paranothosaurus* is undoubtedly fully grown, its pectrum is very weakly developed and greatly reduced relative to that of *Nothosaurus*. It differs also by its open coracoid notch and barlike interclavicle.

Another apparently distinct genus is also known only from its (incomplete) type specimen. Its skull is not preserved and many details of its remaining anatomy are unclear. Nevertheless, it has generally been treated as a valid taxon. *Psilotrachelosaurus* apparently has a uniquely long and slender coracoid (Fig. 37F) and ulnae which are two-thirds the length of the radii. In his listing of reptilian genera, Nopcsa (1982a) identifies this fossil as "*Philotrachelosaurus.*" However, as the full description and designation of the fossil as a new genus appears in a separate paper (Nopcsa, 1928b) consistently naming the animal *Psilotrachelosaurus,* the former name is obviously a misprint and the latter should be considered the available name.

Several specimens of *Proneusticosaurus* are known; yet these are no less fragmentary. *Proneusticosaurus* is seemingly different from all presently known 'nothosaurs' in possessing six sacral vertebrae (Arthaber 1924; Volz 1902). Although

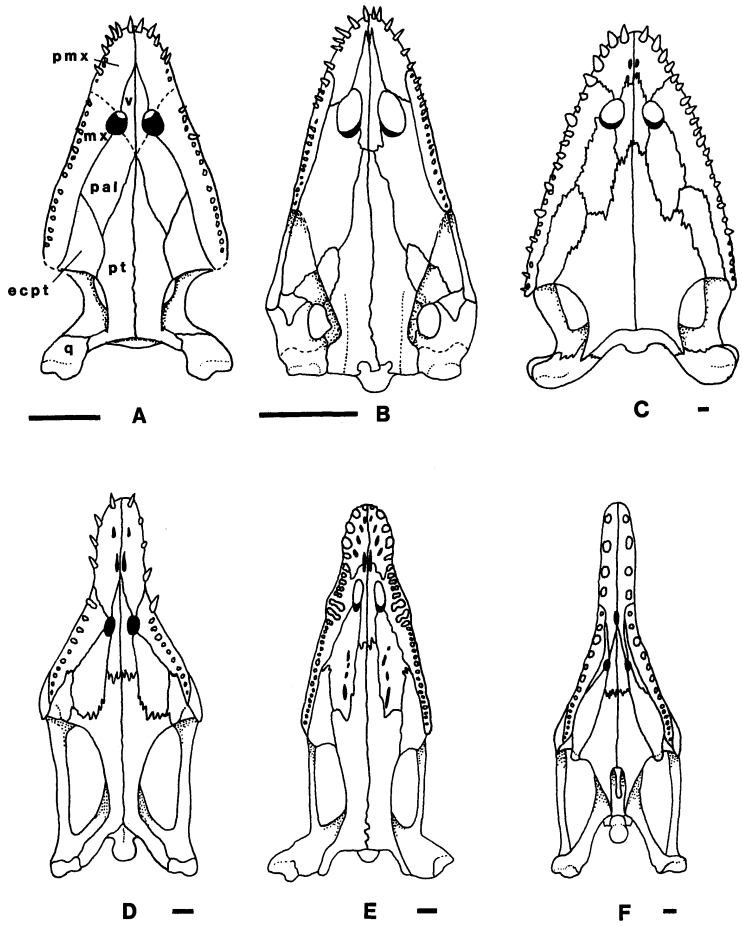

FIG. 32. Reconstructed skulls of various 'nothosaurs' and *Pistosaurus* in palatal aspect. A, *Anarosaurus* after Carroll (1981); B, "*Pachypleurosaurus*" after Carroll and Gaskill (1985); C, *Simosaurus* after Jaekel (1910) and von Huene (1921); D, *Cymatosaurus* after Arthaber (1924), Fritsch (1894), and Schrammen (1899); E, *Nothosaurus* after Schroeder (1914); F, *Pistosaurus* after von Meyer (1847–55) and Schrammen (1899). ecpt = ectopterygoid; mx = maxilla; pal = palatine; pmx = premaxilla; pt = pterygoid; q = quadrate; v = vomer. Scale bars = 1.0 cm.

from a large animal, the ribs of *Proneusticosaurus* are thickened and the sacral ribs have little or no distal expansion. The large calcaneum and astragalus are subequal in size. The ischia are noteworthy by virtue of their relatively great breadth and length. The thyroid fenestra is rather small. Cranial material of *Proneusticosaurus* is unknown.

Finally, of the aforementioned genera, *Simosaurus* (Figs. 30B, 32C, 33C, 35A, and 37A) is perhaps the most distinctive. Its large, round, supratemporal fenestrae and moderately long postorbital region combined with the brevirostrine antorbital area make the skull easily recognizable. This skull is large and massive. Whereas most 'nothosaurs' seem to have had long, slender, conical teeth, those of *Simosaurus* are short, squat, and deeply striated. On the basis of such teeth, and by virtue of similar size, locality, and age, von Huene (1952) attributed a partial postcranial skeleton to *Simosaurus*. A second postcranial skeleton (this time with skull) was described in 1959 (v. Huene 1959a). These display other diagnostic features including five sacral ribs, stout limb girdles, and a large, posteriorly projecting interclavicle.

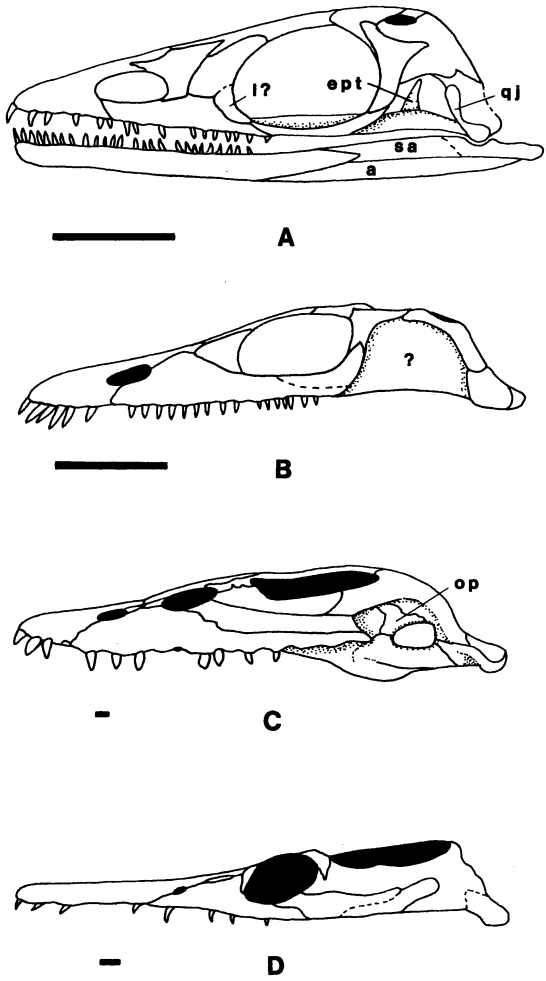

FIG. 33. Reconstructed skulls of various 'nothosaurs' and *Pistosaurus* in lateral aspect. A, "*Pachypleurosaurus*" modified from Carroll and Gaskill (1985); B, *Anarosaurus* after Carroll (1981); C, *Simosaurus* after von Huene (1921); D, *Pistosaurus* after von Meyer (1847–55) and Schrammen (1899). Compare with Fig. 8, A. a = angular; ept = epipterygoid; op = opisthotic; l = lachrymal; qj = quadratojugal; sa = surangular. Scale bars = 1.0 cm.

Some additional fossils possibly represent valid 'nothosaur' (primitive sauropterygian) genera, although they are rather poorly known. *Rhaeticonia* Broili, 1927 [initially anglicized by Woodward (in Zittel 1932) from the original *Rhäticonia* to conform with English nomenclatural practice] was known only from a single, very small (juvenile?) skeleton (destroyed during World War II). It had thick, "pachyostotic" ribs and vertebrae, and stout humeri. The skull was possessed of a conspicuously narrow, medium-length rostrum which seems to set this 'nothosaur' apart from most others which are presently known. The nature of the skull roof and temporal fenestrae is unknown. *Metanothosaurus* Yabe and Shikama, 1948 from Japan is certainly a 'nothosaur' in the traditional usage, but the headless, partial vertebral column of the holotype (now lost) is of little diagnostic value. It is a large animal and, being the first 'nothosaur' discovered in Asia, was made the type of a new genus, primarily on the basis of its large size, high neural spines, and extremely slender ribs ("costae"). This status is dubious but may be

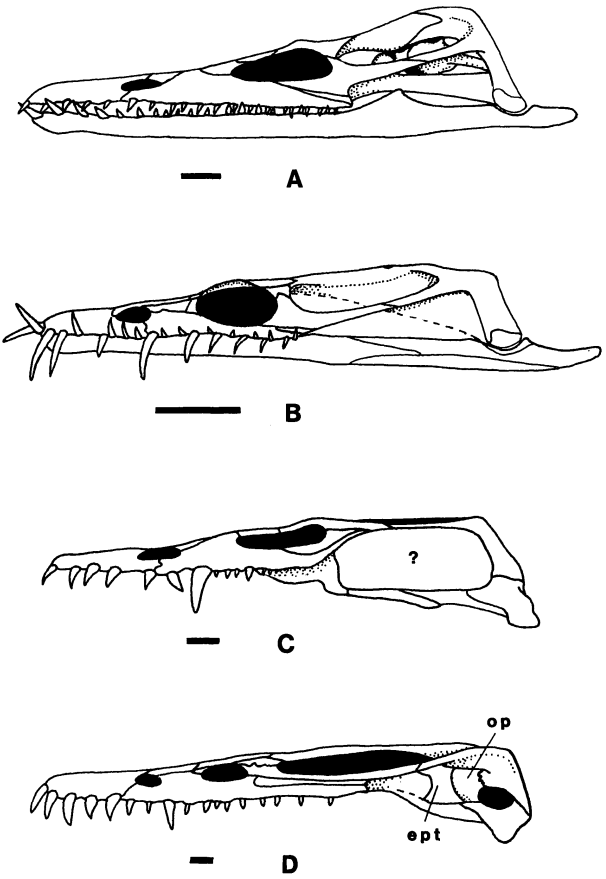

FIG. 34. Reconstructed skulls of nothosauriform 'nothosaurs' in lateral aspect. A, *Corosaurus*; B, *Lariosaurus* modified from Mazin (1985), Kuhn-Schnyder (1987) and Tschanz (1989); C, *Cymatosaurus* modified from Arthaber (1924) and Schrammen (1899); D, *Nothosaurus* modified from Carroll (1981). Compare with Fig. 8, A. ept = epipterygoid; op = opisthotic. Scale bars = 1.0 cm.

tentatively maintained in the hope that new, more definitive material may be forthcoming.

Young (Yang) has more recently described several additional Asian 'nothosaurs,' including *Keichousaurus*. While *Keichousaurus,* as noted above, is an animal with a relatively well-understood anatomy, *Chinchenia* Young, 1965a; *Kwangsisaurus* Young, 1959; *Sanchiaosaurus* Young, 1965a; and *Shingyisaurus* Young, 1965a are known from fewer, and more fragmentary, specimens. Each of these forms is from the Triassic of China and the morphology of each appears to justify its position as a separate taxon. Young (1958, 1959, 1960, 1965a, 1972, and 1978) has discussed their differences in greater detail but, for our purposes, *Chinchenia* is noted for its deep and massive lower jaw and mandibular symphysis, and sharply anisodont dentition; *Kwangsisaurus* for its stout femur and small pes; and *Sanchiaosaurus* for its large size, relatively long mandibular symphysis, squat teeth, constricted coracoid with very small supracoracoid foramen, broad ischia, and robust propodials. The only skull of *Shingyisaurus* is of a mesorostrine, large fenestra format which is similar in general appearance to that of *Simosaurus*. It likewise has a short mandibular symphysis and rounded rostrum. Its temporal

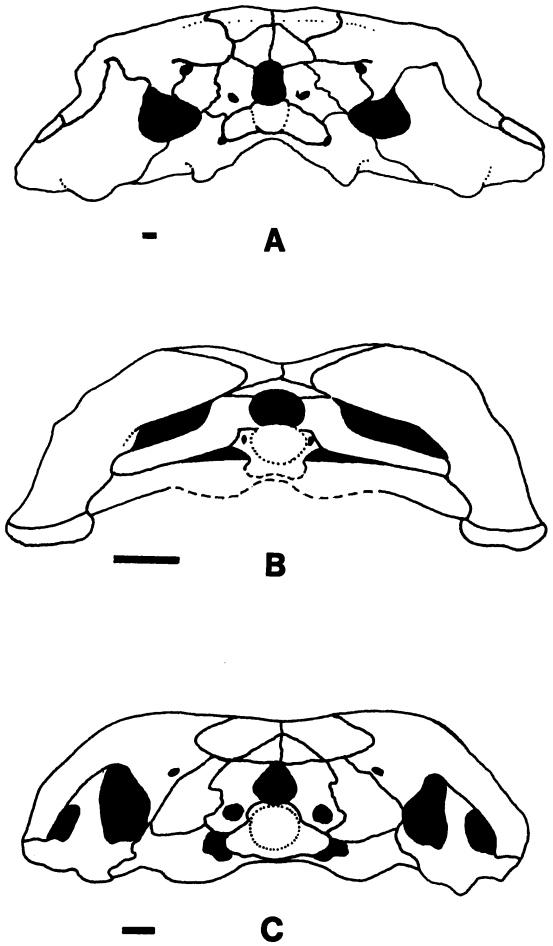

FIG. 35. Reconstructed skulls of various 'nothosaurs' in occipital aspect. A, *Simosaurus* after von Huene (1921), Kuhn-Schnyder (1961) and Schultze (1970); B, *Corosaurus*; C, *Nothosaurus* after Koken (1893) and Schroeder (1914). Compare with Fig. 8, B. Scale bars = 1.0 cm.

fenestrae are slightly more elongate than are those of *Simosaurus*. Though coarsely ridged, the teeth of *Shingyisaurus* are slender.

Partanosaurus Skuphos, 1893a *emend.* 1893b from the Middle Triassic of Vorarlberg, western Austria, is a final problematic genus which may be tentatively retained. It is unusual in possessing: tall, ridged, neural spines; ovate vertebral centra; distally expanded dorsal ribs; and a very slender scapular blade. The small *Microleptosaurus* Skuphos, 1983c, introduced along with a full description of *Partanosaurus,* is from the same unit and general locale as the latter and may represent merely the juvenile form of *Partanosaurus*. Unfortunately, it is known only from fragmentary material and thus is of little use in an ontogenetic study. Also proposed in the same reference is *Kolposaurus* Skuphos, 1893c from the Muschelkalk of Upper Silesia. This, as well as numerous other genera described from fragmentary specimens or only a few, isolated bones is here considered *nomen dubium,* although often equated with *Nothosaurus* (e.g., Romer 1966). These dubious names are listed with all other 'nothosaur' genera and their present status in Appendix B.

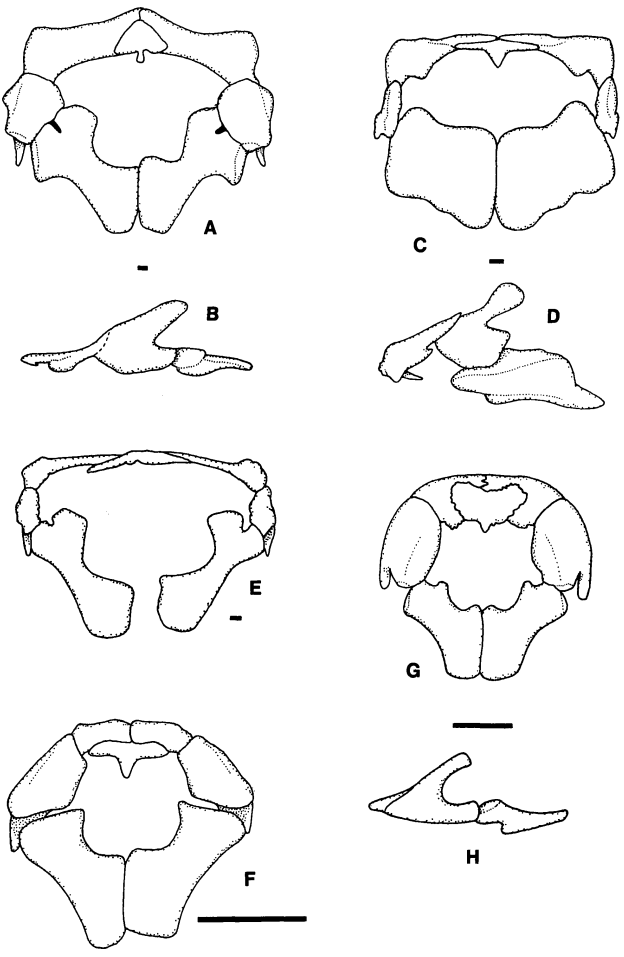

FIG. 36. Pectoral girdles of various 'nothosaurs' in ventral and lateral aspects. A, B, *Nothosaurus* after Romer (1956) and Carroll and Gaskill (1985); C, D, *Corosaurus*; E, *Paranothosaurus* after Peyer (1939); F, *Keichousaurus* after Young (1958); G, H, "*Pachypleurosaurus*" after Carroll and Gaskill (1985). Compare with Figs. 13 and 14. Scale bars = 1.0 cm.

SAUROPTERYGIAN ORIGINS AND RELATIONSHIPS

The probable origin of the Sauropterygia from primitive diapsids has been briefly discussed above. Carroll (1981) described as *Claudiosaurus* a small, aquatic reptile from the Upper Permian of Madagascar (Piveteau 1955) which he considered to be the earliest and most primitive sauropterygian known. The appendicular specializations and lower temporal emargination (presumed arcade loss) of *Claudiosaurus* clearly support this interpretation. The propodials of *Claudiosaurus,* for example, very closely resemble those of 'nothosaurs' and, in fact, share certain derived features with the Sauropterygia such as reduced epicondyles and an ectepicondylar foramen which has been transformed to a notch. Its gross cranial anatomy (apart from the missing lower temporal arch), the existence of an interpterygoid vacuity, the presence of palatal dentition, and certain other skeletal characteristics appear quite similar to those of younginiform 'eosuchians' (Suborder Younginiformes Romer, 1945) such as *Hovasaurus, Tangasaurus, Thadeosaurus,* and *Youngina* (Carroll 1981; Currie 1981, 1982; Currie and Carroll 1984) but these are plesiomorphic characteristics. They are, however, united by the

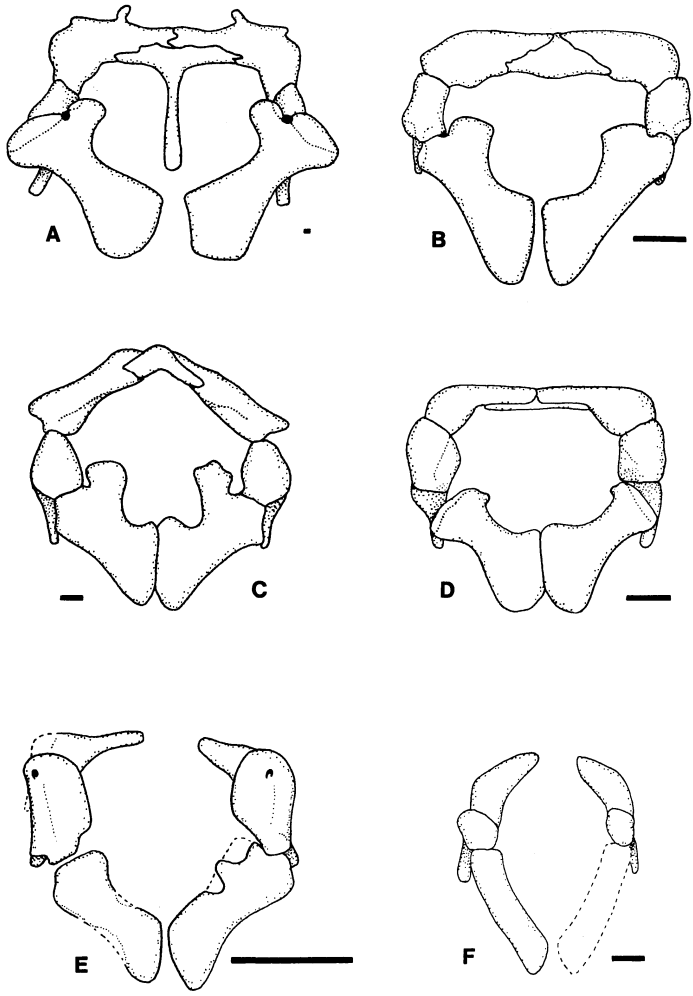

FIG. 37. Pectoral girdles of various 'nothosaurs' in ventral aspect. A, *Simosaurus* after von Huene (1952); B, *Lariosaurus* after Mazin (1985); C, *Ceresiosaurus* after Kuhn-Schnyder (1963b); D, *Serpianosaurus* after Arthaber (1924), Deeke (1886), and Rieppel (1989); E, *Dactylosaurus* after Nopsca (1928b) and Sues and Carroll (1985); F, *Psilotrachelosaurus* after Nopsca (1928b). Compare with Fig. 13. Scale bars = 1.0 cm.

derived features of present suborbital and posttemporal fenestrae, reduced lachrymals, single headed dorsal ribs, and a reduced olecranon process. Further examination of *Claudiosaurus* and comparison with the Younginiformes has revealed numerous derived characteristics that clearly distinguish *Claudiosaurus* from 'eosuchians' (Carroll 1981). These traits include the apparent loss of the subtemporal arch and concomitant reduction of the quadratojugal and jugal [a reasonable proposal contrary to Rieppel (1989)], the reduction of the suborbital fenestra and interpterygoid vacuity, the loss of the transverse flange of the pterygoid, and an unossified sternum. It is commonly felt that both *Claudiosaurus* and the Sauropterygia have likely diverged from a basal diapsid (younginiform?) stock as suggested by Kuhn-Schnyder (1962, 1963a, 1967, 1980). Following Sues (1987), the Sauropterygia are mostly closely related to the Lepidosauromorpha of Benton (1985).

From this point, it has been possible to utilize the Captorhinomorpha, the

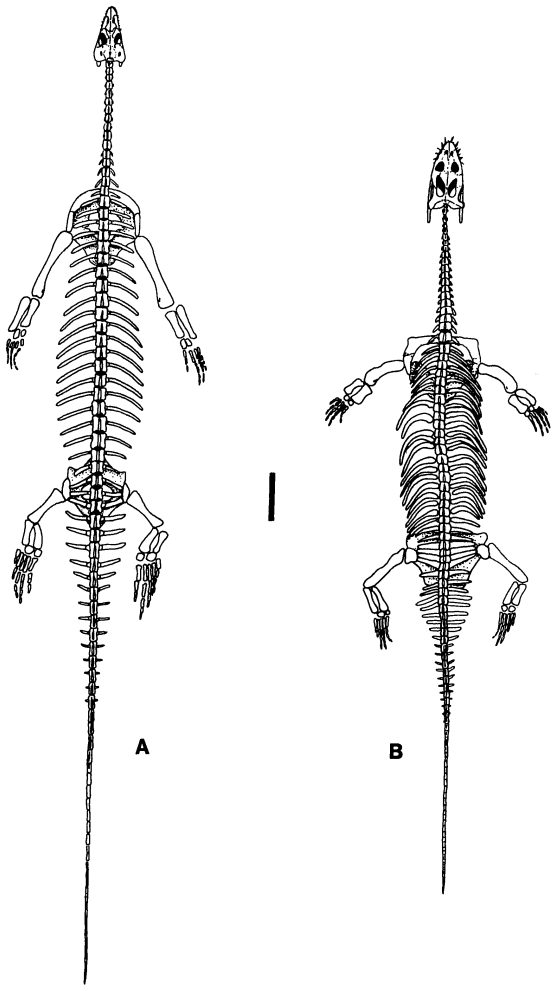

FIG. 38. Reconstructed 'nothosaur' skeletons in dorsal aspect. A, "*Pachypleurosaurus*" (= *Neusticosaurus*) modified from Carroll and Gaskill (1985) and Peyer (1944); B, *Lariosaurus* after Peyer (1933). Compare with Fig. 21. Scale bar = 5.0 cm. (Most specimens of *Neusticosaurus* smaller.)

primitive diapsid *Petrolacosaurus* (following Rieppel 1989), the Younginiformes, and *Claudiosaurus* as primitive outgroups for comparison with the traditional Sauropterygia during rigorous character analysis. It is a happy circumstance that *Claudiosaurus* and the Younginiformes, as potential structural "ancestors" and sister-groups to the unknown ancestors of the mainstream Sauropterygia, are Permian in age, whereas no undisputed 'nothosaur' or plesiosaur is known from before the Triassic (although by definition the lineage must have been present). Most 'nothosaurs' are Middle Triassic in age and the group does not appear to enter the Jurassic. Plesiosaurs are primarily Jurassic and Cretaceous animals.

Each of the major groups of the Sauropterygia have likewise been examined for presumably derived characteristics and these are listed in Table 2. Appendix C details discussions of each character and its significance. Figure 40 provides a hypothetical cladogram of sauropterygian relationships which was constructed from these characters and which places each derived suite in perspective. The 84 characters of the data matrix were analyzed with the branch and bound algorithm of PAUP (Phylogenetic Analysis Using Parsimony) for the MacIntosh v.3.0 (Swofford 1989). Six equally parsimonious trees of 150 steps were produced at

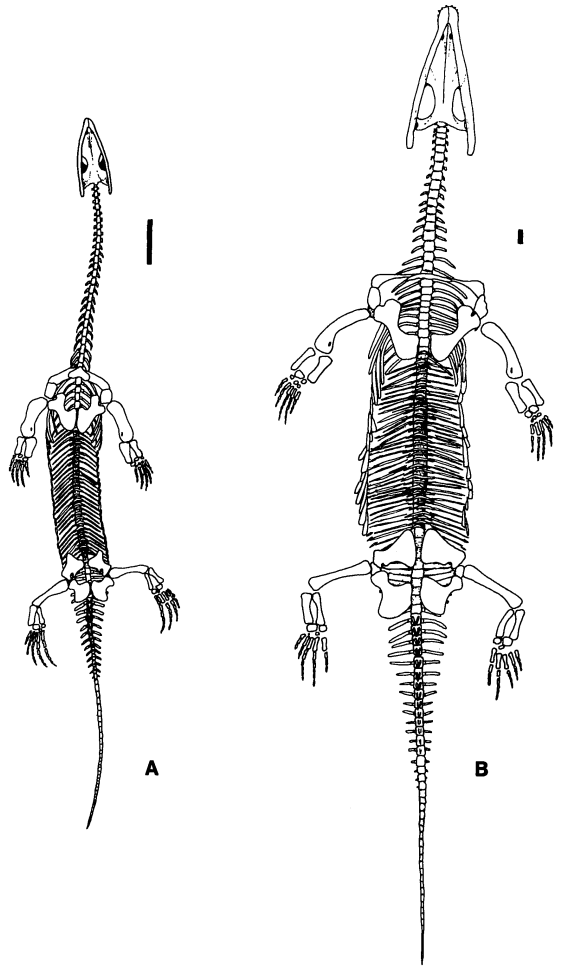

FIG. 39. Reconstructed 'nothosaur' skeletons in ventral aspect. A, *Ceresiosaurus* after Kuhn-Schnyder (1964) and Peyer (1931, 1944); B, *Paranothosaurus* after Peyer (1939). Compare with Fig. 21. Scale bars = 10.0 cm.

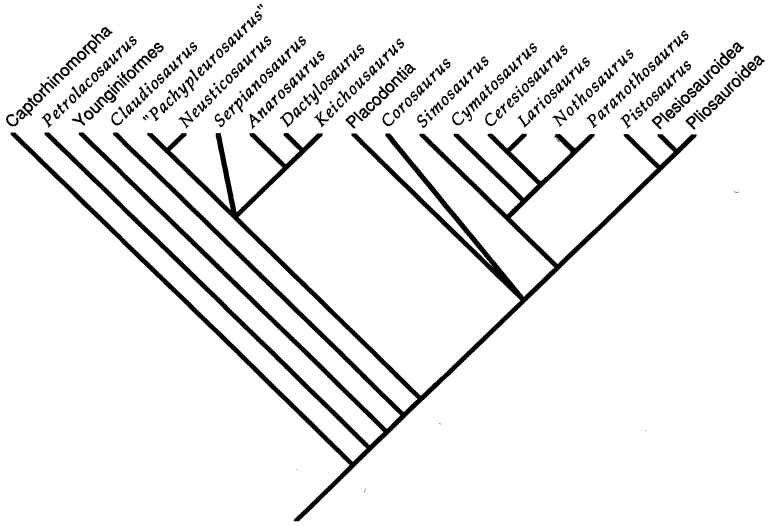

FIG. 40. Cladogram of hypothetical relationships of the Sauropterygia and outgroups.

TABLE 2. Data matrix of sauropterygian character states for 21 taxa (including outgroups). Each character is fully discussed in Appendix C.

		1 size	2 neck	3 skull	4 arch	5 stf	6 tem	7 qj	8 notch
1	Captorhinomorpha	0	0	0	?	?	?	0	0
2	*Petrolacosaurus*	0	0	0	0	0	?	0	0
3	Younginiformes	0	0	0	0	0	?	0	1
4	*Claudiosaurus*	0	0	0	1	0	0	0	1
5	*Pachypleurosaurus*	0	1	?	1	0	0	0	1
6	*Neusticosaurus*	0	1	?	1	0	0	0	1
7	*Serpianosaurus*	0	1	?	1	0	0	0	1
8	*Anarosaurus*	0	1	?	1	0	0	?	?
9	*Daciylosaurus*	0	1	?	1	0	0	?	?
10	*Keichousaurus*	0	1	?	1	0	0	?	?
11	Placodontia	1	0	1	1	1	1	0	1
12	*Simosaurus*	1	1	1	1	1	0	0	0
13	*Corosaurus*	1	1	1	1	1	0	?	0
14	*Ceresiosaurus*	1	1	1	1	1	0	1	0
15	*Lariosaurus*	0	1	1	1	1	0	1	0
16	*Cymatosaurus*	1	1	1	1	1	0	1	0
17	*Nothosaurus*	1	1	1	1	1	0	1	0
18	*Paranothosaurus*	1	1	1	1	1	0	1	0
19	*Pistosaurus*	1	1	1	1	1	1	1	0
20	Plesiosauroidea	1	1,2	1	1	1	1	1	0
21	Pliosauroidea	1	1	1	1	1	1	1	0

Continued on next page

a consistency index of 0.607. This is a high index for analysis of 21 taxa. Figure 40 is a strict consensus of these trees. No *a priori* character weighting was assumed, for such cannot be empirically supported. Characters chosen were, however, presumed to have phylogenetic significance. Although the data exhibit less structure at 151 steps, a strict consensus tree still differentiates between the major clades of Figure 40.

Claudiosaurus was undoubtedly an aquatic reptile with an origin among terrestrial forebears as discussed by Carroll (1981, 1988). It would appear to follow that 'nothosaurs,' placodonts, and plesiosaurs also represent a return to an aquatic environment, in spite of the doubts expressed by Romer (1974). How are these groups related to *Claudiosaurus* and to each other? They retain (as primitive features) the derived characters exhibited by *Claudiosaurus* over the Younginiformes, but of course, also display unique characters of their own (Table 2). *Claudiosaurus,* while probably not the ancestor of the Sauropterygia, represents a suitable structural analog for the animal that was. From this transitional grade, and following the results of cladistic analysis, can be postulated the origin of two divergent sauropterygian lineages currently recognized as placodonts + 'nothosaurids' + plesiosaurs, and the pachypleurosaurs. These monophyletic sister clades may hereafter be referred to as the **Nothosauriformes** (new taxon) and the Pachypleurosauria, respectively. These groups largely correspond to those produced by Sues (1987), Rieppel (1989), and Tschanz (1989). Tschanz's (1989) Eusauropterygia is similar to the Nothosauriformes but excludes the placodonts. The pachypleurosaurs are monophyletic whereas the monophyletic plesiosaurs arose from the paraphyletic 'nothosaurids.' The taxon Nothosauria is paraphyletic and therefore no longer tenable. I believe that Tschanz's (1989) use of a restricted Nothosauria is confusing and ill-advised in light of the strong historical connotations of the word.

TABLE 2 -- *Continued*

		9	10	11	12	13	14	15	16
		subf	pal/pt	vacuity	flange	pmx/n	n/prf	st	stf shape
1	Captorhinomorpha	?	0	0	0	0	0	0	?
2	*Petrolacosaurus*	0	0	0	0	0	0	0	0
3	Younginiformes	0	0	0	0	0	0	0	0
4	*Claudiosaurus*	0	0	0	1	0	0	0	0
5	*Pachypleurosaurus*	1	0	1	1	1	0	1	0
6	*Neusticosaurus*	1	0	1	1	0,1	0	1	1
7	*Serpianosaurus*	1	0	1	1	0	0	1	0
8	*Anarosaurus*	1	0	1	1	0	0	1	0
9	*Dactylosaurus*	1	0	1	1	0	0	1	1
10	*Keichousaurus*	1	0	1	1	1	0	1	1
11	Placodontia	0	1	1	0	0	0	1	0
12	*Simosaurus*	1	0	1	1	1	1	1	1
13	*Corosaurus*	1	?	?	0	0	0	1	0
14	*Ceresiosaurus*	1	?	1	1	0	0	1	1
15	*Lariosaurus*	1	0	1	1	0,1	0	1	1
16	*Cymatosaurus*	1	0	1	1	1	1	1	1
17	*Nothosaurus*	1	0	1	1	0	1	1	1
18	*Paranothosaurus*	1	0	1	1	0	1	1	1
19	*Pistosaurus*	1	0	0	1	1	0	1	1
20	Plesiosauroidea	1	0	0	1	?	?	1	0,1
21	Pliosauroidea	0,1	0	0	1	?	?	1	0,1

Continued on next page

The time of origin of the nothosauriform and pachypleurosaur phyletic lines is likely to have been the latest Permian to earliest Triassic but is poorly represented by contemporary sauropterygian fossil material. The presence of *Claudiosaurus,* the relatively plesiomorphic sister taxon to the Pachypleurosauria, in the Upper Permian suggests a Late Permian minimum time of divergence for these two groups. Thus, by definition, the sauropterygian lineage must also have been present by at least the Upper Permian. Once thought to have been ancestral to plesiosaurs (e.g., Seeley 1882; Tarlo 1967), 'nothosaurs' in general were later often excluded from this role on the basis of one discrete character, namely their lack of interpterygoid fenestrae (Romer 1966). Plesiosaurs retain the primitively "open" format of 'eosuchians' in which the basicranium is largely exposed between the pterygoids. The functional significance, if any, of an open versus a closed palate is not yet understood and the apparent character (evolutionary) reversal from a closed to open palate has not been evaluated. However, the most parsimonious explanation in this case, considering the numerous nothosauriform synapomorphies of Table 2, should be adopted: the ancestral plesiosaur stock probably arose from within the traditional 'nothosaurids' and they coincidentally with the Placodontia (Fig. 40).

In the present analysis, the placodonts as currently known are confirmed as sauropterygians, for they share the derived features of: a single upper temporal opening; no interpterygoid vacuity (plesiosaurs seemingly reverse this character); loss of supratemporal, postparietal, tabular, and lachrymal; retracted nares; prominent retroarticular process; loss of trunk intercentra; minimum of three sacral vertebrae; no sternum; divided scapulocoracoid; scapula superficial to the clavicle; a straight clavicular bar with a pronounced anterolateral corner (reversal in plesiosaurs); and pectoral and thyroid fenestration. Perhaps surprisingly, they sort out in the analysis as nothosauriforms in sharing: large size; a large supratemporal fenestra; a posterolateral process to the frontal; an elongate jugal that extends caudad from the orbit; a stout mandibular symphysis; platycoelous ver-

TABLE 2 -- *Continued*

		17 po/stf	18 pf shape	19 pf/stf	20 pp	21 tabular	22 1	23 l/en	24 jugal/o
1	Captorhinomorpha	?	0	?	0	0	0	0	0
2	*Petrolacosaurus*	0	0	0	0	0	0	0	0
3	Younginiformes	0	0	0	0	0	0	1	0
4	*Claudiosaurus*	0	0	0	0	0	0	1	0
5	*Pachypleurosaurus*	1	0	0	1	1	?	?	0
6	*Neusticosaurus*	1	0	0	1	1	1	?	0
7	*Serpianosaurus*	1	0	0	1	1	1	?	0
8	*Anarosaurus*	0	0	0	1	1	1	?	0
9	*Dactylosaurus*	0	0	0	1	1	1	?	0
10	*Keichousaurus*	0	?	?	1	1	1	?	0
11	Placodontia	0	0	0	1	1	1	?	0
12	*Simosaurus*	0	1	0	1	1	1	?	0
13	*Corosaurus*	0	0	0	1	1	1	?	1
14	*Ceresiosaurus*	0	?	?	1	1	1	?	?
15	*Lariosaurus*	0	0	0	1	1	1	?	1
16	*Cymatosaurus*	0	1	0	1	1	1	?	0
17	*Nothosaurus*	0	1	0	1	1	1	?	1
18	*Paranothosaurus*	0	1	1	1	?	?	?	1
19	*Pistosaurus*	0	0	0	1	1	1	?	0
20	Plesiosauroidea	0	?	0	1	1	1	?	0
21	Pliosauroidea	0	?	0	1	1	1	?	0

Continued on next page

tebrae; and a strongly curved humerus (reversal in plesiosaurs). The obvious diagnostic features of the placodonts such as a stout coronoid process, palatines that usually meet to separate the pterygoids, crushing palatal and marginal teeth, hyposphene/hypantrum articulations, and occasional dermal armor are all synapomorphies for the group that under the present systematic philosophy can potentially be ascribed to evolution following the placodont/'nothosaurid' + plesiosaur divergence. Similarly, the large jugal and quadratojugal may have been reelaborated as an evolutionary reversal in response to function. The Placodontia are presumably monophyletic; however, this group requires substantially more anatomical elucidation.

No clear synapomorphies can as yet resolve a basal trichotomy between the Placodontia and the remaining nothosauriforms. The loss of the quadratojugal is significant beyond the *Simosaurus* node, but if *Simosaurus* in reality also lacks a quadratojugal, traditional 'nothosaurids' + plesiosaurs might be resolved in the future. Unfortunately, this character is presently equivocal in *Corosaurus* (although likely to be derived). Nothosauriformes minus the Placodontia also have no quadrate notch, usually reduced nasals and prefrontals, and largely platycoelous vertebral centra. Reversals and convergences in the various lineages are enumerated in Appendix C.

The possible functional changes, in light of nothosauriform anatomy, that might have allowed the evolution of plesiosaurs from an animal structurally akin to 'nothosaurids,' have been discussed in Chapter 3. *Pistosaurus,* a Middle Triassic (Upper Muschelkalk) contemporary of the 'nothosaurids,' had an open palate, but the postcrania sometimes assigned to this genus are rather primitive in several respects (Carroll and Gaskill 1985; E. von Huene 1949; F. von Huene 1948c; von Meyer, 1847–55; Sanz 1983b; Sues 1987). The body appears to have been relatively long and narrow; accessory vertebral articulations were present; the humerus and femur were slender; the epipodials were long; and the ilium was in contact with the pubis in *Pistosaurus* as in primitive nothosauriforms. Conversely, *Pistosaurus* had ventral nutritive foramina in the vertebral centra, long transverse

TABLE 2 -- *Continued*

		25	26	27	28	29	30	31	32
		jugal/qj	j shape	parietals	p for	frontals	f shape	pfr	plt dent
1	Captorhinomorpha	0	0	0	0	0	0	0	0
2	*Petrolacosaurus*	0	0	0	0	0	0	0	0
3	Younginiformes	0	0	0	0	0	1	0	0
4	*Claudiosaurus*	1	1	0	0	0	1	0	0
5	*Pachypleurosaurus*	1	1	0	0	0,1	1	0	1
6	*Neusticosaurus*	1	1	0	0	0,1	1	0	1
7	*Serpianosaurus*	1	1	0	0	0,1	1	0	1
8	*Anarosaurus*	?	1	0	0	?	1	0	1
9	*Dactylosaurus*	?	1	0	1	0	1	0	1
10	*Keichousaurus*	?	1	0	1	0	1	0	1
11	Placodontia	0	2	0	0	0	0	0	0
12	*Simosaurus*	1	2	0	0	0	0	1	1
13	*Corosaurus*	?	2	0	0	0	1	0	1
14	*Ceresiosaurus*	?	?	0	0	?	0	0	1
15	*Lariosaurus*	?	?	0	1	0	0	1	1
16	*Cymatosaurus*	?	?	0	0	0	0	1	1
17	*Nothosaurus*	?	2	1	1	1	0	1	1
18	*Paranothosaurus*	?	2	1	1	1	0	1	1
19	*Pistosaurus*	?	2	0	0	0	?	?	1
20	Plesiosauroidea	?	2	0	0	0	0	1	1
21	Pliosauroidea	?	2	0	0	0	1	1	1

Continued on next page

processes, tall neural spines, elongate coracoids, no entepicondylar foramen, and relatively broad epipodials which are synapomorphic for plesiosaurs. Vertebral nutritive foramina (foramina subcentralia) are a uniquely derived character shared by virtually all plesiosaurs (excepting the very unusual *Brachauchenius* of the North American Cretaceous), and are unknown in pachypleurosaurs, placodonts and 'nothosaurid' grade nothosauriforms. While the skull of *Pistosaurus* retains the nasals, unlike that of advanced plesiosaurs, the nasals no longer contact the borders of the external nares as they do in more plesiomorphic nothosauriforms. On the basis of these characters as well as the open palate, *Pistosaurus* must be considered a primitive plesiosaur (Fig. 40).

Several problematic Permo-Triassic sauropterygian specimens may also occupy a place in the plesiosaur lineage, but these are usually too fragmentary to be of any real taxonomic value. Others may be the bones of 'nothosaurids,' pachypleurosaurs, or even of representatives of the pre-nothosauriform/pachypleurosaur grade. Von Huene (1929) described two amphicoelous dorsal vertebrae and a dorsal rib from the German Upper Keuper (Late Triassic), probably correctly, as those of a plesiosaur. In overall appearance, these remains differ little from those of undoubted Liassic plesiosaurs. Similar vertebral centra with obvious ventral nutrient foramina, apparently from primitive plesiosaurs, are occasionally contained in collections of assorted Triassic material. Two such specimens are in the British Museum (Natural History) and are associated with isolated centra of "*Nothosaurus*" (BMNH 1103 and 8201). These vertebrae are from the Bavarian Muschelkalk. A third is figured by Sanz (1983b), again as "*Nothosaurus,*" while a similar isolated sauropterygian centrum from the Ladinian of the Lena Basin of the Soviet Union has been assigned to "*Nothosaurus*(?)" (Lazurkin and Ochev 1968).

The genus *Elmosaurus* v. Huene, 1957 from the Upper Muschelkalk has been commonly referred to the 'Nothosauria' (Carroll 1988; Carroll and Gaskill 1985; v. Huene 1957) but is enigmatic. Known only from a single, intermediately-sized, fragmentary skull, *Elmosaurus* displays a cranial morphology profoundly different

TABLE 2 -- *Continued*

		33	34	35	36	37	38	39	40
		rostrum	nasal	en	n/en	diastema	dent or	dentition	t shape
1	Captorhinomorpha	0	0	0	0	0	0	0	0
2	*Petrolacosaurus*	0	0	0	0	0	0	0	0
3	Younginiformes	0	0	0	0	0	0	1	0
4	*Claudiosaurus*	0	0	0	0	0	0	1	0
5	*Pachypleurosaurus*	0	0	1	0	0	1	1	0
6	*Neusticosaurus*	0	0	1	0	0	1	1	0
7	*Serpianosaurus*	0	0	1	0	0	1	1	0
8	*Anarosaurus*	0	0	1	0	0	1	1	0
9	*Dactylosaurus*	0	0	1	0	0	1	1	0
10	*Keichousaurus*	0	0	1	0	0	1	1	0
11	Placodontia	1	0	1	0	1	1	0,1	2,3
12	*Simosaurus*	0	0	1	0	0	1	1	1
13	*Corosaurus*	0	0	1	0	0	1	0	0
14	*Ceresiosaurus*	0	0	1	1	0	1	?	0
15	*Lariosaurus*	0	0	1	0	0	1	0	0
16	*Cymatosaurus*	1	0	1	0	0	1	0	0
17	*Nothosaurus*	1	0	1	0	0	1	0	0
18	*Paranothosaurus*	1	0	1	0	0	1	0	0
19	*Pistosaurus*	1	0	1	1	0	1	1	0
20	Plesiosauroidea	0	1	1	?	0	1	1	0
21	Pliosauroidea	0,1	1	1	?	0,1	1	0,1	0

Continued on next page

from those of all other known sauropterygians. The skull is of apparent euryapsid configuration, but the supratemporal fenestra is bounded on three sides by the huge squamosal, excluding both the postorbital and the postfrontal from the temporal opening. Unlike the case in other sauropterygians, an extremely large lachrymal is present. The nature of the posterior palate is unknown and without more material the animal must be considered ?Sauropterygia *incertae sedis*.

F. Von Huene (1944) has described an isolated left humerus of a primitive sauropterygian from the Lower Muschelkalk. This curved element is very reminiscent of 'nothosaurs' but lacks both epicondylar foramina and thus appears to be part of the plesiosaur radiation. Its plesiomorphic curvature may be the result of an ontogenetic or paedomorphic effect. Von Huene (1951) has also described a possible sauropterygian epipodial from a stromatolitic unit of the Lower Triassic (Scythian) Lower Buntsandstein of Germany. This bone is difficult to interpret but has the appearance of a 'nothosaur' tibia. Von Huene (1951) identified the bone as that of a pachypleurosaur, but as its characteristics are primitive, it is also *incertae sedis*. Its stratigraphic position is, nevertheless, interesting. Lastly, *Nothosauravus* Kuhn, 1958a was named for a single, small, amphicoelous sacral vertebra (Kuhn 1939) from the lower Upper Permian Kupferschiefer. This problematic bone has a 'nothosaurian' appearance and may be that of a primitive sauropterygian. The specimen is, however, generically nondiagnostic.

The environmental condition(s) and evolutionary mechanism(s) that might have led to the origin of the Sauropterygia, and then more specifically to the respective origins of the pachypleurosaurs and nothosauriforms, including plesiosaurs and placodonts, are unknown. The limited sample sizes and temporal ranges of the animals involved also preclude any knowledge of the tempo(s) and mode(s) of their evolution. Examination of the ontogenetic series provided by Currie (1981) for the tangasaurid *Hovasaurus,* by Currie and Carroll (1984) for *Thadeosaurus,* by Carroll (1981) for *Claudiosaurus,* and by numerous, isolated, juvenile remains of 'nothosaurs' and plesiosaurs (e.g., Andrews 1910) suggests, however, that the various forms of sauropterygians might have been derived in part through a process of paedomorphic (heterochronous) development. The juvenile humeri of

TABLE 2 -- *Continued*

		41	42	43	44	45	46	47	48
		mx can	pmx can	sym	ret p	intc	centrum	fo sub	z
1	Captorhinomorpha	0	?	0	0	0	0	0	0
2	*Petrolacosaurus*	0	?	0	0	0	0	0	0
3	Younginiformes	1	?	0	0	0	0	0	0
4	*Claudiosaurus*	1	0	0	0	0	0	0	0
5	*Pachypleurosaurus*	1	1	0	1	1	0	0	0
6	*Neusticosaurus*	1	0	0	1	1	0	0	0
7	*Serpianosaurus*	1	0	0	1	1	0	0	0
8	*Anarosaurus*	1	0	0	1	1	?	0	0
9	*Dactylosaurus*	1	0	0	1	1	?	0	0
10	*Keichousaurus*	1	0	0	1	1	?	0	0
11	Placodontia	1	0	1	1	1	0	0	0
12	*Simosaurus*	1	0	?	1	1	1	0	0
13	*Corosaurus*	1	0	1	1	1	0	0	0
14	*Ceresiosaurus*	?	?	1	1	1	?	0	0
15	*Lariosaurus*	0	1	1	1	1	0	0	0
16	*Cymatosaurus*	0	0	1	?	?	?	?	?
17	*Nothosaurus*	0	1	1	1	1	1	0	0
18	*Paranothosaurus*	0	1	1	1	1	1	0	0
19	*Pistosaurus*	1	0	1	?	1	1	1	0
20	Plesiosauroidea	1	0	1	1	1	1	1	1
21	Pliosauroidea	0	0,1	1	1	1	1	1	1

Continued on next page

each taxon, for example, are remarkably similar in form, becoming less similar only in later ontogenetic stages (Baer's law). The humeri of pachypleurosaurs and primitive nothosauriforms, especially, are very much like those of the juveniles of *Hovasaurus* and *Thadeosaurus* and in particular lack the prominent condyles of the adult 'eosuchians.' Similarly, juvenile pectra of the Jurassic plesiosaur *Cryptocleidus* resemble the generalized 'nothosaur' pattern with a large pectoral fenestra and relatively reduced coracoids (Carroll and Gaskill 1985). Mosaic, variable rates of embryologic and juvenile development, the retention of juvenile traits, and hypertrophic elaboration of characters during ontogeny are probably major sources of morphologic variability and macroevolutionary change in all phyla. The reduced and latent ossification of marine reptile skeletons may increase the susceptibility of these animals to such change. In the Sauropterygia, specifically, morphologic diversity is largely the result of proportional variation.

Carroll and Gaskill (1985) have discussed the possible evolutionary reduction and reelaboration of the sauropterygian pectrum in relation to the reversed endochondral and dermal pectoral elements of this group. The scapulae and interclavicle are superficial to the clavicles in the Nothosauriformes and Pachypleurosauria but in few other groups. According to Rieppel (1989) this may also be true for the Placodontia. Such a change could conceivably only occur at an early stage of ontogenetic development prior to the ossification of the pectrum. Additional examples of presumed proportional and structural change during ontogeny can be hypothesized but, because of the likelihood of allopatric speciation and possible evolutionary punctuations (for whatever reason), few transitional fossils are to be expected. I cannot accept Schmidt's (1987) interpretation of the dermal elements of the sauropterygian pectrum as new endochondral ossifications.

'NOTHOSAUR' RELATIONSHIPS

By using the discussions presented above, the relationships of the two 'nothosaur' groups—one monophyletic, the other paraphyletic—and the specific position of *Corosaurus* can be examined. It seems clear that the pachypleurosaurs are mono-

TABLE 2 -- *Continued*

		49	50	51	52	53	54	55	56
		zo/za	ho/ha	sac v	sac r	pachy	gastralia	armour	sternum
1	Captorhinomorpha	0	0	0	0	0	?	0	?
2	*Petrolacosaurus*	0	0	0	0	0	?	0	?
3	Younginiformes	1	0	0	0	0	0	0	0
4	*Claudiosaurus*	1	0	0	0	0	0	0	1
5	*Pachypleurosaurus*	1	0	1	1	1	1	0	2
6	*Neusticosaurus*	1	0	1	1	1	1	0	2
7	*Serpianosaurus*	1	0	1,2	1	0	0	0	2
8	*Anarosaurus*	?	0	1	1	1	0	0	2
9	*Dactylosaurus*	?	0	1	1	0,1	0	0	2
10	*Keichousaurus*	?	0	0	1	1	?	0	2
11	Placodontia	0	1	1	?	0	0	0,1	2
12	*Simosaurus*	1	0	3	0	0	?	0	2
13	*Corosaurus*	1	0	1	0	0	0	0	2
14	*Ceresiosaurus*	?	0	2,3	1	1	0	0	2
15	*Lariosaurus*	?	0	3	1	1	0	0	2
16	*Cymatosaurus*	?	?	?	?	?	0	?	?
17	*Nothosaurus*	1	0	1,2,3	0	0	?	0	2
18	*Paranothosaurus*	1	0	3	0	0	?	0	2
19	*Pistosaurus*	1	0	1	0	0	?	0	2
20	Plesiosauroidea	0	0	1	0	0	0	0	2
21	Pliosauroidea	0	0	1	0	0	0	0	2

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phyletic and distinct from the remaining sauropterygians. Rieppel (1989) contends that the loss of the ectopterygoid characterizes the pachypleurosaurs. This character is, however, difficult to evaluate in most nothosauriform specimens. A ventral quadrate projection for suspension of the tympanum may also be diagnostic (Rieppel 1989). In spite of Rieppel's (1989) objections, there may be a divergent trend for supratemporal fenestra reduction in the pachypleurosaurs and a general "pachyostotic" thickening of the ribs accompanied by narrowed distal ends of the sacral ribs may also be significant.

As in the works of Rieppel (1989), Tschanz (1989), Sues (1987), and Sues and Carroll (1985), the present study suggests that the Pachypleurosauria are the relatively plesiomorphic sister group to the remaining sauropterygians; they certainly exhibit fewer derived characters than do the nothosauriform 'nothosaurs.' These differences are discussed in the above noted works and can be found also in Table 2.

Under the present hypothesis of relationships the known members of the Pachypleurosauria are *Anarosaurus, Dactylosaurus, Neusticosaurus,* "*Pachypleurosaurus*" (probably a specific variant of *Neusticosaurus*), *Keichousaurus,* and *Serpianosaurus.* These genera share the basic pachypleurosaur suite of derived characteristics as discussed above and in Appendix C. *Psilotrachelosaurus,* as a poorly known taxon, has not been included in the analysis but, if distinct, is most likely a pachypleurosaur. The interrelationships of the Pachypleurosauria are known with far less certainty than is its probable composition. Enough anatomical knowledge is available for construction of the clade, but very little for clarification of its internal genealogy. However, with the few additional derived characters gleaned from individual pachypleurosaur anatomies (Table 2), a preliminary, hypothetical cladogram of part of the group is suggested (Fig. 40). Certainly *Neusticosaurus* and "*Pachypleurosaurus*" (sensu Carroll and Gaskill 1985) form a clade because of their many synapomorphies (Table 2), while *Anarosaurus, Keichousaurus,* and *Dactylosaurus* apparently also form a distinct clade. The present analysis suggests a basal trichotomy between these two pachypleurosaur groups and *Serpianosaurus.* If the impedance matching middle ear of Rieppel (1989) and Sander (1989), and

TABLE 2 -- *Continued*

		57 cleitrum	58 icl	59 icl size	60 cl corner	61 sc/cor	62 scapula	63 cor ex	64 sup f
1	Captorhinomorpha	0	0	0	0	0	0	?	0
2	*Petrolacosaurus*	0	0	0	0	0	0	?	0
3	Younginiformes	0,1	0	0	0	0	0	?	0
4	*Claudiosaurus*	1	0	0	0	0	0	?	0
5	*Pachypleurosaurus*	1	0	1	0,1	1	1	0	0
6	*Neusticosaurus*	1	0	1	0,1	1	1	0	0
7	*Serpianosaurus*	1	0,1	1	1	1	1	0	0
8	*Anarosaurus*	1	?	?	?	1	1	0	1
9	*Dactylosaurus*	1	?	?	1	1	1	0	1
10	*Keichousaurus*	1	0	1	0,1	1	1	0	1
11	Placodontia	1	0	1	1	1	1	?	0
12	*Simosaurus*	1	0	0	1	1	1	0	0
13	*Corosaurus*	1	0	1	1	1	1	0	1
14	*Ceresiosaurus*	1	1	?	?	1	1	0	0
15	*Lariosaurus*	1	1	?	1	1	1	0	0
16	*Cymatosaurus*	?	?	?	?	?	?	?	?
17	*Nothosaurus*	1	0	1	1	1	1	0	0
18	*Paranothosaurus*	1	1	?	1	1	1	0	0
19	*Pistosaurus*	1	?	?	?	1	1	1	1
20	Plesiosauroidea	1	1	?	0	1	1	1	1
21	Pliosauroidea	1	1	?	0	1	1	1	1

Continued on next page

the bone ornamentation of Sander (1989) are accepted as synapomorphies for *Neusticosaurus*, "*Pachypleurosaurus*," and *Serpianosaurus*, the trichotomy is resolved with *Serpianosaurus* forming the plesiomorphic sister of the neusticosaurs (Fig. 41).

Similarly, for the nothosauriform 'nothosaurs' Figure 40 presents a hypothetical cladistic hierarchy that includes *Ceresiosaurus, Corosaurus, Cymatosaurus, Lariosaurus, Nothosaurus, Paranothosaurus* and *Simosaurus*. *Sanchiaosaurus* may be provisionally placed in this group but is, however, too poorly known for inclusion in the cladogram. The characters forming the basis of relationship are again listed in Table 2. *Nothosaurus* and *Paranothosaurus* form a closely related unit, as expected.

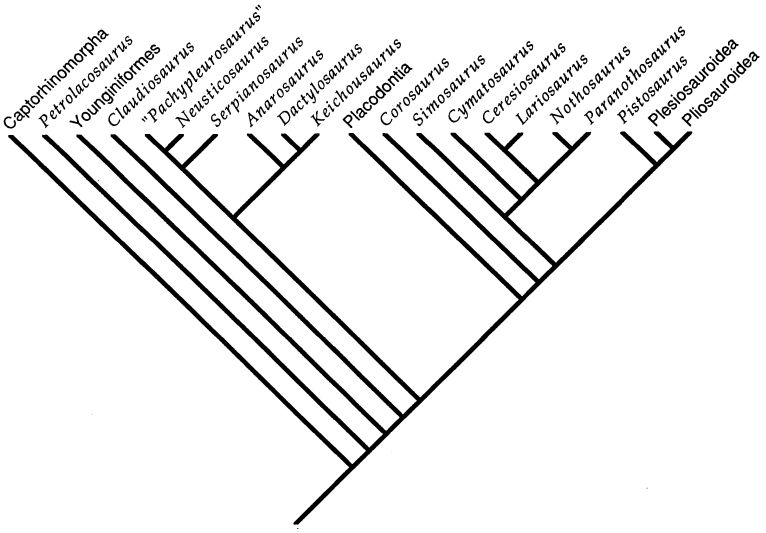

FIG. 41. Revised cladogram of hypothetical sauropterygian and outgroup relationships indicating likely resolutions of analysis trichotomies as discussed in text.

TABLE 2 -- *Continued*

		65 pec f	66 pec b	67 ilc b	68 ilm/pub	69 pub	70 obt f	71 thy f	72 forelimb
1	Captorhinomorpha	0	?	0	0	0	0	0	0
2	*Petrolacosaurus*	0	?	0	0	0	0	0	0
3	Younginiformes	0	?	0	0	0	0	0	0
4	*Claudiosaurus*	0	?	0	0	0	0	0	0
5	*Pachypleurosaurus*	1	0	1	0	0	0	1	0
6	*Neusticosaurus*	1	0	1	0	0	0	1	0
7	*Serpianosaurus*	1	0	1	0	0	0	1	0
8	*Anarosaurus*	1	0	?	0	0	?	1	0
9	*Dactylosaurus*	1	0	1	0	0	0	1	0
10	*Keichousaurus*	1	0	1	0	0	?	1	0
11	Placodontia	1	0	0	0	0	0	1	0
12	*Simosaurus*	1	0	0	0	0	0	1	0
13	*Corosaurus*	1	0	0	0	1	0	1	0
14	*Ceresiosaurus*	1	0	1	0	0	0	1	1
15	*Lariosaurus*	1	0	1	0	?	0	1	0
16	*Cymatosaurus*	?	?	0	?	?	?	?	?
17	*Nothosaurus*	1	0	1	0	0	0	1	0
18	*Paranothosaurus*	1	0	1	0	0	0	1	0
19	*Pistosaurus*	1	0	2	0	?	?	1	0
20	Plesiosauroidea	1	0,1	2	1	1	1	1	0
21	Pliosauroidea	1	0,1	2	1	0,1	1	1	0

Continued on next page

A clade united primarily by distally unexpanded sacral ribs, "pachyostosis," and no interclavicular posterior process contains *Ceresiosaurus* and *Lariosaurus* as the sister group to *Nothosaurus* + *Paranothosaurus*. Small size was apparently developed in *Lariosaurus* independently of the pachypleurosaurs. The two groups form a larger monophyletic clade which is the sister of *Cymatosaurus*. These groups plus *Cymatosaurus* exhibit the greatest number of uniquely derived traits of the known 'nothosaurids,' variously including increased sacral vertebral number, elongate temporal region and fenestrae, elongate skull and rostrum, fused frontals and parietals, maxillary caniniform teeth, the loss of a nasal/prefrontal contact, the presence of a rostral constriction, and a subrectangular postfrontal. The relative position of *Cymatosaurus* is based, of course, almost entirely upon cranial material.

Simosaurus seems to represent a separate lineage with an earlier origin and displays its own unique suite of derivations. The unusual autapomorphies of *Simosaurus,* such as its brevirostrine format and short, striated teeth cannot at this time support any hypothesis of relationship, although if shared by the poorly known *Shingyisaurus,* may indicate kinship. *Simosaurus* is apparently linked to the above nothosauriforms through the shared absence of a pterygoid flange, elongate supratemporal fenestrae, a prefrontal which is normally significantly smaller then the postfrontal, and an increased number of sacral vertebrae.

The sister to all of these 'nothosaurids' is the monophyletic Plesiosauria (containing *Pistosaurus* + typical Jurassic and Cretaceous forms). Future work is required to determine the phylogenetic validity of the traditional plesiosaur (sensu stricto) and pliosaur lineages.

Corosaurus, with its several derived postcranial features, nevertheless appears to have had the least recent common descent of all 'nothosaurids.' It has retained the presumably primitive characteristics of only three sacral vertebrae, a relatively unlengthened skull with a short temporal region, round supratemporal fenestrae, noncaniniform premaxillary teeth, amphicoelous vertebral centra, elongate femur, and similar traits. It would seem that only in a latter stage in the history of this

TABLE 2 -- *Continued*

		73 humerus	74 epic	75 ect f	76 ent	77 spa int	78 radius	79 joint	80 hyp
1	Captorhinomorpha	0	0	0	0	0	0	0	0
2	*Petrolacosaurus*	0	0	0	0	0	0	0	0
3	Younginiformes	0	0	1	0	0	0,1	0	0
4	*Claudiosaurus*	0	1	2	0	0	0	0	0
5	*Pachypleurosaurus*	0	1	2	0	0	1	0	0
6	*Neusticosaurus*	0	1	2	0	0	1	0	0
7	*Serpianosaurus*	0	1	2	0	0	1	0	0
8	*Anarosaurus*	0	1	2	0	0	?	0	1
9	*Dactylosaurus*	0	1	2	0	0	1	0	1
10	*Keichousaurus*	0	1	2	0	0	1	0	1
11	Placodontia	1	1	2	0,1	0	2	0	?
12	*Simosaurus*	1	1	2	0	0	?	0	?
13	*Corosaurus*	1	1	2	0	0	2	0	?
14	*Ceresiosaurus*	1	1	2	0	0	2	0	1
15	*Lariosaurus*	1	1	2	0	0	2	0	1
16	*Cymatosaurus*	?	?	?	?	?	?	?	?
17	*Nothosaurus*	1	1	2	0	0	2	0	1
18	*Paranothosaurus*	1	1	2	0	0	2	0	?
19	*Pistosaurus*	1	1	0	1	0	2	0	?
20	Plesiosauroidea	1,2	1	0	1	0,1	2	1	2
21	Pliosauroidea	2	1	0	1	1	2	1	2

Continued on next page

lineage did *Corosaurus* acquire its confusingly derived features or autapomorphies, particularly the expanded coracoid and pubis through which it is slightly reminiscent of plesiosaurs. We have already seen how such similarities might arise independently in parallel lineages. The expanded coracoid of *Corosaurus* is, in fact, only superficially like those of plesiosaurs and lacks the exceptional posterior development of the latter. The unresolved phylogenetic position of *Corosaurus* with regard to the placodonts has been discussed above and hinges on the equivocal presence or absence of a quadratojugal in *Corosaurus* and possibly *Simosaurus*. Assuming such a loss, and incorporating the resolutions of the above discussed trichotomies, a reasonable cladogram of sauropterygian relationships is presented in Figure 41.

The preliminary phylogenetic hypotheses presented here are, of course, falsifiable and likely to be altered by the acquisition of future data. Several additional nothosaurian-grade sauropterygians are so poorly known that they cannot yet be satisfactorily included in any classification scheme. These forms include *Chinchenia, Kwangsisaurus, Metanothosaurus, Partanosaurus, Proneusticosaurus,* and *Rhaeticonia.* All save *Rhaeticonia* are large forms possibly having some relationship to the Nothosauriformes but lacking conclusive cranial material. *Rhaeticonia* could be either an unusual pachypleurosaur with a constricted rostrum, a small 'nothosaurid' like *Lariosaurus,* or even the juvenile of some known form (e.g., *Cymatosaurus*?), but neither is its temporal configuration known. Each of these taxa is presently considered Sauropterygia *incertae sedis.*

HIERARCHICAL CLASSIFICATION

DIAPSIDA Osborn, 1903
NEODIAPSIDA Benton, 1985
LEPIDOSAUROMORPHA Benton, 1985
SAUROPTERYGIA Owen, 1860

Diagnosis. Small to large lacertiliform aquatic reptiles with derived diapsid ("euryapsid") cranial configuration. Deep lateral temporal emargination (reversal

TABLE 2 -- *Continued*

		81 car/tar	82 hindlimb	83 ulna	84 pisiform
1	Captorhinomorpha	0	0	0	0
2	*Petrolacosaurus*	0	?	0	0
3	Younginiformes	0	0	0	0
4	*Claudiosaurus*	0	0	0	0
5	*Pachypleurosaurus*	1	0,1	0	1
6	*Neusticosaurus*	1	1	0	1
7	*Serpianosaurus*	1	0,1	0	1
8	*Anarosaurus*	1	0	0	?
9	*Dactylosaurus*	1	1	0	0,1
10	*Keichousaurus*	1	0	1	1
11	Placodontia	1	?	0	?
12	*Simosaurus*	1	1	0	?
13	*Corosaurus*	1	0	0	1
14	*Ceresiosaurus*	1	1	1	0
15	*Lariosaurus*	1	0	1	1
16	*Cymatosaurus*	?	?	?	?
17	*Nothosaurus*	1	0	0	1
18	*Paranothosaurus*	1	0	0	1
19	*Pistosaurus*	?	0	0	?
20	Plesiosauroidea	0	1	1	0,1
21	Pliosauroidea	0	0	1	0,1

in Placodontia and Plesiosauria); no lower temporal fenestra or arcade. Jugal reduced; quadratojugal reduced or absent (reversal in Placodontia); nasals reduced or absent, nares retracted; supratemporal, tabular, and postparietal absent; lachrymal reduced or absent; no interpterygoid vacuity (reversal in Plesiosauria); prominent retroarticular process; cervical region elongate (reversal in Placodontia); trunk intercentra absent; three or more sacral vertebrae; sternum absent; scapulocoracoid divided; scapula and interclavicle superficial (ventral) to clavicle; straight clavicular bar with pronounced anterolateral corner (reversal in Plesiosauria); prominent pectoral and thyroid fenestration; ectepicondylar foramen reduced to notch or lost.

Range. ?Upper Permian–Upper Cretaceous (Maastrichtian).

PACHYPLEUROSAURIA Sanz, 1980

Diagnosis. Plesiomorphic sauropterygians with small supratemporal fenestrae (much smaller than orbits); ectopterygoid perhaps lost; quadrate hooked with pronounced otic notch; general "pachyostotic" thickening of bones (variably present in *Dactylosaurus*); sacral ribs reduced in diameter distally; slight hyperphalangy.

Range. Middle Triassic (lower Anisian–upper Ladinian).

NOTHOSAURIFORMES, new taxon

Diagnosis. Large sauropterygians (reversal in *Lariosaurus*) with large supratemporal fenestrae (larger than orbits); frontal with prominent posterolateral process; quadratojugal lost (independently?) in most lineages; no quadrate notch (except in Placodontia); stout mandibular symphysis; normally anisodont dentition with procumbent or caniniform teeth or both; vertebrae tending towards platycoely; humerus strongly curved (reversal in Plesiosauria); modified (flattened) epipodials.

Range. Lower Triassic (Scythian)–Upper Cretaceous (Maastrichtian).

PLACODONTIA Zittel, 1887–90

Diagnosis. Broad-bodied nothosauriforms with (secondarily?) short cervical region; quadratojugal contacts jugal; no temporal emargination (reelaboration?); pterygoids separated by palatines; stout coronoid process; crushing palatal and marginal dentition with diastema; hyposphene/hypantrum accessory articulations; dermal armor common.

Range. Triassic (upper Scythian–upper Rhaetian).

PLESIOSAURIA de Blainville, 1835

Diagnosis. Highly transformed nothosauriforms with stout thoracic and elongate cervical regions; interpterygoid vacuity (reversal); nasals reduced or, more commonly, lost; zygosphene/zygantrum articulations absent; high neural spines; zygapophyses narrower than centrum; foramina subcentralia; clavicular arch reduced; occasional pectoral and pelvic longitudinal "bars"; posterior ramus of iliac blade and iliopubic contact lost; no obturator foramen, anterior border of pubis expanded; propodials massive and largely straight; entepicondylar and ectepicondylar foramina lost; reduced or lost spatium interosseum; epipodials extremely short and flat; no midlimb joint; extreme hyperphalangy.

Range. Middle Triassic (upper Anisian)–Upper Cretaceous (Maastrichtian).

5. STRATIGRAPHY

INTRODUCTION

The Alcova Limestone of central Wyoming is a unique carbonate unit in an otherwise uninterrupted stratigraphic sequence of Triassic red bed deposits. Because of its striking departure from the lithologies of over- and under-lying units, the Alcova is readily identifiable in the field and has long had formal stratigraphic status. It has also enjoyed protracted importance as a marker unit and datum in outcrop and subsurface stratigraphic and structural studies. However, the age, regional correlation, and paleoenvironmental interpretation of the Alcova Limestone have proven difficult to resolve, largely because of its unusual character and position, its limited geographic extent, the stratigraphic and structural complexity of the Triassic System in Wyoming, and the rarity of fossils within, above, and below the Alcova. An excellent overview of these difficulties and of the Wyoming Triassic in general is provided in McKee et al. (1959).

The Alcova Limestone was originally defined by Lee (1927) as a member of the Chugwater Formation of Darton (1904) on the basis of outcrops near Alcova, Natrona County, Wyoming, at the southeastern edge of the Wind River Basin. Since that time, the Alcova has been widely noted and discussed (e.g., Burk 1953; High and Picard 1967a, 1969; Hubbell 1956; Kummel 1954; Love 1948, 1957; Picard 1967, 1978; Picard et al. 1969; Pipiringos 1953; Tohill and Picard 1966; etc.), but rarely studied in detail. The Alcova has generally maintained its member status, although Branson and Branson (1941) and Pipiringos (1968) elevated the unit to formational rank within the Chugwater Group. While the Alcova Limestone is easily recognized in the field, its slight thickness and local discontinuity make it generally unmappable at a scale of 1:25,000, a definitional requirement of a formation, and member status should be retained for this stratigraphic unit. Its genetic history, discussed below, is also relevant to its member rank.

The nomenclatural histories of the surrounding rocks are somewhat more complex. Love (1939) was first to divide the red beds of the Chugwater into subunits, including in part, the Red Peak, Crow Mountain, and Popo Agie members. There was no mention of the Alcova in Love's field area where it was

TABLE 3. Nomenclature and principal rock types of the Chugwater Group. Oldest units at bottom (modified from Picard 1978).

STRATIGRAPHIC UNIT	PRINCIPAL ROCK TYPES
Popo Agie Formation	arkosic silts, carbonates
Crow Mountain Formation	
"upper sandstone/siltstone unit"	arkosic sandstone, siltstone
"basal sandstone unit"	arkosic sandstone
Alcova Limestone Member	carbonates
"variegated sandy facies"	arkosic sandstone
Red Peak Formation	arkosic clay, silts, sands

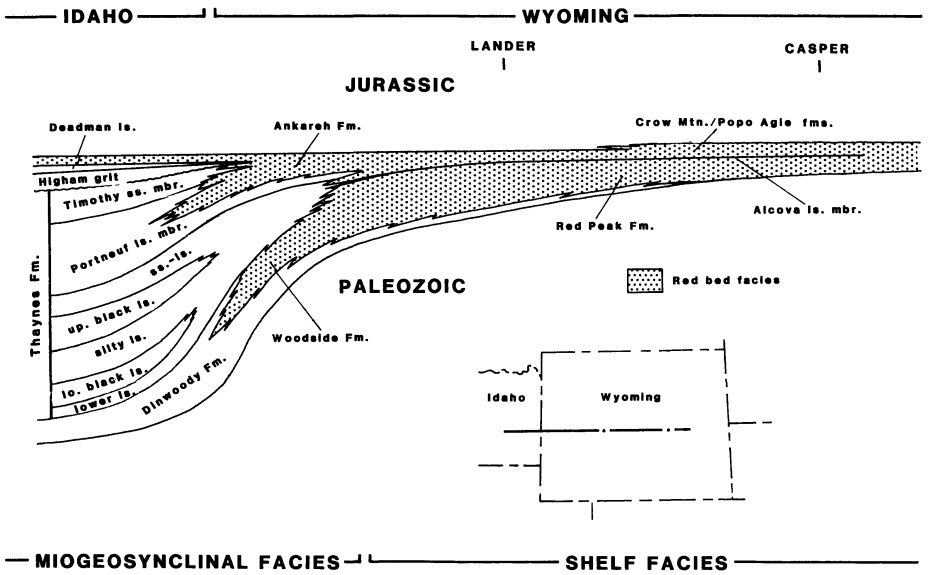

FIG. 42. Generalized stratigraphic diagram of inferred Triassic rock relations in Wyoming. Not to scale. Redrawn from Carini (1964) with modifications from Kummel (1955) and Picard et al. (1969).

apparently absent. A series of studies by High and Picard (1967a, b, 1969), Picard (1964, 1965, 1966, 1967, 1978), Picard et al. (1969), and Tohill and Picard (1966) have refined the boundaries of these units and identified several informal lithologic subdivisions of each. The nomenclature resulting from this work (High and Picard 1967a; Picard, 1978; etc.) is adopted here as the most workable and appropriate available (Table 3). The Chugwater red beds are thus considered a stratigraphic group comprising, from oldest to youngest, the Red Peak Formation, the Crow Mountain Formation, and the Popo Agie Formation. The Crow Mountain Formation consists of a lower "variegated sandy facies," the Alcova Limestone Member, and an upper part including a "basal sandstone unit" and an "upper sandstone and siltstone unit" (High and Picard 1967a). Pipiringos (1968) has proposed a formal nomenclature for similar subunits, but his less descriptive terminology is somewhat cumbersome in practice. In southeastern and central southern Wyoming the Alcova is disconformably overlain by the Jelm Formation, an equivalent of the upper Crow Mountain.

REGIONAL SETTING

The Chugwater Group and its Alcova Member form only a small part of the extensive Triassic sequence of rocks in the Northern Rocky Mountain Province. Containing a variety of microenvironmental facies, the units of the Chugwater grade both upwards and to the east into terrestrial sediments. To the west, the Chugwater red beds grade into the Ankareh and Woodside formations which themselves intertongue with the nonred Dinwoody and Thaynes formations of western Wyoming and Idaho (Fig. 42). The Dinwoody and Thaynes formations are of Early Triassic age and represent shallow to deep water marine deposits (silts, sands, shales, and limestones) in a broad, subsiding, miogeosynclinal basin at the western edge of the North American craton during Scythian times. This geosyncline trended northeast through what are now south-central California, Nevada, Utah, and Idaho and was fed by detrital sediments originating from

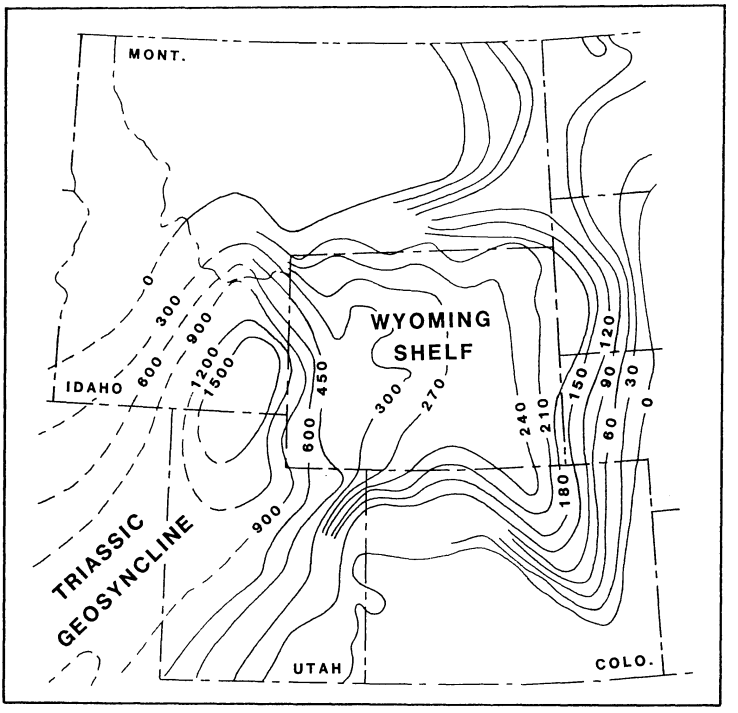

FIG. 43. Inferred western interior paleogeography of the Early Triassic and approximate isopachs (in meters) of Lower Triassic sediments of the Dinwoody and Red Peak formations (modified from Picard and High 1968).

terrestrial highs in the north, east, and southeast, including the Uncompaghre Uplift. In places these sediments reach a thickness of 2,000 m (Kummel 1955). At the same time, central Wyoming was home to a broad, shallow, westward sloping, marine shelf (Fig. 43). This shelf witnessed several eastward transgressive pulses during the Early, and perhaps the Middle, Triassic (Collinson and Hasenmueller 1978). The eastern expanse of the Dinwoody Formation, consisting of grey siltstones and shales, represents the first such invasion of the Triassic sea.

Lying above the Dinwoody, the rocks of the lower Chugwater reveal a complex history of transgression and regression, and lithofacies indicative of marine shelf, coastal, and tidal flat environments (Picard 1978). As, however, most past attempts have failed to correlate the Alcova Limestone with the normal marine sediments of the miogeosyncline, it has been uncertain whether or not the Alcova represents a similar marine shelf transgression. The uppermost Chugwater, particularly the Popo Agie Formation, is unquestionably of terrestrial—fluvial and lacustrine—origin. These rocks comprise red clays, sands, and conglomerates and are the materials that filled the structural basins of Wyoming during Late Triassic times. By the Late Triassic, the western miogeosyncline had withdrawn. Its departure is marked by an erosional unconformity at the top of the Timothy Sandstone Member of the Thaynes Formation (Carini 1964).

PHYSICAL STRATIGRAPHY AND PETROGRAPHY

In addition to a synthesis of published data, field studies on the Alcova Limestone were conducted during the summers of 1983, 1989, and 1990. As much of this

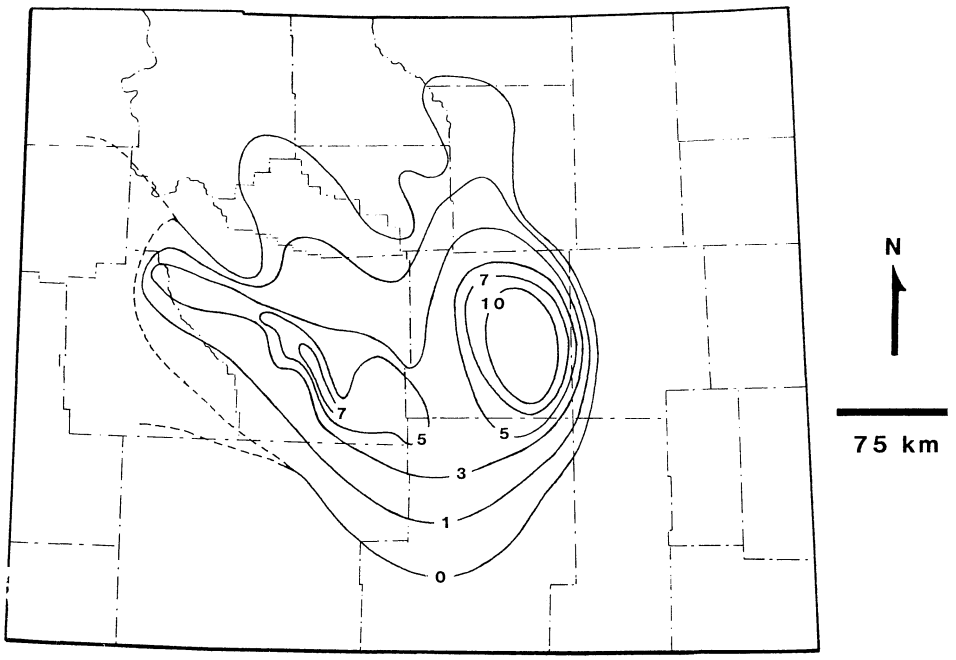

FIG. 44. Inferred distribution and approximate isopachs (in meters) of the Alcova Limestone within the state of Wyoming. Original distribution extended primarily westward. Wyoming counties indicated. Data from various sources.

work coincided with the collection of *Corosaurus* specimens, most sampling was done in Natrona County, primarily in the regions of Alcova, Casper, Freeland Junction, and Muddy Mountain (see Fig. 1). However, exposures of the Alcova and of adjacent red beds were also examined in Freemont County near Lander, and Hot Springs County near Thermopolis, and outcrops of the Ankareh, Thaynes, and Woodside formations were studied for comparison in Teton County.

DISTRIBUTION AND THICKNESS

The Alcova Limestone is a thin but strikingly persistent unit that is recognized throughout central Wyoming and adjacent areas, most notably in the Wind River Basin, but also in the southern margin of the Big Horn Basin, the eastern edge of the Powder River Basin, and along the northern edges of the Hanna, Great Divide, Shirley, Laramie, and Washakie basins (Carini 1964; Love, in Reeside et al. 1957; Picard 1978; Pipiringos 1953). The unit can be traced with difficulty into western Wyoming and has been reported in Jackson Hole and the southern part of Yellowstone National Park (Love 1957). In eastern and southern Wyoming the Alcova is absent through erosional stripping or nondeposition. Present inferred distribution of the member covers approximately 80,000 square km (Fig. 44). Because of extensive Cretaceous–Tertiary cordilleran deformation, outcrops of the Alcova, and Chugwater in general, are geographically discontinuous and border structural and topographic highs. Where the Alcova is upended or overturned as a result of this structural deformation the limestone is characterized by shatter fractures and faults that mask lithologic relationships and have probably destroyed any contained fossils.

The Alcova is a very thin unit, averaging 2 to 4 m. In places it is less than one m thick, in others it reaches a maximum of nine m. Locally, the Alcova may

pinch out altogether as it does in the southern Big Horn Basin and in parts of the Wind River Basin. At such points, the "variegated sandy facies" of the Crow Moutain Formation is overlain directly by the "basal sandstone unit" of the upper Crow Mountain and these two informal units cannot be distinguished. Only where the Alcova is present has variegated staining been produced in the lower sandstone, apparently due to diagenetic fluid percolation downwards from the fetid, petroliferous limestone (High and Picard 1967a).

Argument has existed concerning the nature of the present Alcova edge in the north, south, and east; i.e., is this edge a primary depositional feature representing the original extent of the unit, or a result of post-Alcova erosional stripping? Burk (1953) on the basis of electric log correlation has maintained that, at least along the southeastern margin of the unit, the thinning wedge-edge of the Alcova probably represents the original margin of deposition. In this area it appears that only the Alcova Member is missing, whereas the entire "variegated sandy facies" of the Crow Mountain is preserved—a perhaps unlikely circumstance in the event of erosion. This conclusion is consistent with data accumulated by Downs (1952) and Love (1957).

The Alcova appears to be similarly lenticular along the northwest margin of the Wind River Basin and the northern part of the Laramie Basin. This unit disappears eastward in the Power River Basin, probably also because of non-deposition (Love, in Reeside et al. 1957). East of the Freezeout Mountains the Alcova becomes arenaceous and pinches out (High and Picard 1969). However, evidence of Jurassic erosion of Triassic rocks in parts of the Big Horn and Power River basins, and the eastern edge of the Laramie Basin does exist (Love 1957; Love, in Reeside et al. 1957). Additionally, the top of the Alcova is everywhere an irregular disconformity, and eroded Alcova clasts are often contained in the overlying sandstones (Carini 1964; Love et al. 1945, 1947; Picard 1967; Pipiringos 1968; Pipiringos and O'Sullivan 1978; Tohill and Picard 1966; Woodward 1957). Nevertheless, the original extent of the Alcova Limestone was unlikely to have exceeded the presently inferred distribution in the north and east by any great amount, and its present edge must largely reflect paleoshoreline configuration. Complete erosional stripping of the Alcova has no doubt occurred in some areas of the south.

Maximum thickness of the Alcova is developed in the general region of the type area and extends throughout eastern Natrona County. Stratigraphic section compilations from various sources have resulted in the inferred isopach map of Figure 44.

Lithology

The Alcova is a very hard, dense, resistant, microsparitic (terminology of Folk 1974) limestone in beds approximately 2–25 cm thick. It commonly forms a cap rock lying above cliffs of the Red Peak Formation and "variegated sandy facies" of the Crow Mountain Formation (Fig. 45). The limestone is microlaminated, slightly fossiliferous, and locally dolomitic. Clastic content is generally low but variable; quartz silt particles are locally common, increasingly so near pinchout boundaries. This silt is good evidence for natural lateral termination in these areas. Carbonate-pebble conglomerate is occasionally present in the unit (Picard 1978). The Alcova Limestone is usually grey in color, but can exhibt mottling of pink, red, yellow, and brown as a result of staining by ferric iron (hematite).

Algal stromatolites are abundant in the lower portion of the unit, creating a

FIG. 45. Alcova Limestone Member, Milne Ranch, southern flank of Muddy Mountain, Natrona County, Wyoming. Obvious ledge of Alcova amid red beds of the Chugwater Group.

zone that ranges up to 1 m in thickness (Carini 1964). These stromatolites are the most significant organic component of the limestone, all other fossils being sporadically distributed. The limestone is ubiquitously petroliferous but is particularly high in organic content in the Alcova area where the rock is dark grey in color. Fracturing of the Alcova generally produces a strongly bituminous odor.

The horizontal-to-wavy algal laminations of the Alcova are the principal bedding structures of the unit and are differentially affected by chemical weathering and etching (Fig. 46). Styolites are common and can be oriented both parallel and perpendicular to bedding. Styolitic amplitudes have been reported from less than 1 mm to more than 8 cm (Carini 1964). Diagenetic dissolution of the limestone along fractures has created a secondary vuggy porosity. These cavities are usually lined with coarsely crystalline calcite. Carini (1964) has also noted localized secondary porosities resulting from dolomitization of the limestone and from dissolution of limonite pseudomorphs after epigenetic pyrite.

The Alcova Limestone Member is easily recognized in electric logs (Burk 1953; Love 1957). Both short and long spacing resistivity curves are consistently very high for the Alcova, and indicative of its dense, largely impermeable quality (Fig. 47). The self-potential curve is variable but usually shows little departure from the log shale line.

MINERALOGY

Previous studies of the petrology of the Alcova Limestone have largely been limited to gross lithological descriptions. Only Carini (1964) has analyzed the mineralogic content of the Alcova in detail. As a test of, and supplement to, his investigations, detailed petrographic examinations of Alcova limestone from *Corosaurus* localities were conducted for the present study.

FIG. 46. Detail of wavy algal bedding, Alcova Limestone Member, Milne Ranch, southern flank of Muddy Mountain, Natrona County, Wyoming.

Carbonate Minerals

These are, of course, the major mineralogic components of the Alcova, which has been variously described as a limestone, a dolomitic limestone, and a dolomite (Branson and Branson 1941; Carini 1964; Love 1957; Picard 1978; etc.). Both calcite and dolomite occur in the Alcova Member, but their proportional ratios vary widely with geographic position. Considering the unit as a whole, however, and particularly where it is structurally undeformed, calcite is by far the dominant constituent. This is the case at all known *Corosaurus* localities and Figure 48 presents the pattern results of X-ray powder diffraction analysis on a typical sample from Muddy Mountain, Natrona County (associated with YPM 41037). The powdered rock sample allows random orientation of crystal faces, permitting simple analysis under the Bragg equation and accurate distinction between calcite and dolomite.

The Bragg equation stipulates that $\lambda = 2d \sin \theta$, where d is the spacing in angstroms between the molecular layers of a mineral, θ is half the angle between the diffracted and incident X-radiation, and λ is the wavelength of the incident X-radiation. Standard copper K-alpha radiation (wavelength of 1.5418 Å) was used. When molecular spacing data for calcite and dolomite obtained from Berry (1974) was applied, the scanning run of 26° to 33° for 2θ (Fig. 48) indicates an intense diffraction peak for pure calcite (d = 3.0357 Å) at approximately 29.5° with no dolomite diffraction (approximately 31°). Small amounts of quartz and feldspar are also indicated.

The origin of the primary Alcova calcite is presumed to have been fourfold. Initial calcite sediment was probably deposited as a micritic, phytochemical precipitate amid the prominent fabric of stromatolitic algae in the lower part of the unit. To this were added carbonate precipitates from other biologic sources and from inorganic processes. Detrital calcitic (and aragonitic) macroinvertebrate

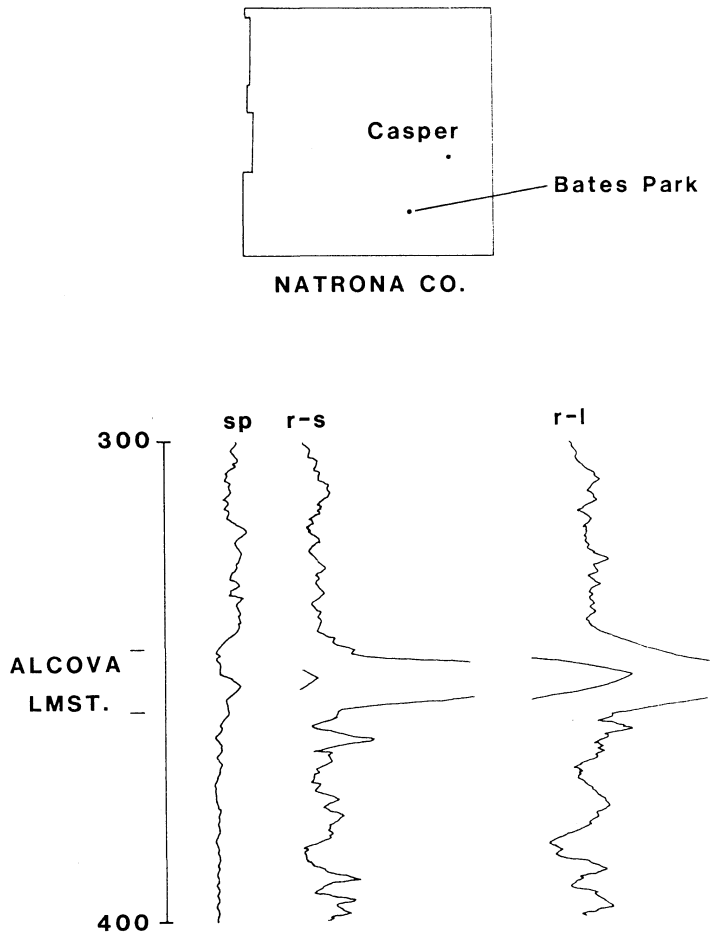

FIG. 47. Electric log curves for the Alcova Limestone from Bates Park, Natrona County, Wyoming, Sec. 3, T30N, R81W (from Burk 1953). Vertical depth scale (along shale line) in meters. No correction for dip. r-1 = long spacing resistivity; r-s = short spacing resistivity; sp = self-potential.

skeletal remains (primarily pelecypods) constitute a relatively minor component of the rock but can be locally abundant, resulting in a biosparitic composition (Fig. 49), while microorganismal remains were probably common. Lastly, chemically precipitated primary sparite formed within primary cavities of the sediment. The calcite (and aragonite) from all of these sources has undergone diagenetic recrystallization and neomorphism. The Alcova also presently contains secondarily deposited sparry calcite within fractures and cavities.

All dolomite found in the Alcova Limestone is the result of diagenetic replacement of calcite and is not of primary origin. Carini (1964) has conducted X-ray powder diffraction analyses on the Alcova for a range of structurally deformed areas and has indicated partial dolomitizations of 1 to 98 percent. Alcova dolomitization has thus been shown to be directly related to tectonic deformation and to structural control of magnesium-rich ground-water circulation. Preferential dolomitization of individual beds within the Alcova is an auxiliary result. Dolomite and calcite combined form between 59 and 98 percent (geographically dependent) of the Alcova Limestone (Carini 1964). The average carbonate percentage is greater than 80.

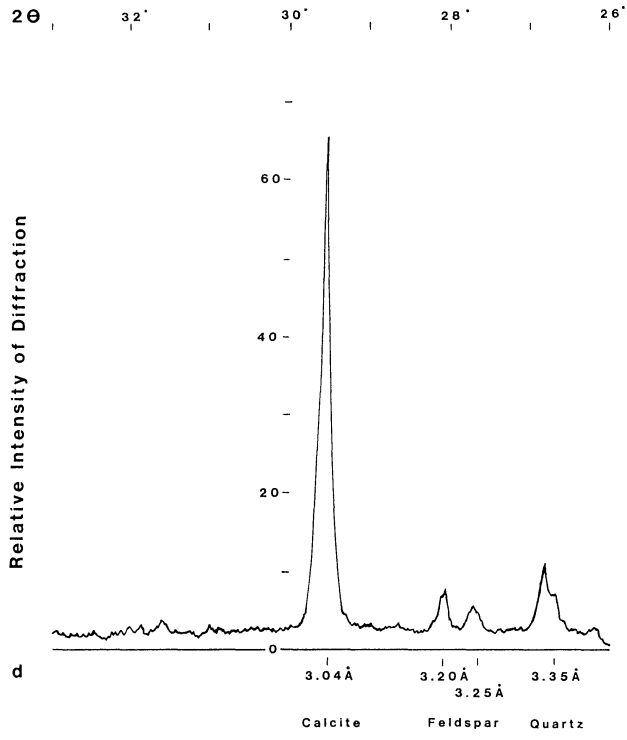

FIG. 48. X-ray powder diffraction pattern for a typical undeformed Alcova Limestone sample, Muddy Mountain, Natrona County, Wyoming (associated with YPM 41037). Abscissa is calibrated in degrees of 2θ; ordinate is relative intensity of diffraction. Molecular d spacings represented in sample are indicated.

Noncarbonate Minerals

Minerals other than calcite and dolomite present in the Alcova Member are all clastic introductions. Approximately 90 percent of these detritals are silt-sized, angular to rounded particles; over 60 percent quartz. Occasional isolated feldspar- and mica-group minerals can also be identified in petrographic thin section but are of minor significance. Quantitative insoluble residue analyses have been carried out by Carini (1964) to characterize these clastic assemblages. Identified feldspars are dominantly orthoclase, but also albite, microcline, and perthite. Micas include biotite, chlorite, and muscovite.

Accessory heavy minerals are present in trace amounts in samples of the Alcova Limestone silt fraction. Among these heavy minerals are, most notably, grains of garnet, hematite, ilmenite, magnetite, rutile, tourmaline, and zircon. This assemblage is not unexpected as resistant residuals of long distance transport.

The remaining 10 percent of detrital grains consists of clay minerals, principally illite, kaolinite, and montomorillonite. Glauconite was reported in the Alcova of the Freezeout Mountains by Pipiringos (1957), but this record is disputed by Carini (1964). No glauconite was discovered in the present study.

FABRIC

Throughout the Alcova Limestone the dominant factor affecting the fabric of the rock is recrystallization of original calcite and aragonite. All aragonite, such as that originally comprising molluscan remains, has been inverted to calcite. Virtually all calcite has been subjected to aggrading neomorphism, and in places,

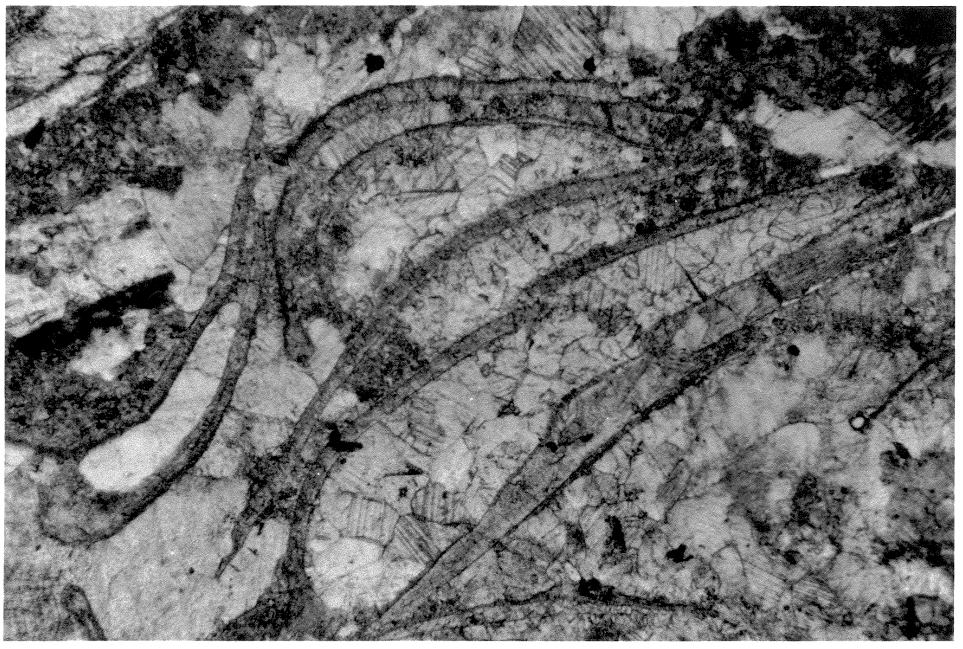

FIG. 49. Petrographic thin-section of Alcova Limestone depicting pelecypod debris creating biosparitic texture. Field of view is 3.70 mm across.

much or all of the primary carbonate component of the rock has undergone replacive dolomitization as noted. Because of these changes, much of the original microstructural fabric of the rock has been obscured. Nevertheless, certain characterizations may be made of localized rock types within the member.

The orthochemical contribution to the Alcova, or that component that has been precipitated within the depositional basin and is presumably relatively untransported, has been most greatly disguised by diagenetic recrystallization. Of the several genetic types discussed above, carbonate produced by inorganic chemical precipitation, phytochemical precipitation, and by the disintegration of pelagic microorganisms is presumed to constitute the major orthochemical foundation of the rock. This foundation was probably a microcrystalline carbonate ooze (micrite) of calcitic and aragonitic composition or both. Following recrystallization, however, this ooze was transformed into a calcitic microcrystalline sparite or microsparite with a typical crystal diameter of 5 microns.

Also of an orthochemical nature but present in much smaller amounts is primarily deposited sparry calcite. Sparite may have formed some of the original matrix cement of the rock, but was certainly more notably present as penecontemporaneous crystal growths in primary cavities of the sediment at the time of deposition. Most such cavities were those located in piles of molluscan skeletal debris. Original sparite cannot now, however, be reliably differentiated from aggraded recrystallized micrite (Folk 1965).

Certain allochems, or elements of the rock which, although formed within the depositional basin, are not precipitates as discussed above and have been potentially or actually transported, have been less affected by Alcova recrystallization. These are principally molluscan remains which, while completely inverted to calcite, remain recognizable although the structure of the shells has been partially obscured (Figure 49). Also present are textural ghosts of dissolved bivalved microorganisms, possibly ostracods.

The stromatolites which form a major textural constituent of the Alcova Member, particularly in the lower part of the unit, are an *in situ* biohermal component

(see, e.g., Fig. 46). Where present, they necessitate a separate carbonate rock classification (below). Other special features affecting the fabric of the Alcova Limestone are the localized secondary deposition of sparry calcite in fractures and dissolution cavities, and the epigenetic preferential overprinting of dolomitization creating characteristic sparry dolomite rhombs (see Carini 1964).

Rock Classification

As nowhere in the Alcova Member does the terrigenous component of the rock exceed 50 percent, the unit is strictly a carbonate; yet numerous carbonate rock types exist locally due to subtle mineralogic and textural variations within the member. While carbonate rocks are prone to complex compositional variations, a workable and flexible systematics of carbonates has been developed by Folk (1959, 1962, 1974). Several Alcova rock types can be recognized under this system. As calcite is the dominant mineral, the unit is overall a true limestone, and as dolomitization is nowhere primary, the member is locally a dolomitized limestone or replacement dolomite. Although even the calcitic portion of the Alcova Limestone has been recrystallized, several intraunit limestone categories exist. Most of these categories have been independently recognized by Carini (1964).

The principal rock type of the Alcova is a recrystallized micrite or microsparite of Folk (1959, 1962, 1974). Carini (1964) notes that microsparite is most commonly developed in the upper half of the Alcova in beds 5 to 15 cm thick. Microlamination is commonly evident and usually reflects parallel orientation of terrigenous particles.

The abundance of *in situ* stromatolites makes them the second major Alcova rock type—stromatolite biolithite. Wavy stromatolitic layers form the framework of this intraunit rock. Recrystallization has not hidden the gross morphology of the stromatolitic banding, but has eradicated any trace of cellular structure. The stromatolitic laminae average approximately 1 mm in thickness.

Microsparitic rock types with a significant (greater than 10 percent) allochemical contribution are more rarely and locally encountered in the Alcova. Occasionally, a coquinoid texture of detrital shells is achieved. Such rocks probably possessed a large percentage of original sparry cement in the open-space interstices of the shell debris framework, as the pelecypod shells are commonly disarticulated, but rarely fragmented.

Oomicrosparites are rare in the Alcova but are encountered in the Freezeout Mountains at the top of the unit (Carini 1964; Pipiringos 1957). Occasional intraclastic rocks have been observed and Picard (1978) has identified a pelmicrosparite ("pelmicrite") near Rawlins, Carbon County. Quite probably, ooliths, pellets, and intraclasts were common in the original fabric of the rock but have been largely destroyed by recrystallization. Sedimentary structures (discussed more fully in Chapter 6), particularly small-scale cross laminations, indicate local movement of allochems and terrigenous clasts, but also of authigenic microcrystalline calcite particles resulting in calcilutites. Alcova calcilutites fall in the fine to medium (0.008–0.031 mm) range of the Wentworth scale.

STRATIGRAPHIC CORRELATION

The Alcova Limestone has generally been believed to represent an eastward extension of the Triassic sea from the miogeosyncline of Idaho and western

Wyoming. The setting of the Alcova on the Triassic Wyoming shelf, its relatively large geographic area, and its nearness to the Triassic cordilleran miogeosyncline argue for a marine origin for the unit. Alternative suggestions that the member is an isolated unit laid down by an inland sea or lake (Bower 1964; Carini 1964) are invalidated by paleoenvironmental data (Chapter 6). Marine Triassic rocks are also present in Canada but, because of their distance from the Alcova and the regional framework of the western interior, are not considered correlative with it.

The general lack of significant fossil material, the different lithofacies of eastern and western Wyoming sediments, and the structurally complex transition zone between them have long prevented precise correlation of the miogeosynclinal and epicratonic units. Attention has often focused on the Alcova as the most significant marker unit in the Wyoming Triassic sequence, but little agreement on its age or position has been reached. The presence of the primitive nothosauriform *Corosaurus* in the Alcova has led some workers to assign a Middle or Late Triassic age to this unit (Colbert 1957; Zangerl 1963). Other vertebrate fossils in the Chugwater partially bracket the Alcova. The Popo Agie Formation has yielded Late Triassic vertebrates (Branson 1948; Colbert 1957; Williston 1904) and presumably Early Triassic footprints have been found in the Red Peak Formation (Lull 1942). The Red Peak Formation is stratigraphically equivalent to the Lower Triassic Moenkopi Formation of Utah and Arizona, whereas that part of the Crow Mountain Formation above the Alcova contains Late and possibly Middle Triassic rocks (Pipiringos and O'Sullivan 1978).

Most workers have correlated the Alcova Limestone with part of the Thaynes Formation (Newell and Kummel 1942; Pipiringos 1953, 1957; Thomas 1949), and particularly with part of the Portneuf Limestone Member of the upper part of the Thaynes (Kummel 1954, 1955, 1957; Love 1948; McKee et al. 1959). The Lanes Tongue of the Ankareh Formation, which intertongues with the Portneuf, has been cited as equivalent to the Alcova (Kummel 1953; Reeside et al. 1957). Love (1957) labeled the Alcova a tongue of either the uppermost Thaynes or of a younger unit. As the Thaynes/Ankareh sequence is a thick one, such studies have variously called the Alcova Lower, Middle, and Upper Triassic.

Correlation of the Alcova Member with the Thaynes Formation by Picard et al. (1969) has now convincingly demonstrated that the Alcova is an eastward marine extension of the "sandstone and limestone unit" of the upper part of the Thaynes (nomenclature of Kummel 1954). Several limestones are included in this unit. This conclusion is based upon detailed study of subsurface and surface sections, as well as the paleontology, petrology, mineralogy, and sedimentary structures of the Thaynes Formation and the Chugwater Group. The "variegated sandy facies" of the Crow Mountain and "upper platy facies" of the Red Peak also grade into the "sandstone and limestone unit" of the Thaynes (Fig. 50). The precise location of the Alcova within this latter unit is unknown (Picard et al. 1969). High and Picard (1969) have shown the basal parts of the Ankareh and Jelm formations and the "basal sandstone unit" of the Crow Mountain to be equivalent. The lower Red Peak grades into the Woodside Formation. These correlations suggest that the Alcova is an uppermost Lower Triassic or Scythian (Spathian) rock unit, or perhaps lowermost Middle Triassic or Anisian. Little if any time transgression appears possible from west to east. The numerous invertebrate fossils from the Thaynes below the "sandstone and limestone unit" are certainly Early Triassic in age (Collinson and Hasenmueller 1978; Kummel 1954). Fossil faunas are poorly represented in the miogeosynclinal sequence in the "sandstone and limestone unit" of the Thaynes Formation, the Lanes Tongue,

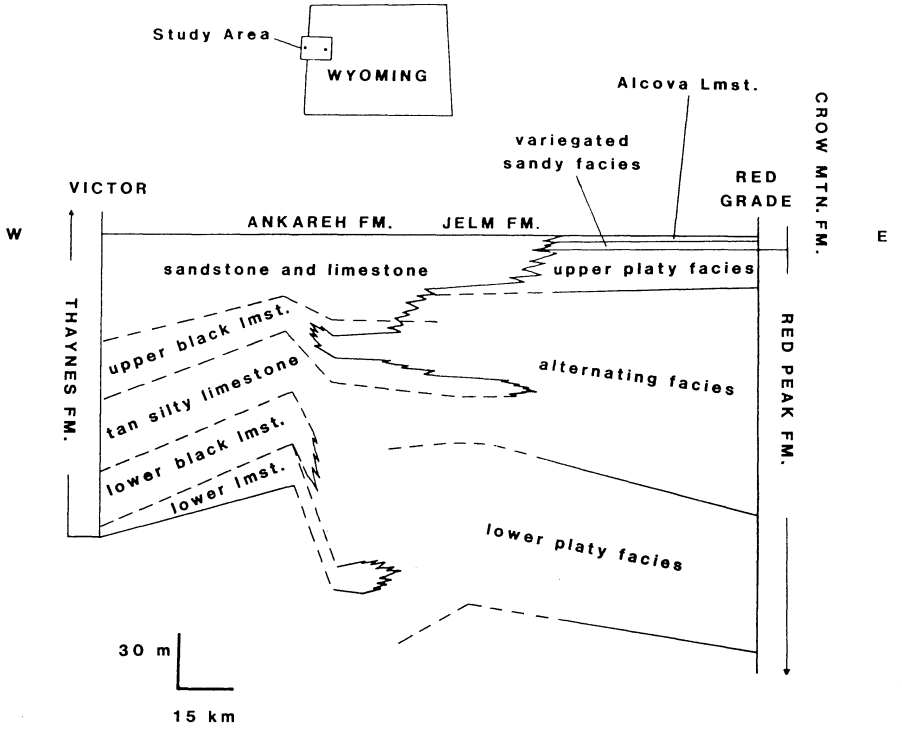

FIG. 50. Simplified correlation of the Alcova Limestone and enclosing units with the Triassic miogeosynclinal sequence of the Idaho–Wyoming border (modified from Picard et al. 1969).

the Portneuf Member, and above. They may range from late Early Triassic to Late Triassic (Kummel 1954; Oriel in McKee et al. 1959). Invertebrates from the Alcova are not age-definitive (Chapter 6). The Tr-2 unconformity of Pipiringos and O'Sullivan (1978), which ubiquitously marks the top of the Alcova, probably represents a Middle Triassic depositional hiatus. The rocks immediately below Tr-2 are thus of Early Triassic or questionably lower Middle Triassic age (Pipiringos and O'Sullivan 1978).

The Middle to Late Triassic ages of the Alcova suggested by Colbert (1957) and Zangerl (1963) were based upon what they perceived as an advanced degree of aquatic specialization in *Corosaurus*. These ages have been accepted by most workers. Case (1936), however, wisely made no more specific assignment than Triassic in his initial description of the animal. The presence and morphology of *Corosaurus* are not sufficient to determine the stage/age of the Alcova and have assumed inordinate importance in previous studies. The anatomy of *Corosaurus* and the presumably early differentiation of the *Corosaurus* lineage from the remaining Nothosauriformes (Chapter 4) are each compatible with, but are not by themselves indicative of, the apparent Early/Middle Triassic boundary position of the Alcova Limestone.

6. PALEOENVIRONMENT

The position of the Alcova on the Wyoming shelf and its unusual physical character indicate a unique paleoenvironment bearing directly on the paleobiology of *Corosaurus*.

SEDIMENTARY STRUCTURES

Although the recrystallization of the Alcova Limestone has locally obscured the fabric of the rock, sedimentary structures of several types are preserved in the unit. These structures can be divided into two distinct genetic categories, structures of the physical environment and those with a biologic origin.

Physical Sedimentary Structures

The major physical structure present in the Alcova is horizontal microlamination. These parallel laminae, approximately 1 mm thick, are widespread and usually undisturbed. They predominate throughout the unit where thick stromatolite sequences are absent. The slow, continuous precipitation of calcium carbonate accompanied by intermittent pulses of terrigenous detritus, largely silt-sized grains of hematite-stained quartz, account for Alcova microlamination. The undisturbed nature of stratification indicates that the laminae were deposited under low energy conditions where there was no homogenization of the beds through bioturbation. Occasional, locally non-laminated beds probably reflect the preferential destruction of microlaminae by recrystallization.

Less abundant, yet still common in the Alcova, are wavy and small-scale, trough cross-stratified laminae that represent small irregularities in the bottom sediment. The most common cause of these irregularities was probably bottom scour and fill by local low-to-moderate energy, polydirectional bottom currents. Sediment from scoured horizontal laminae, composed of clasts and authigenic crystals, was locally transported and redeposited in shallow bottom depressions.

Higher energy wave and current action is responsible for the construction of ripple structures. Ripple marks are relatively common in the Alcova. Most observed ripples have been of low amplitude, long wavelength, and have symmetrical ridges. These are oscillation ripples produced by wave action, not currents. As such they represent shallow water, perhaps intertidal conditions. Occasionally, interference ripple structures are found superimposed upon stromatolites, producing a lineation among the algal mounds. Waves and currents both may be responsible for the rarer occurrence of Alcova intraclast conglomerates and rip-up structures (Fig. 51). Partially consolidated carbonate mud was torn from the bottom sediments of the Alcova water body and redeposited as brecciated limestone, possibly by storms. However, no evidence of grading, common to tempestites, has been seen in these rip-up deposits. Diagenetic recrystallization of the limestone has possibly removed some fine-scale grading. Picard (1978) notes that carbonate pebble conglomerates are rare to common in the Alcova.

In the present study, a single example of dessication polygons was discovered in a bed of Alcova algal laminae at Milne Ranch, Muddy Mountain, Natrona County. The up-turned edges of these mud cracks are typical of the thick, subaerially exposed algal mats of the intertidal zone.

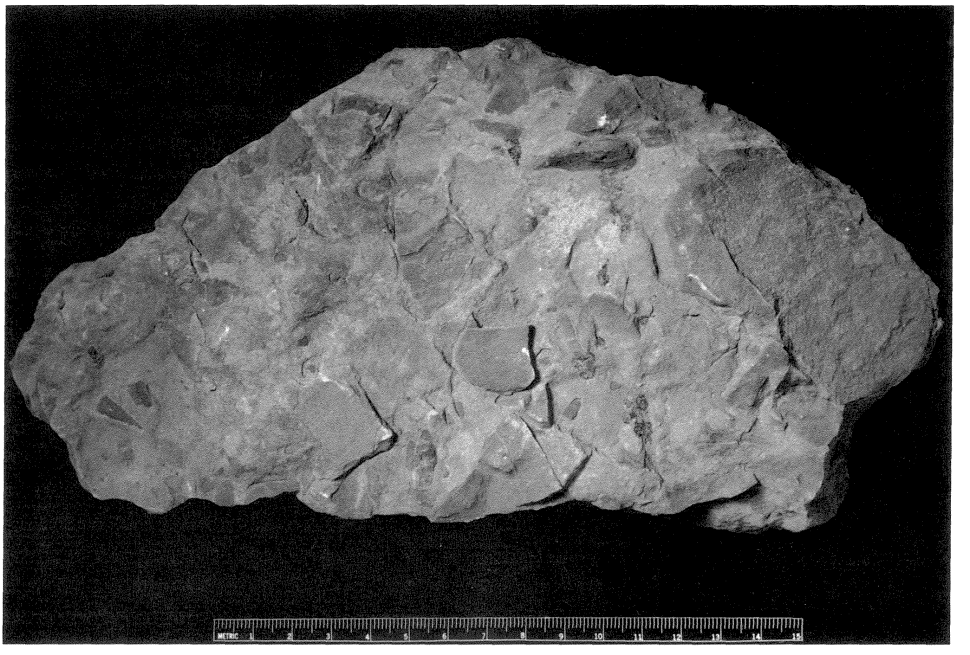

FIG. 51. Rip-up intraclast conglomerate of the Alcova Limestone, Milne Ranch, Muddy Mountain, Natrona County. Upper bedding surface viewed. Scale in centimeters.

BIOGENIC SEDIMENTARY STRUCTURES

The only significant biogenic structure of the Alcova is the prominent wavy algal stratification, found largely in the lower part of the unit (see Fig. 46). These laminations average approximately 2 mm in thickness and display considerable stromatolitic mounding (but no columns). Mounds average approximately 10 cm in diameter, but rare mounds 1 m in diameter have been observed. The algal mats caught and retained free-floating particles of carbonate mud and now make up much of the framework of the rock. Most of the mats apparently lay continuously subaqueously as only one example of dessication cracks is known. Phanerozoic subtidal-zone stromatolites generally develop only in areas of hypersalinity where they are free from the browsing of gastropods (James 1979); high salinity restricts the presence of algae-controlling gastropods. The abundance of stromatolites throughout the member indicates that much of the Alcova was warm, well aerated, and shallow, with its bottom within the photic zone. Their presence also indicates, as does the ubiquitous microlamination, that the sea floor was predominantly stable. Algal mats are unable to grow on shifting sediments. The absence of stromatolite columns belies limited wave action, although occasional ripple marked mats have been noted.

Very little bioturbation is apparent in the Alcova but some rare possible invertebrate trails are present (Fig. 52). These seem to be branching, horizontally oriented, hypichnial groove casts of probable feeding trails. Such horizontal traces are typical of sediment feeders and are often indicative of deepwater deposits where there are few suspended particles (Seilacher 1967, 1978). In this case, where shallow water conditions are suspected, the potential trails may be supporting evidence for the hypothesis of a low energy regime. The general paucity of bioturbation is a probable result of inhospitable chemical conditions, perhaps hypersalinity.

FIG. 52. Possible hypichnial groove casts of invertebrate horizontal feeding trails from Alcova Limestone, Milne Ranch, Muddy Mountain, Natrona County. Scale in centimeters.

FOSSIL ASSEMBLAGE

Few fossils are known from the Alcova Limestone. They occur sporadically, are generally poorly preserved, and have been only questionably identified. Few taxa are represented in the Alcova biota, which has generally been regarded as marine, but lacks the unequivocal occurrence of a marine organism.

VERTEBRATE FAUNA

The most conspicuous component of the Alcova fauna is the 'nothosaur' *Corosaurus alcovensis,* remains of which, while not extremely abundant, are not rare. It is assumed that this animal was an inhabitant of the Alcova basin and not a chance import, for it is a distinct genus and species uniquely known from the Alcova Limestone, and is unassociated with typical open marine faunas. If an occasional immigrant, obvious and well-known marine forms would be expected as well. Skeletal material of *Corosaurus* is so far restricted to the Casper–Muddy Mountain area of Natrona County, the section of maximum unit thickness. This may, however, be a function of the greater amount of rock exposed in this area. If a natural restriction, *Corosaurus* perhaps preferentially inhabited the relatively open waters of the central basin. As many of the bones have come from talus debris, the precise stratigraphic horizon from which they originated within the member is unknown. They were perhaps randomly distributed, although few specimens have been discovered in association with stromatolites. On the other hand, all Field Museum specimens were collected *in situ* from the upper half of the local profile.

Most *Corosaurus* fossils consist of scattered or isolated elements; others are only partially articulated skeletons, sections of vertebral columns, or accumulations of gastralia. This disposition of fossils might suggest violent transport, but none of

the bones exhibit signs of abrasion. There is also no current orientation of the elements and most bone accumulations are those naturally maintained by remnant ligamentation. The likeliest explanation for the occurrence of isolated *Corosaurus* bones is the combination of the natural disarticulation of floating carcasses and the low-energy winnowing of bones deposited under slow sedimentation rates. There is no evidence of disturbance by scavengers.

Corosaurus has usually been cited as evidence for a marine origin for the Alcova. While the hundreds of specimens of other 'nothosaurs' known worldwide are primarily from marine deposits, there is, however, no reason to suppose that the pachypleurosaurs and 'nothosaurids' were restricted to normal marine environments. Indeed, some are known from marginal environments (Chapter 7). Reptiles, with their protective dermal covering of scales, are particularly well suited to existence in a variety of osmotic regimes (Schmidt-Nielsen and Fange 1958). While the Alcova paleoenvironment was evidently not freshwater, the possibility of hypersaline waters exists. In this light, the possible maxillary pits of *Corosaurus* described in Chapter 2 may have been receptacles for subcutaneous salt glands. Salt glands are those responsible for osmo-regulatory secretions of sodium and/or potassium, necessitated by hostile ionic environments and/or salt-rich diets (Schmidt-Nielsen 1963; Taplin 1989; Whybrow 1981). Salt glands, however, are not restricted to animals living in hypersaline environments. Reptilian kidneys are less efficient in concentrating salt than are those of mammals and facial and other salt glands are well known in modern reptiles—for example, the marine iguana, sea snakes and turtles, and crocodiles (Schmidt-Nielsen and Fange 1958; Taplin 1989; Whybrow 1981).

The only other vertebrate reported from the Alcova was a fragmentary reptile supposedly collected by the Field Museum party during the 1948 expedition. This was identified by Zangerl (written communication to Oriel 1956, in McKee et al. 1959) as a possible thecodont (phytosaur?) or *Coelophysis*-like dinosaur. It may have been washed, post-mortem, into the Alcova depositional basin from a terrestrial source. However, the whereabouts of this specimen are presently unknown and Zangerl (personal communication, 1986) now has no recollection of it.

While from its dentition it may be assumed that *Corosaurus* was primarily piscivorous, no fish remains have yet been recovered from the unit. Possibly, such remains have been destroyed by taphonomic processes. Fish skeletons are fragile and easily disarticulated. Furthermore, some resident fish may have been cartilaginous. Very small, isolated, skeletal elements would be difficult to detect in the Alcova matrix without a tedious insoluble residue analysis.

Invertebrate Fauna

Rather problematic invertebrate fossils are known from the largely unfossiliferous Alcova Limestone. They are of patchy distribution, poor preservation, and very low species diversity. All are totally recrystallized. Pelecypod molluscs predominate in the available assemblage. These bivalves are preserved most commonly as external casts and molds, but also as anhedral calcite-filled hollows, voids where such sparite has secondarily dissolved, and as recrystallized shell debris (Figs. 53, 54, 55, 56, and 57). Rarely is any indication of internal shell structure zonation present in cross-sectioned shells. Darton (1906) first noted invertebrates from a Chugwater limestone in the Owl Creek Mountains which Lee (1927) later identified as the Alcova. Bivalves in Darton's assemblage were identified as *Aviculi-*

FIG. 53. Alcova Limestone block from Milne Ranch with bivalves preserved as randomly oriented calcite-filled voids. Scale in centimeters.

pecten cf. *A. curticardinalis, Bakewellia* sp., and *Pleurophorus*? sp., all marine forms, to which Lee (1927) added *Naiadites*? sp. True *Naiadites* is a Pennsylvanian freshwater pelecypod. Although Branson and Branson (1941) claim that these fossils were collected from a limestone in the Chugwater above the Alcova, Pipiringos (1953, 1957) has identified *Pleurophorus*? *bergeri* from the Alcova of the

FIG. 54. External casts and molds of pelecypod bedding plane brood in apparent life position, Alcova Limestone, Milne Ranch, Muddy Mountain, Natrona County. Scale in centimeters.

FIG. 55. External molds of pelecypod bedding plane brood in apparent life position, Alcova Limestone, Milne Ranch, Muddy Mountain, Natrona County. Scale in centimeters.

Freezeout Mountains. None of these specimens have been described or illustrated and Carini (1964), in describing new specimens, maintains that the Alcova bivalve fauna, while consisting of at least two species, is generically indeterminate. Numerous bivalves collected for the present study (and now in the YPM Inver-

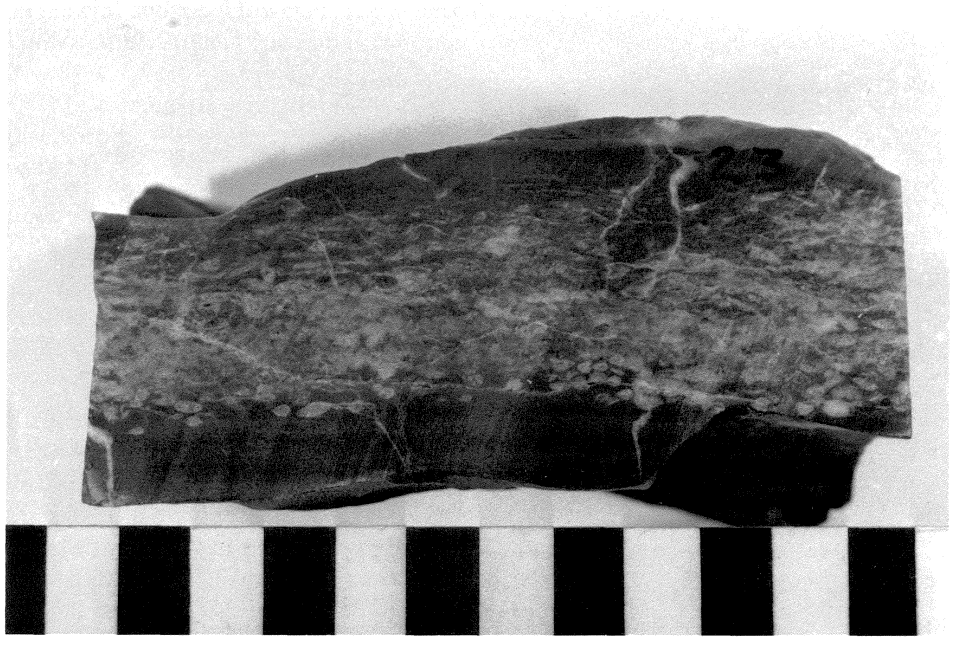

FIG. 56. Alcova Limestone block, Milne Ranch, Muddy Mountain, Natrona County, sectioned normal to stratification, showing brief accumulation of successive bivalve generations in possible life position; preserved as casts and recrystallized shell. Scale in centimeters.

FIG. 57. Death assemblage of disarticulated, recrystallized pelecypod shells, Alcova Limestone, Milne Ranch, Muddy Mountain, Natrona County. Scale in centimeters.

tebrate Paleontology Collection) appear to belong to one or two genera, but are insufficiently preserved to permit identification. Most range from approximately 2 to 18 mm in length and have horizontally elongate or elliptical valves. The umbo is small. Concentric growth striae are sometimes evident. Their internal anatomy is unknown.

The Alcova pelecypods appear largely restricted to the central and southern portions of the Alcova basin (Carini 1964). Where found, they are numerous and closely packed over relatively small areas (patches approximately 30–60 square cm). Most Alcova bedding planes are devoid of fossils. Often, where lying upon undisturbed microlaminae, the shells remain articulated in what may have been their possible life position, parallel to stratification. These clusters form single or several successive beds of similarly-sized, albeit small, animals suggesting individual, short-lived broods of an r-selected, opportunistic or stress-tolerant species. The apparently episodic nature of high individual mortality events is in agreement with the notion of a disturbed or high-stress environment. As the sedimentology of the Alcova indicates relatively stable bottom deposits, the environment was not one of frequent physical disturbances. However, chemical perturbations, for example salinity fluctuations, produce identical records of population dynamics. Again, paleoecologic data suggest a possible paleoenvironment of variable greater or less than normal marine salinity for the Alcova.

In areas of scour and fill cross-beds and bivalve clusters, the fossils are often preserved as pockets of redeposited, disarticulated, but unfragmented shells. Their unfragmented nature suggests a lack of reworking, predation, and/or bioturbation. Occasionally, calcite-filled molds of indeterminate pelecypods are found oriented perpendicular to bedding but in the same horizontal plane. These are perhaps life assemblages of shallow-burrowing bivalves.

Gastropods are far less frequently found in the Alcova and those present are of minute to small (2–7 mm) size. They are most common in the basal Alcova

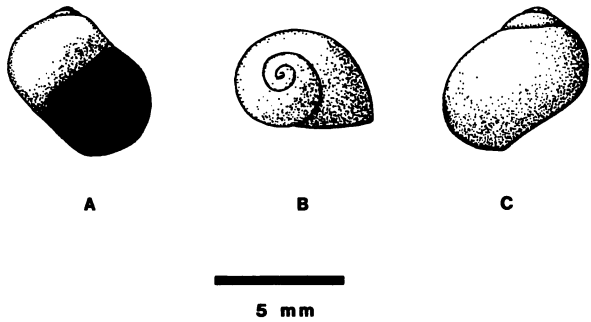

FIG. 58. Typical gastropod of the Alcova Limestone. A, apertural aspect; B, apical aspect; C, lateral aspect. (Redrawn from Carini 1964).

(Carini 1964). They are sometimes found in conjunction with bivalves but rarely in association with stromatolites. Bivalves are also rarely found with stromatolites. The gastropods, representing a single species, are preserved both as recrystallized shells and as external casts. They are dextral, ovoid, gently sloping conispiral shells without marked ornamentation (Fig. 58). Darton (1906) and Lee (1927) have identified this gastropod as *Natica lelia,* whereas Pipiringos (1953, 1957) has more properly called it *Natica? lelia. Natica? lelia* was described by Hall and Whitfield (1877) from an indeterminate (Triassic?) limestone near Rawlings, Wyoming. It is similar to the Alcova form and probably not a true *Natica.* Carini (1964) has shown that the Alcova gastropod is also not a true *Natica,* having no parietal lip callus, but likely represents a new genus. Once more, possibly abnormal salinity is suggested by the uncommon occurrence of a single gastropod species in the Alcova. Gastropod diversity decreases under brackish and hypersaline conditions. High salinity is particularly deadly for most, though not all, gastropods.

Carini (1964) has described the rare problematic occurrence of certain other possibly organic structures. These have been tentatively considered possible ostracods or nepionic pelecypods, conchostracans, and crustacean gastroliths. All have dubious paleoenvironmental significance.

ALGAL FLORA

The macrostructure, occurrence, and significance of Alcova stromatolitic algae have been detailed above. The colonial mound structure of these probable blue-green algae is sinuate and biostromal with generally hemispherical domes (Fig. 59). Individual laminae, representing thin mats of nonskeletal algal threads are preserved in cross section (Fig. 60), but recrystallization has destroyed cellular structure. They cannot, therefore, be generically identified. Although stromatolites are known worldwide from a variety of environments, from freshwater to brackish, marine, and hypersaline (Walter 1976), their abundance in the Alcova may be related to a lack of invertebrate consumers, particularly gastropods, through abnormally saline conditions as discussed above.

GEOCHEMISTRY

Carbonate rocks, particularly limestones, are well suited to isotopic chemical analysis because of the fractionation characteristics of carbon and oxygen. Mass

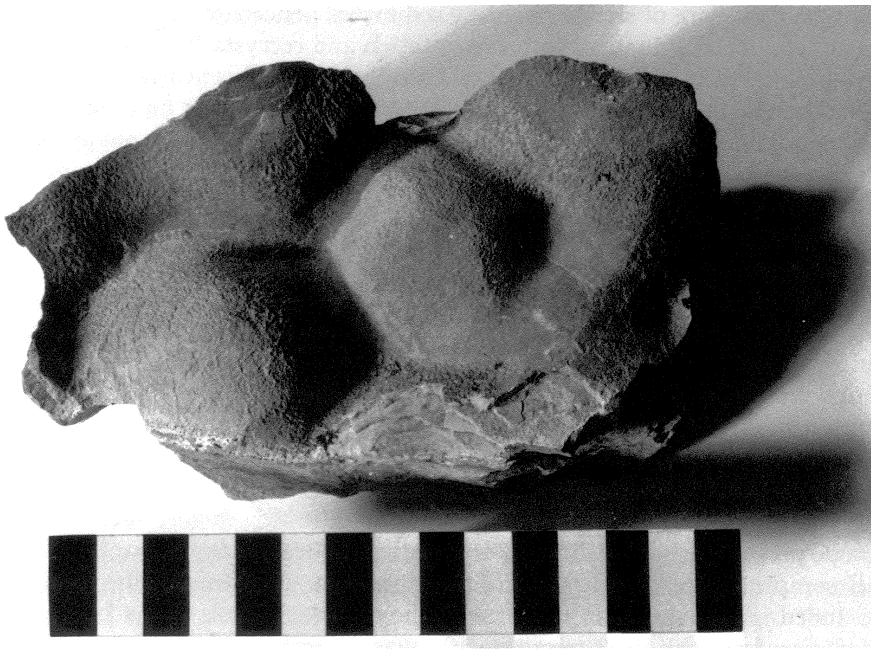

FIG. 59. Stromatolite hand specimen, Alcova Limestone, Muddy Mountain, Natrona County. Upper bedding surface view of hemispherical mounds. Scale in centimeters.

spectrometric examination of the stable isotopes of carbon and oxygen in a rock can often shed light upon the conditions of formation of the carbonate (Anderson and Arthur 1983; Hoefs 1980; Hudson 1977; Keith and Weber 1964). Although the Alcova Limestone has undergone complete recrystallization and presumably isotopic reequilibration, the possibility exists that this was an early diagenetic

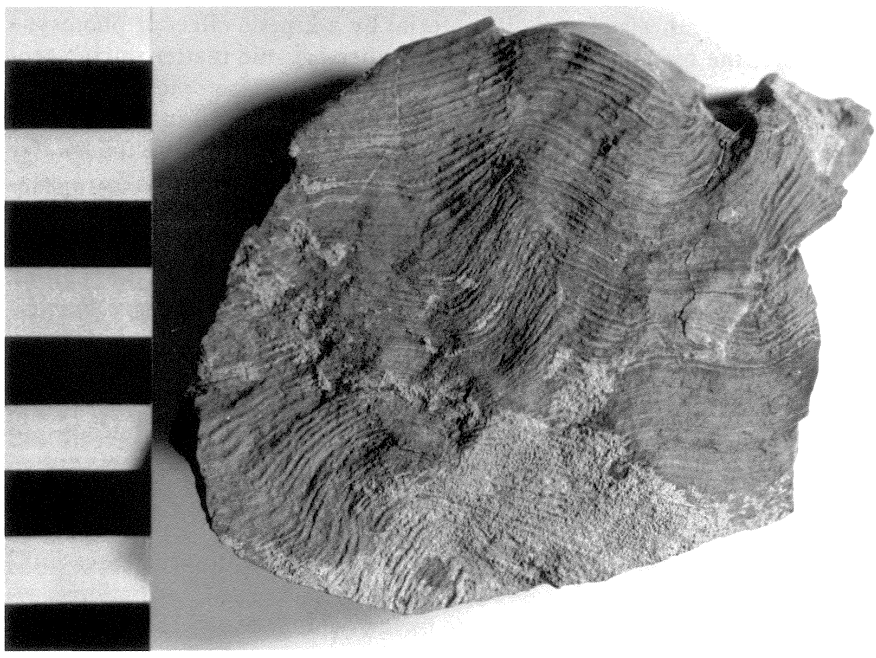

FIG. 60. Stromatolite hand specimen, Alcova Limestone, Muddy Mountain, Natrona County. Cross-sectional view of wavy algal laminae. Scale in centimeters.

change. Exposure of shallow-marine sediments penecontemporaneously with deposition can result in diagenetic cementation and recrystallization. In such a case, formational pore waters would be chemically little different from the depositional water column. Furthermore, various isotopic changes might be predicted to occur under particular diagenetic conditions. If these changes are not observed, the diagenetic history of the rock and the extent to which this history has affected the original isotopic content of the unit may be illuminated. Thus, the usefulness of geochemical analysis of the Alcova should not be prematurely discounted. It must be stressed, however, that data obtained from mass spectrometry are subject to many variables and cannot prove the existence of certain paleoenvironmental conditions. They must be used in conjunction with sedimentologic and paleontologic data as possible corroborative evidence.

In the present study (including also Storrs 1988b), only samples associated with specimens of *Corosaurus* from Muddy Mountain were used. A typical sample is that associated with YPM 41037, previously discussed as a sample analyzed by X-ray power diffraction (Chapter 5) and therefore known to be free of dolomitization, a diagenetic/postdiagenetic complicating factor. With calcite as the single present carbonate, final interpretation of the samples is simplified. Virtually all samples were of microsparitic composition. No stromatolite samples were included. A single sample contained invertebrate shell debris but no isotopic variation from the strict microsparites was observed.

Carbon Isotopic Composition

Carbon has two stable isotopes, C^{12} and C^{13}, and two major reservoirs, the biosphere and carbonate sediments. These reservoirs are isotopically separated by different fractionation mechanisms (Hoefs 1980). In the organic realm, the heavy isotope C^{13} within carbon dioxide is relatively depleted and the light isotope C^{12} concentrated in synthesized organic material by a kinetic effect of photosynthesis. Therefore, the oxidation of humus and other organic matter during terrestrial decay, transport, and deposition, lightens the carbon isotopic composition of freshwater. Freshwater carbonates are preferentially enriched in light carbon (C^{12}). Marine waters (and carbonates), particularly those with little freshwater contribution (e.g., distanced from deltaic and estuarine environments), are relatively rich in heavy carbon (C^{13}).

Examination of the Alcova Limestone gives δC^{13}PDB values of 1.0–3.4‰ with an average of 1.8‰ [PDB is the international reference standard for carbon isotopes measured from *Belemnitella americana* of the Cretaceous Pedee Formation, South Carolina (Hoefs 1980)]. These values are relatively high, indicating a heavy isotopic composition. Freshwater limestones typically have a negative δC^{13} value, thus the Alcova sample is apparently confirmed as marine. It also appears that little or no freshwater, with its supply of oxidized C^{12}, was input to the Alcova depositional basin. The organic matter associated with Alcova stromatolite construction would have naturally equilibrated with the heavy carbon of oceanic reservoir.

Carbon isotopic compositions of carbonates are less liable to diagenetic reequilibration than are oxygen isotopic compositions. This is because formational solutions contain little carbon as compared to oxygen (Hudson 1977). The Alcova heavy carbon values are thus considered reliable ones.

Oxygen Isotopic Composition

Three stable isotopes of oxygen exist, O^{16}, O^{17}, and O^{18}. Because of their greater abundance and mass difference, the O^{16}/O^{18} ratio is generally measured (Hoefs 1980). The oxygen isotopic composition of a carbonate is largely dependent upon the temperature and isotopic composition of the water in which it formed. Variations found in the oxygen isotopic compositions of natural waters are themselves due to differences in vapor pressure. Heavy oxygen (O^{18}) is concentrated in the condensed phase of water in all evaporation and precipitation. In general, water vapor is preferentially enriched in light oxygen (O^{16}), the extent depending upon temperature, so that rainwater, and thus freshwater, is relatively depeleted in O^{18}. Evaporation of a limited reservoir concentrates O^{18} in the body of water subjected to evaporation (Anderson and Arthur 1983). Ultimately, freshwater carbonates are generally lighter in oxygen isotopic composition than marine carbonates.

The δO^{18}SMOW (SMOW = Standard Mean Ocean Water) value of the Alcova Limestone ranges from 28.3‰ to 32.0‰ with an average of 30.0‰. These are very high relative values for carbonate of this age (Triassic); thus the Alcova Limestone is enriched in O^{18}. Keith and Weber (1964) have shown that marine carbonates tend to be isotopically lighter with increasing geologic age. This is perhaps a result of diagenetic neomorphism and reequilibration with meteoric (light) water over time, although this point is still debated. Nevertheless, it is diagenetically very difficult to push a carbonate heavy with respect to oxygen. The particularly high δO^{18} values for the Alcova Limestone strengthens the view that recrystallization in this instance came early in the unit's history and that heavy original pore waters were involved. Such O^{18} enrichment suggests strong evaporation of the restricted Alcova reservoir. The low latitude position of Wyoming during the Triassic and the presumably warm, equable climate of the time may have facilitated a high evaporation rate.

FACIES INTERPRETATION

In light of the previous discussions, the Alcova Limestone appears to have been laid down in a low energy, restricted marine, almost lagoonal, hypersaline environment. This interpretation is the only one that is consistent with all observed environmental indicators. The shallow, though stable, bottom indicates that the Alcova shelf embayment was protected from high energy influences of the open ocean of the miogeosyncline. The presumed geography of the basin in conjunction with the low-diversity fauna, abundant stromatolites, low clastic input, high evaporation rate, and other factors argues for hypersaline waters.

The history of the Triassic Wyoming shelf, as discussed in Chapter 5, has been one of marine transgressions and regressions (Table 4). It is now presumed that the Alcova is immediately under- and overlain by marine units that are genetically similar. That is, the Alcova represents a carbonate break in the clastic dominated marine sedimentation of the "variegated sandy facies" and "basal sandstone unit" of the Crow Mountain Formation (High and Picard 1967a, b; etc.). Obviously, the terrestrial input to the shelf basin was largely interrupted at this point. The Alcova was probably a short-lived static phase between periods of transgression and regression. Additionally, Picard et al. (1969) have discussed the likely existence of a restricted apron/oolite shoal between the open shelf of the Red Peak

TABLE 4. Inferred environments of deposition of the Alcova Limestone and enclosing units (Chugwater Group). Oldest rocks at bottom (modified from Picard 1978).

STRATIGRAPHIC UNIT	DEPOSITIONAL FACIES
Popo Agie Formation	fluvial, lacustrine
Jelm Formation	deltaic plain
Crow Mountain Formation	
"upper sandstone/siltstone unit"	tidal flat complex, beach
"basal sandstone unit"	marine shelf/nearshore marine
Alcova Limestone Member	hypersaline restricted shelf
"variegated sandy facies"	nearshore marine
Red Peak Formation	tidal flat complex, shelf

Formation to the east and the miogeosynclinal trough of the Thaynes Formation to the west. Tectonic uplift along the shelf hinge zone may have perpetuated this restriction into Alcova times. This cannot be directly confirmed as the hinge area of the Alcova is poorly preserved.

Presumably, the relatively quiet, restricted shelf conditions with little terrestrial contribution facilitated the intiation of phytochemical carbonate precipitation at the beginning of Alcova deposition. The water column was obviously shallow, perhaps averaging no more than 10 or 20 m. The high degree of evaporation, low freshwater influx, and partial oceanic isolation would have significantly raised the salinity of the water in the basin. A salt-tolerant, probably stenohaline, biota of low diversity developed within. This was occasionally subjected to salinity fluctuations and resultant high invertebrate mortality, possibly as storm surges breached the hinge shoals and flooded the basin with water of normal marine, and therefore lower, salinity. Such periodic marine influence and replenishment also prevented the development of evaporite sequences by averting the precipitation of salts from supersaturated waters.

7. PALEOBIOGEOGRAPHY

INTRODUCTION

The presence of *Corosaurus* in the western United States creates an interesting biogeographic problem. 'Nothosaurs,' of both the pachypleurosaur and nothosauriform varieties, are common in the marine Triassic of the Old World, but why so rare in the New? Is this an ecologic or a stratigraphic phenomenon? Is *Corosaurus* truly a geographic isolate? The question of early sauropterygian abundance and distribution, both spatially and temporally, bears directly upon their evolutionary history—their place of origin and their subsequent radiation. It is also relevant to discussions of habitat preference and paleoecology.

'NOTHOSAUR' GEOGRAPHIC DISTRIBUTION

Old World 'nothosaurs' are rather widely distributed, with new specimens continuing to come to light in a variety of locations. The specific age and locality data, where known, of the generic types are presented in Appendix B. The classic 'nothosaur' localities are in the Middle Triassic shales of south and central Europe, particularly those of the German Muschelkalk epicontinental sea and the Alpine border of Tethys to the south. Notable among the Germanic Triassic localities are important deposits in Bavaria and Württemberg (see, e.g., Geissler 1895; Kuhn-Schnyder 1974; von Meyer 1847–55; Schmidt 1928; Wild 1972, 1980; and other authors). The most productive of the Alpine sites are found in northern Italy near Perledo and Besano, and in southern Switzerland at Monte San Giorgio (Tessin) (e.g., Gilardoni 1964; E. Kuhn 1941; Kuhn-Schnyder 1963b, 1964, 1987; Kuhn-Schnyder and Vonderschmitt 1953; Peyer 1933, 1934, 1944; Wild 1972; and other authors). Muschelkalk deposits containing pachypleurosaurs and primitive nothosauriforms ('nothosaurids') extend westwards into the Netherlands (Hooijer 1959) and eastwards into eastern Germany and Poland (e.g., Gürich 1884; Gürich and Dames 1891; Schrammen 1899; Tarlo 1959c; Volz 1902). The notice of a 'nothosaur' vertebra from the Lena Basin of the USSR (Lazurkin and Ochev 1968) probably represents a primitive plesiosaur (Chapter 4). Additional 'nothosaur' occurrences in the Alpine province along the margin of Tethys are found in France (Corroy 1933; Mazin 1985), Spain (Sanz 1976, 1983a), and the East Alpine Overthrust of Austria (Skuphos 1893c).

It is apparent that the Triassic Tethyan marine province and adjacent epicontinental environs controlled the distribution of early European sauropterygians to a very large extent. It is therefore to be expected that coastal animals of the tethyan faunal province would be found along Triassic coasts throughout the geographic range of Tethys. This is obviously the case for the Sauropterygia (Fig. 61). Numerous 'nothosaur' specimens occur along the northern Gondwana coast in Tunisia (Gorce 1960; Halstead and Stewart 1970), Israel (Brotzen 1955, 1957; Haas 1963, 1967, 1980; Peyer 1955; Swinton 1952), and Saudi Arabia (Thulborn, personal communication 1982). Tarlo (1959b) reports a 'nothosaur' vertebra from northern India, although this identification is questioned by Robinson (1959). No other indication of Triassic sauropterygians in India is yet known (Chatterjee and Roy-Chowdhury 1974). They remain unknown from Australia. Lazurkin and Ochev (1968) report *Nothosaurus giganteus* in the Upper Triassic of Australia but this is apparently an error (Thulborn, personal communication, 1982).

At the farthest eastern influence of Tethys, and bordering on the western edge

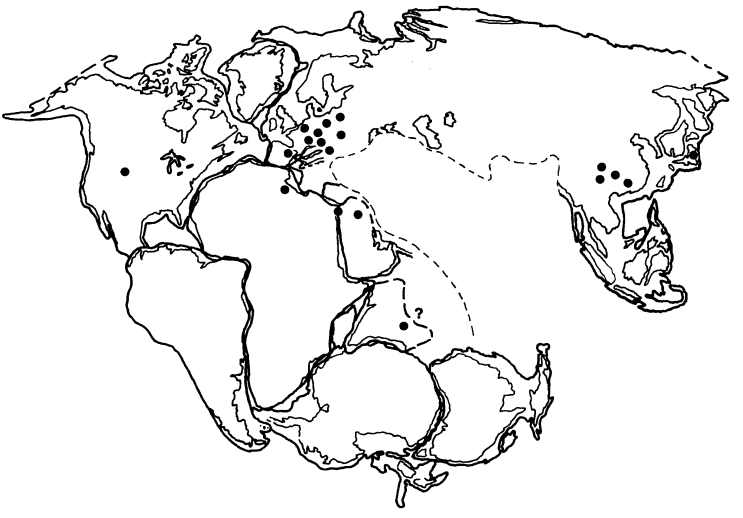

FIG. 61. Generalized world paleogeographic reconstruction for Middle Triassic time (Anisian–Ladinian) and known distribution of 'nothosaurs' (including Lower and Upper Triassic occurrences). Modified from Smith and Briden (1977).

of the Pacific province, 'nothosaurs' have been discovered in Japan (Yabe and Shikama 1948; Mazin 1986) [and possibly Hasegawa and Ota (1975), although the described tooth is impossible to assign to any genus] and with increasing frequency in the Hupeh, Kwangsi, Yunnan, Szechuan, and especially Kweichou (Keichow) provinces of China (Dong 1979; Young 1958, 1959, 1960, 1965a and b, 1972, 1978; Zhen et al. 1985). The Triassic marine deposits of China are very widespread and yield an interesting and diverse vertebrate fauna. Future work in this area will greatly add to our knowledge of the plesiomorphic sauropterygians and may clarify the relationships of the group.

Corosaurus, in being restricted to western North America, is situated well outside of the generally accepted Tethyan province. It may be considered to form part of an eastern Pacific faunal province, although its apparently unique paleohabitat (Chapter 6) evidently set it apart from typical Pacific faunas. The extensive Middle to Upper Triassic marine deposits of Nevada, California, Oregon, and Idaho have not yet yielded sauropterygian remains although numerous other vertebrates, particularly ichthyosaurs and thalattosaurs, are known, most notably from the Hosselkus Limestone of California and Luning Formation of Nevada (Merriam 1895, 1902, 1904, 1908; Camp 1976, 1980). As Case (1936) has observed, one such ichthyosaur was originally referred to "*Nothosaurus*?" by Smith (1894) and reassigned to *Shastasaurus* by Merriam (1902). [*Purranisaurus* from the Jurassic of Argentina was described initially as a plesiosaur (Rusconi 1948a, b) and then assigned to the Nothosauridae (Rusconi 1956), but is actually a thalattosuchian (metriorhynchid) crocodile (Gasparini 1980). Romer (1956, 1966) and Gasparini (1980) have provisionally equated this genus with *Metriorhynchus.*].

An additional western hemisphere 'nothosaur' may be represented by numerous fossils of a small, poorly known reptile from the Wupatki Member of the Moenkopi Formation of northeastern Arizona. These possible pachypleurosaurs, as yet undescribed, were collected near Leupp, Arizona, in 1949 by S. Welles of the University of California Museum of Paleontology, and more recently by K. Thiessen of the Museum of Northern Arizona in 1988. These animals are currently under study by Thiessen (personal communication 1988) and may lend important new evidence elucidating the early history and biogeography of the Sauropterygia.

It must be noted, however, that as yet the resemblance of these fossils to pachypleurosaurs is only superficial. No sauropterygian synapomorphies have been firmly identified among them and they may merely represent 'eosuchian'-grade aquatic animals, possibly younginiforms. The Wupatki Member is middle Spathian (upper Scythian) in age, and like the Alcova, represents an unusual paleoenvironment for sauropterygians—in this case apparently a fluvial regime.

'NOTHOSAUR' TEMPORAL RANGE

Having examined the geographic range of the pachypleurosaurs and 'nothosaurids,' it remains to discuss the distribution of these animals through time. The possible sauropterygian, *Nothosauravus,* of the Permian (Chapter 4) notwithstanding, all unequivocal nonplesiosaurian sauropterygians are restricted to the Triassic. Yet within this period a certain amount of temporal variation is evident, in spite of often poor stratigraphic resolution. Romer (1966) and Anderson and Cruickshank (1978) have crudely depicted 'nothosaur' zonation but numerous refinements can be made to their schemes.

As noted above, most known forms are Middle Triassic in age. More than anything else, this is probably a result of the stratigraphic bias presented by the abundance of Middle Triassic marine rocks, especially in Europe, where paleontologic investigation has had a long history. The Middle Triassic was a time of widespread marine transgression. However, although rare, there are some Lower Triassic sauropterygians. *Kwangsisaurus* from Kwangsi, China is purported to be of Early Triassic age (Young 1959, 1965a). Yabe and Shikama (1948) indicate *Metanothosaurus* to be from upper Scythian or lower Anisian rocks, although Mazin (1986) suggests that it may be upper Anisian, and *Corosaurus* is either Spathian or lowermost Anisian in age (this study, Chapter 5). Fragmentary material questionably referable to *Nothosaurus* is present in the uppermost Scythian at the top of the Buntsandstein of Germany (Edinger 1921; v. Meyer 1847–55; Schmidt 1986). These are all likely to be nothosauriforms, although *Kwangsisaurus* and *Metanothosaurus* are incompletely known. They are all at least large forms. The general lack of the smaller and presumably more plesiomorphic pachypleurosaurs is again likely to be an artifact of the stratigraphic record. The undescribed aquatic reptiles from the Scythian Wupatki Member of Arizona may correct this situation.

If the Indian occurrence (Tarlo 1959b) proves to be a 'nothosaur' (sensu lato), it is also Lower Triassic, for Chatterjee and Roy-Chowdhury (1974) note the Panchet Beds to be equivalent to the "*Lystrosaurus*" zone of the Scythian. Obviously, sauropterygians were already widely distributed by the end of the Lower Triassic. Mazin (1984) has assumed a Gondwana origin and Tethys-restricted dispersal for the group, based upon the positions of *Claudiosaurus* from the Permian of Madagascar (Carroll 1981), *Kwangsisaurus,* and *Metanothosaurus.* However, the possible presence of sauropterygians in Europe during the Permian and the early appearance of *Corosaurus* in the western hemisphere leave these questions in some doubt. Even allowing that sauropterygians may have originated in Gondwana, the relative scarcity and incomplete paleontologic exploration of Lower Triassic marine rocks limits our knowledge of their subsequent dispersal.

By the Middle Triassic both nothosauriforms and pachypleurosaurs are common and widely dispersed. For example, *Keichousaurus* is common in the Anisian of Kweichou and Hupeh provinces, China. *Neusticosaurus,* "*Pachypleurosaurus*" (= *Neusticosaurus*), and *Serpianosaurus* are frequently encountered in the Alpine

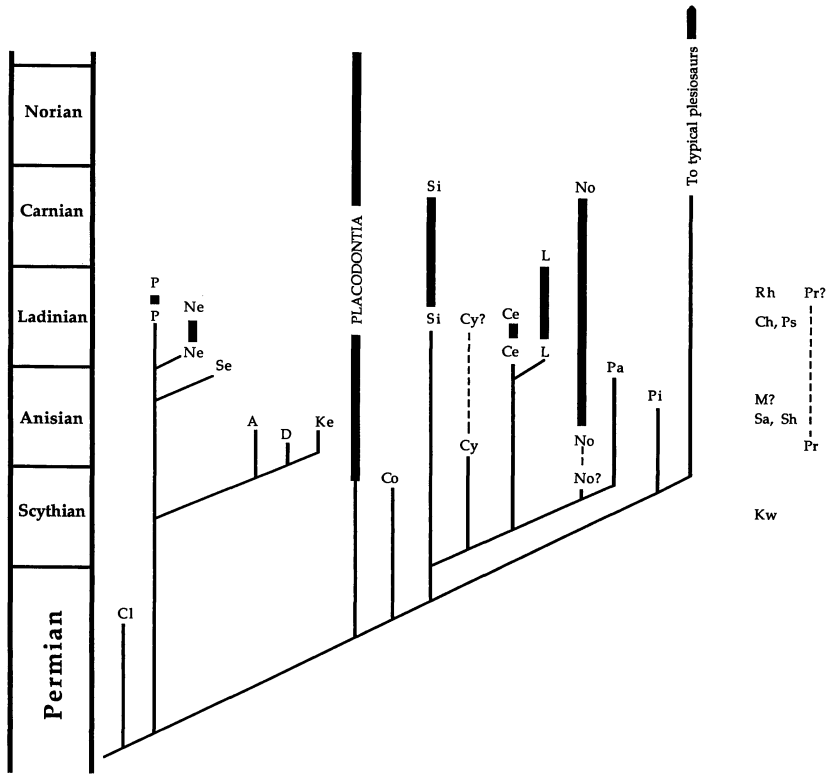

FIG. 62. Dendrogram of *Claudiosaurus, Pistosaurus,* selected 'nothosaurs,' and other sauropterygians incorporating presumed cladistic relationships and crude stratigraphic positions (ranges) of genera. See text for discussion. Relative stratigraphic positions of problematic genera indicated at right. Data from various sources. A = *Anarosaurus*; Ce = *Ceresiosaurus*; Ch = *Chinchenia*; Cl = *Claudiosaurus*; Co = *Corosaurus*; Cy = *Cymatosaurus*; D = *Dactylosaurus*; Ke = *Keichousaurus*; Kw = *Kwangsisaurus*; L = *Lariosaurus*; M = *Metanothosaurus*; Ne = *Neusticosaurus*; No = *Nothosaurus*; P = "*Pachypleurosaurus*"; Pa = *Paranothosaurus*; Pi = *Pistosaurus*; Pr = *Proneusticosaurus*; Ps = *Psilotrachelosaurus*; Rh = *Rhaeticonia*; Sa = *Sanchiaosaurus*; Se = *Serpianosaurus*; Sh = *Shingyisaurus*; Si = *Simosaurus.*

province and *Neusticosaurus* is representative of pachypleurosaurs in southern Germany; *Neusticosaurus* ranges through the Ladinian, and *Serpianosaurus* is known from the Grenzbitumen horizon at the Anisian/Ladinian boundary. The Ladinian to lowermost Carnian nothosauriform *Lariosaurus* is known from Italy, Switzerland, France, and Spain. The genus *Nothosaurus* has the greatest known temporal and geographic range. It is reported from the Anisian (possibly uppermost Scythian) to the uppermost Carnian, and in both the Germanic and Tethyan provinces—in Germany, Poland, the Netherlands, Spain, Tunisia, and Israel. Some of these specimens may, however, actually represent distinct but closely related genera such as *Paranothosaurus* (or perhaps *Silvestrosaurus,* see Appendix B). Simosaurus from southern Germany ranges from the Ladinian to the uppermost Carnian. If *Cymatosaurus* is truly congeneric with *Micronothosaurus* (Schultze 1970), this genus is Anisian and Ladinian, from Germany and Israel, respectively. E. von Huene (1944) has assigned a maxilla from the Upper Buntsandstein (lower Anisian) of Germany to *Cymatosaurus.* A similar maxilla from the Lower Muschelkalk of the Netherlands was described by Hooijer (1959). While *Proneusticosaurus* is originally known from the lower Anisian of Upper Silesia (Volz 1902), a possible specimen of *Proneusticosaurus* from Kärnten, Austria, has been identified as upper Ladinian by Arthaber (1924). The affinities of

this specimen, however, are rather dubious. The stratigraphic horizons (as limited by our present knowledge) of the remaining 'nothosaur' genera may be found in Appendix B.

Figure 62 presents the relative stratigraphic and evolutionary relationships of the nonplesiosaurian sauropterygians as they are presently understood. The relative recency of common descent indicated is extracted from the cladistic analysis of Chapter 4. Node stratigraphic positions are only relative, however, and should not be seen as representative of absolute times of divergence. A second limitation of the diagram is its rather platformed appearance. This is due both to the poor stratigraphic resolution provided by the record for many of these fossils and to the existence of isolated deposits exhibiting exceptional preservation (Lagerstätten), such as that at Monte San Giorgio, to which our knowledge of certain of the taxa (faunas) is restricted. Nevertheless, a preliminary picture of overall temporal relationships is gained. Refinement of this picture may be expected as our knowledge is increased. *Nothosaurus, Lariosaurus, Simosaurus, Neusticosaurus,* and perhaps *Cymatosaurus* and *Proneusticosaurus* are the only genera for which any significant stratigraphic range is known. It can also be seen that few 'nothosaurs' are known from the Upper Triassic—again only *Nothosaurus, Simosaurus,* and *Lariosaurus.* The apparent decline of the nonplesiosaurian sauropterygians in the Late Triassic is briefly discussed by Mazin (1987).

'NOTHOSAUR' HABITAT DIVERSITY

It is now increasingly apparent that 'nothosaurs' do not represent a natural monophyletic group, that their habits and habitats varied, and that their occurrences are not restricted only to typical marine sediments. The interpretation of the Alcova Limestone as a variably hypersaline, restricted marine basin, and the presumption that *Corosaurus* was an endemic faunal element within it, is one of the most obvious exceptions. The unique morphology of *Corosaurus* can perhaps be partly explained by its geographic isolation and restricted occurrence in a unique paleohabitat. Furthermore, fragments of *Nothosaurus* have been recovered from a primarily freshwater deposit in the lower Keuper of Kupferzell, Germany (Wild 1980). This discovery may indicate a short-lived marine influence over deltaic flood plains as suggested by Wild (1980), but may be equally indicative of a localized brackish environment. It is, of course, another question whether or not *Nothosaurus* actually lived in this environment or was simply transported to it post-mortem.

Among the Triassic deposits of Europe, those of the Germanic Basin generally represent distinct environmental facies from those of the western Tethys–Alpine geosyncline (Kummel 1961). The Middle Triassic Muschelkalk of the Germanic province includes not only marine marls and limestones of the epeiric sea, but also evaporites and marginal sands of lagoonal environments. Nothosauriform remains occur in many of these deposits. Similar lagoonal rocks and fossils are contained within the regressive Keuper of the Germanic Upper Triassic. Alpine Triassic rocks are representative of unrestricted, miogeosynclinal marine conditions and consist largely of shales, limestones and dolomites. 'Nothosaurs' are rare in the deepwater reef facies but, where common, are still fully marine. Apparently the two European marine provinces were more or less separated by an intermittent land barrier or arch during the Triassic. The juvenile 'nothosaur' cave fauna of southwest Poland may consist of immature shore dwellers along a subaerially exposed part of this arch (Tarlo 1967).

The physical separation of the two European provinces seems to have resulted

in the development of two distinct faunas (Wild 1972). Many genera, such as *Lariosaurus* and *Simosaurus,* are as yet restricted to their respective basins. However, the common and readily recognizable genus *Nothosaurus* is known from both provinces, as well as from the northern edge of Gondwana. The sauropterygian-bearing deposits of North Africa represent flat, open shoreline facies (Halstead and Stewart 1970). *Neusticosaurus,* and possibly *Cymatosaurus* and *Proneusticosaurus,* also cross the European arch barrier. Thus, faunal isolation, while genuine, may not have been complete and may partially reflect preservational biases and localized habitat variations.

The Chinese pachypleurosaurs and 'nothosaurids' are both morphologically distinct and geographically distant from their European counterparts. The marine Triassic of China has not been fully characterized but contains numerous limestones and shales of a shallow epicontinental seaway. Young (1958) has likened these to rocks of the calcareous Alps of Tessin (Alpine province). [It should be noted that one 'nothosaur' occurrence reported in Young (1960) is in error (Young 1965b).]

The one common factor among virtually all 'nothosaur' occurrences is their littoral or paralic position. Plesiomorphic sauropterygians were predominantly near-shore animals. All are from shallow-water environments and, as discussed in Chapter 3, may have been amphibious. In general, 'nothosaurs' appear to have been ecologically separate from, and are rarely found amid, pelagic faunas containing plesiosaurs and ichthyosaurs. This may partially account for their absence in the open marine Triassic of the westernmost United States where ichthyosaurs, at least in the Upper Triassic, are common. The Tessin (Monte San Giorgio) Grenzbitumen horizon is one of the few places where 'nothosaurs' are associated with ichthyosaurs. As noted, Sues (1987) has proposed that the Triassic plesiosaur *Pistosaurus* is not found with more plesiomorphic forms because of its ecologic restriction to more open waters.

This review of pachypleurosaur and 'nothosaurid' distributions has been necessarily brief but serves to indicate a greater range of geographic, temporal, and habitat dispersal than has been previously supposed. Many of the apparent spatial and temporal restrictions of the early sauropterygians are probably of a geologic (preservational) nature rather than a biologic one. The ecologic problem of local habitat restrictions is more likely to be real, although the relative abundances of individuals and diversity of faunas within them cannot be accurately determined.

8. SUMMARY

Several aspects of *Corosaurus* and its occurrence have been addressed in this study. These include the morphology and systematic position of *Corosaurus*; its functional morphology, behavior and paleoecology; the evolution and systematics of the Sauropterygia; the paleobiogeography and biostratigraphy of pachypleurosaurs and 'nothosaurids'; and the geology, age, and paleoenvironment of the Alcova Limestone. It is clear that the anatomy of *Corosaurus* is unique and that it represents a distinct, valid taxon which is plesiomorphically sauroptergian and not closely similar to plesiosaurs. The skull is mesorostrine with large supratemporal fenestrae, a broad skull table, large nasals, reduced jugals, and possibly no quadratojugals. The axial skeleton is generally conservative, notably possessing only three sacral vertebrae, these with distally expanded ribs.

The relatively expanded limb girdles of *Corosaurus,* specifically with respect to the coracoid and pubis, are only superficially like those of plesiosaurs; the limbs are actually less specialized than are those of certain other primitive nothosauriforms. The coracoid, while large, is not elaborated caudad as in plesiosaurs, the pectoral fenestra remains large, the scapula has no ventral, horizontal elaboration, and the clavicular bar is stout. The pubis retains an obturator foramen, and the ilium is strong, possessing a pronounced iliac blade and contacting both the ischium and the pubis.

Corosaurus and the other 'nothosaurids' represent, along with the plesiosaurs and seemingly the placodonts, a monophyletic clade, the sister group of which is the Pachypleurosauria. This clade is designated the Nothosauriformes. A basal dichotomy is therefore evident within the Sauropterygia and the 'nothosaurs' are paraphyletic. Both groups, however, represent a plesiomorphic experiment with, and radiation in, a secondarily aquatic habitus. Primitive nothosauriforms, especially, were apparently functionally antecedent to the plesiosaurs. The partial structural similarities of the appendicular girdles of *Corosaurus* to those of plesiosaurs may reflect a parallel function—i.e., limb-dominated (paraxial) aquatic propulsion. As the girdles are expanded primarily in the horizonal plane, as they are in plesiosaurs, and vertical movement of the limbs was limited by the configurations of the girdle/propodial articulations, a model of "underwater flight" is not a perfect analogy. Rather, reconstructed musculature suggests a rowing, down and back (drag-based) propulsive limb stroke as in modern otariids, but perhaps using both sets of appendages. Some hydrostatic lift may have been provided by hydrofoil action of a feathered return stroke in the horizontal plane as suggested for plesiosaurs by Godfrey (1984). The tail is not considered to have been the primary propulsive organ of *Corosaurus* because of the stiffened nature of the thorax and the aquatic specializations of the limbs. However, limited caudal propulsion was probably utilized at times. Consideration of other 'nothosaurs' indicates that most of them also probably relied primarily upon their limbs for thrust while swimming. The major structural differences in the appendicular skeletons of pachypleurosaurs and 'nothosaurids' vs. the plesiosaurs probably reflect the retention of amphibious or nearshore bottom-dwelling behavior in the nonplesiosaurian Sauropterygia. This probably pertains also to the Placodontia.

An evaluation of the traditional taxonomic characters of the Sauropterygia and 'Nothosauria' implies that some such features of these animals probably reflect individual, ontogenetic, and preservational variations; other characters reflect functional similarities or parallelisms. Many useful characters can be defined, however, and with them a phylogenetic scheme (cladogram) of the Sauropterygia was constructed portraying a most parsimonious hypothesis of relationships. This

analysis concentrated on the adequately known genera of traditional 'nothosaurs.' These consisted of six pachypleurosaur (including "*Pachypleurosaurus*") and seven 'nothosaurid' genera. Other taxa which are believed to be valid but are too poorly known for analysis were briefly discussed. The Pachypleurosauria generally exhibit small size (up to 1 m in length), small supratemporal fenestrae, isodont dentition, and a relatively small postorbital region of the skull. The 'nothosaurid' nothosauriforms are typically of large size (1–4 m), have large supratemporal fenestrae, strongly curved humeri, and are often distinguished by anisodont dentition and a loss of the quadratojugal. *Corosaurus* apparently diverged early from the nothosauriform stock. The Sauropterygia are quite likely derived diapsids as proposed by Kuhn-Schnyder (1980, etc.), possibly with younginiform ancestors, and the closest known sister group of which is the Permian *Claudiosaurus*.

The thin (1–10 m) Alcova Limestone, a member of the Crow Mountain Formation, Chugwater Group, is a dense microsparite which is highly resistant to erosion and often forms cliffs in outcrop. It is slightly fossiliferous, petroliferous, and locally is secondarily dolomitic. The mineralogy of the unit is dominated by phytochemically precipitated carbonate; the few clastic minerals indicate a low terrigenous input. Low-energy microlaminae and algal stromatolites are abundant. Picard et al. (1969) have shown that the Alcova is physically continuous with the (Scythian or lowermost Anisian) Thaynes Formation of the Triassic western geosyncline, but a dramatic facies change from the normal marine conditions of the Thaynes is evident. *Corosaurus,* in some respects a conservative nothosauriform, is thus also of relatively early geolgic age. The morphology of *Corosaurus* alone, however, is not indicative of this fact. From its unique occurrence, relative abundance, and the lack of associated typical marine organisms, *Corosaurus* is presumed to have been an endemic faunal component of the Alcova basin.

The Alcova, as a transgressive tongue of the Thaynes, obviously represents a unique paleoenvironment of relatively low deposition and probably short duration. Newly examined paleontologic, sedimentologic, and geochemical evidence suggests that the Alcova was a shallow, restricted, probably hypersaline embayment of the sea, possibly intermittently cut off from normal marine conditions by western shoals. This hypothesis is in accord with the structural setting of the U.S. Western Interior during the Triassic.

The apparent geographic and ecologic isolation of *Corosaurus* from occurrences of other 'nothosaurs' is increasingly disputed by new discoveries. Frequent finds of Asian Triassic sauropterygians particularly, and a possible discovery in Arizona, increase both the spatial and temporal range of the plesiomorphic sauropterygians. They may also help to elucidate the systematic interrelationships of the clade. The popular belief that 'nothosaurs' are primarily restricted to the marine Middle Triassic of Europe is a biased result of widespread marine deposits of that age on the continent and of the long history of European paleontologic research. Thus the presently known distribution is a stratigraphic rather than a biologic phenomenon. The animals actually spanned most of the Triassic, and perhaps also the Upper Permian, and may have ranged worldwide. As yet, no paleobiogeographic history of the Sauropterygia can be accurately defined. Early sauropterygians also seem to have tolerated a wider variety of osmotic regimes and environments than previously suspected but are most commonly found in paralic marine settings.

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APPENDIX A

COROSAURUS ALCOVENSIS HYPODIGM

The following list comprises the hypodigm of presently known and catalogued specimens of *Corosaurus alcovensis*.

UW 5485	(holotype) partial skeleton; skull, vertebrae, ribs, gastralia, partial pectrum and forelimbs, etc.; also sacrum of second individual and other fragmentary remains
FMNH PR135	lot number comprising widely scattered but associated partial individual(s?), notably including:
	isolated cervical vertebra with ribs/part and counterpart
	caudal vertebra and rib
	right clavicle
	crushed right humerus
	fragmentary cervical series with ribs
	partial ulna
	numerous specimens of ribs and gastralia
	singly pronged gastralium and other fragmentary gastralia
	doubly pronged gastralium
	partial skeleton including vertebrae, ribs, gastralia, isolated tooth, and partial hindlimbs
	partial skeleton including fragmentary ribs, gastralia, metapodials?, etc.
	fragmentary propodial (humerus?)
	isolated vertebra and gastralium
FMNH PR242	impression of partial vertebral column and ribs
FMNH PR243	right ilium and partial metapodial?
FMNH PR244	fragmentary dorsal rib(s?)
FMNH PR245	dorsal neural arch
FMNH PR246	left mandibular ramus/proximal end and indeterminate bone scrap
FMNH PR480	partial skeleton; vertebrae, ribs, gastralia, pelvis, partial hindlimbs, etc.
FMNH PR1368	partial skeleton(s?) including partial mandible, vertebrae, gastralia, caudal chevron, tibia?, etc.
FMNH PR1369	partial skeleton; vertebrae, ribs, gastralia, partial pelvis and hindlimb, etc.
FMNH PR1382	partial mandible with teeth
FMNH PR1383	partial vertebral column
YPM 41030	partial skeleton; vertebrae, ribs, gastralia, etc.
YPM 41031	partial skeleton; vertebrae, ribs; left humerus, scapula, ulna, and radius
YPM 41032	left humerus
YPM 41033	left humerus
YPM 41034	right coracoid
YPM 41035	right humerus/distal end

YPM 41036	right ulna/proximal end
YPM 41037	left clavicle
YPM 41038	left femur
YPM 41039	right femur
YPM 41040	(left?) pubis
YPM 41043	partial mandible
YPM 41044	dorsal rib
YPM 41045	caudal chevron
YPM 41046	gastralium
YPM 41047	median caudal vertebra
YPM 41048	vertebral centrum
YPM 41049	partial neural arch
YPM 41050	dorsal vertebra and rib
YPM 41051	dorsal rib?
YPM 41052	fragmentary epipodial?
YPM 41053	vertebral centrum
YPM 41054	neural arch and spine
YPM 41055	femur/proximal end
YPM 41056	vertebra
YPM 41057	vertebra
YPM 41058	dorsal vertebra
YPM 41059	gastralia
YPM 41060	partial tooth row
YPM 41061	rib fragment
YPM 41062	median caudal vertebra
YPM 41063	vertebra
YPM 41064	partial coracoid
YPM 41065	gastralia
YPM 41066	vertebra
YPM 41067	large median gastralium
YPM 41068	dorsal rib

APPENDIX B

'NOTHOSAUR' GENERIC NAMES

There follows in alphabetical order a list of 72 generic names that have at times been variously assigned to the 'Nothosauria' or considered primitive sauropterygians. A brief discussion of the status of the taxon and its occurrence accompanies each entry.

Anarosaurus Dames, 1890. An apparently valid taxon based upon the part and counterpart of a partial skeleton, including the skull, from the Muschelkalk of Germany (approximately 15 km west of Magdeburg). Noted for the relative length of the femur (longer than the humerus). Pachypleurosauria. Anisian. Type and only specimen destroyed during World War II but casts exist.

Anomasaurus is a misspelling in Tatarinov and Novozhilov (in Orlov 1964) of *Anomosaurus* v. Huene, 1902, and thus a *nomen nudum* unavailable for synonymy.

Anomosaurus v. Huene, 1902. Problematic generic name based on poor material from the Middle Triassic of Europe and equated with *Dactylosaurus* Gürich, 1884 by von Huene (1956). *Anomosaurus* is now believed to be equivalent to the placodont *Placodus* (v. Huene 1959b; Kuhn 1964a).

Ceresiosaurus Peyer, 1929. This 'nothosaurid' was named in an abstract, but officially described by Peyer in 1931 and is notable for its massive pectoral girdle and robust humeri, and for its relatively elongate neck. It is known from several complete skeletons from Monte San Giorgio, Tessin, Switzerland, and is a valid genus. Nothosauriformes. Ladinian.

Charitodon v. Meyer, 1847 is an unjustified emendation of *Charitosaurus* v. Meyer, 1838a.

Charitosaurus v. Meyer, 1838a. Name applied to an undescribed lower jaw fragment which Kuhn (1964a) states to be from either a small 'nothosaur' or a large ganoid fish. The latter is now generally accepted to be the case.

Chinchenia Young, 1965a. This genus is based upon several very fragmentary partial skeletons from the Ladinian, 7 km west of Chinchen, Kweichou, China. The material is very unusual and is diagnostic of a probable nothosauriform but details of its anatomy remain sketchy.

Chondriosaurus is apparently a second generation misspelling in Romer (1966) of *Conchiosaurus* v. Meyer, 1834, after *Condriosaurus* [in von Meyer (1838b)]. *Chondriosaurus* is a *nomen nudum*.

Conchiosaurus v. Meyer, 1834. Described from a fragmentary skull from the Bavarian Muschelkalk, this genus is generally considered equivalent to *Nothosaurus* Münster, 1834. Von Meyer (1847–55) himself suspected that these two taxa might be found to be the same, and allowed that the name *Nothosaurus* should be given priority.

Condriosaurus is presumably a misspelling (v. Meyer 1838b) of *Conchiosaurus* v. Meyer, 1834, and thus a *nomen nudum*.

Corosaurus Case, 1936. A valid nothosauriform genus from the Alcova Limestone Member of the Crow Mountain Formation of central Wyoming. Known from numerous partial specimens near Casper, Wyoming. Limb girdles uniquely expanded. Nothosauriformes. Uppermost Scythian (Spathian) or lowermost Anisian.

Cymatosaurus Fritsch, 1894. This is a valid taxon with some superficially plesiosaur-like features, but which lacks an interpterygoid vacuity and retains

nasals in contact with the external nares. Known only from skull material and gastralia, although Volz (1902) assigned some questionable postcrania to *Cymatosaurus*. Nothosauriformes. Anisian of the Germanic Province (Muschelkalk). *Eurysaurus* Frech, 1903 and *Germanosaurus* Nopsca, 1928a are apparent junior synonyms. The similar *Micronothosaurus* Haas, 1963 (Ladinian) may also be equivalent (Schultze 1970).

Dactylosaurus Gürich, 1884. A distinct pachypleurosaur from the Lower Muschelkalk of Upper Silesia (now Poland). Differs from other pachypleurosaurs primarily in its more gracile nature, particularly with regard to the epipodials. Known from two partial skeletons with skulls, now lost but preserved as casts. Pachypleurosauria. Anisian.

Deirosaurus Owen, 1854. A genus based upon poor material from the Middle Triassic of Europe and considered Nothosauria *incertae sedis* by Romer (1956). In 1966, Romer placed the genus in the Nothosauridae, but the taxon must be considered a *nomen dubium*.

Diplovertebra is an apparent misspelling of *Doliovertebra* v. Huene, 1902 in Kuhn (1934).

Dolichovertebra Schmidt, 1928 is an emendation of *Doliovertebra* v. Huene, 1902.

Doliovertebra v. Huene, 1902. Taxon based upon three vertebrae from the Schaumkalk of Freyburg, Germany. Now generally considered a synonym of *Proneusticosaurus* Volz, 1902, the material is perhaps nondiagnostic.

Dracontosaurus is a misspelling in Agassiz (1846) of *Dracosaurus* Münster, 1834.

Dracosaururus is an apparent misspelling of *Dracosaurus* Münster, 1834, in Romer (1966).

Dracosaurus Münster, 1834. Another taxon described from fragmentary material from the Germanic Triassic and now universally equated with *Nothosaurus* Münster, 1834.

Elmosaurus v. Huene, 1957. Based on a single partial skull (minus rostrum and posterior portion of cranium) from the upper ceratite layer (Upper Muschelkalk) of Braunsweig, Germany. This is a unique taxon with unknown affinities. The unusual structure of the skull table is unlike that of other known sauropterygians; it may represent an early offshoot of the Sauropterygia. Ladinian.

Eupodosaurus Boulenger, 1891a. This name was improperly based upon a plaster cast of a reptile foot from the Triassic Esino beds of Lombardy, Italy and originally referred to the Stegosauria. The cast is, in fact, that of a foot of *Lariosaurus* Curioni, 1847 (Boulenger 1891b). *Eupodosaurus* is therefore a junior synonym of *Lariosaurus*.

Eurysaurus Frech, 1903. This genus most likely represents a junior synonym of *Cymatosaurus* Fritsch, 1894. It is known from several skulls from the lower Muschelkalk of Upper Silesia that differ little from those of *Cymatosaurus*. The name *Eurysaurus* was preoccupied and has been replaced with *Germanosaurus* Nopsca, 1928a. Anisian.

Germanosaurus Nopsca, 1928a. This name was proposed in place of the preoccupied *Eurysaurus* Frech, 1903. It is generally considered equivalent to *Cymatosaurus* Fritsch, 1894.

Keichousaurus Young, 1958. This is a small, distinct form represented by numerous specimens, including articulated skeletons, from Kweichou (Keichow) and Hupeh provinces, China. The greatly expanded ulna of this genus is diagnostic. Pachypleurosauria. Anisian.

Kolposaurus Skuphos, 1893c. Name given to a fragmentary specimen (largely vertebrae and ribs) from the Muschelkalk of Upper Silesia which was earlier

described by Kunisch (1888) as *Nothosaurus*. Interestingly, a large form with swollen ribs and neural arches, the material is not diagnostic and the taxon must be considered *nomen dubium*.

Kwangsisaurus Young, 1959. A taxon consisting of a single, partial postcranial skeleton from Kwangsi Province, China. It is distinguished by its robust femur and small pes but is an apparent nothosauriform which is very poorly known. Scythian.

Lamprosaurus v. Meyer, 1860a. This genus was based upon a single fragmentary maxilla from the Lower Muschelkalk of Silesia. As the type material is indeterminate, the genus must be considered a *nomen dubium*.

Lamprosauroides Schmidt, 1927. This generic name was proposed to replace *Lamprosaurus* v. Meyer, 1860a, a preoccupied name.

Lamprosciuroides is a misspelling in Romer (1966) of *Lamprosauroides* Schmidt, 1927, and thus a *nomen nudum* unavailable for synonymy.

Lariosaurus Curioni, 1847. A valid taxon known from numerous specimens, including articulated skeletons, from the Alpine province of Tethys. A small nothosauriform with five sacral vertebrae with unexpanded sacral ribs. Type specimen destroyed during World War II but preserved as casts. Nothosauriformes. Ladinian–lowermost Carnian of Italy, Spain, Switzerland, and France.

Macromerosaurus Curioni, 1847 *emend.* Cornalia, 1854 is a probable subjective junior synonym of *Lariosaurus* Curioni, 1847, having perhaps been founded on a juvenile specimen of the latter from Perledo, Italy (Boulenger 1896; Dames 1890; Peyer 1934).

Macromirosaurus Curioni, 1847. The incorrect original spelling of *Macromerosaurus* Curioni, 1847 *emend.* Cornalia 1854. *Macromerosaurus* is etymologically correct and was later adopted by Curioni (1863).

Menodon is a name appearing in Romer (1966) as a junior synonym of *Nothosaurus* Münster, 1834. Its origin is obscure.

Metanothosaurus Yabe and Shikama, 1948. This genus is based upon a headless, partial skeleton (now lost) from near Yanaizu, northeastern Japan. Mazin (1986) believes it to be from the Isatomae Formation. A large animal with high neural spines and slender ribs, the fossil is of little diagnostic value but is probably part of the nothosauriform clade. The taxon may be a *nomen dubium* but is tentatively retained by most current workers. Scythian.

Microcleptosaurus is a misspelling in Romer (1966) of *Microleptosaurus* Skuphos, 1893c. It is a *nomen nudum* unavailable for synonymy.

Microcletosaurus is a misspelling in Tatarinov and Novozhilov (in Orlov 1964) of *Microleptosaurus* Skuphos, 1893c and is a *nomen nudum* unavailable for synonymy.

Microleptosaurus Skuphos, 1893c. This taxon is based upon the nondiagnostic ribs of a very small 'nothosaur' from the Middle Triassic Partnachschichten of Vorarlberg, western Austria. It is generally regarded as the juvenile form of the associated *Partanosaurus* Skuphos, 1893a *emend.* 1893b but *Microleptosaurus* is a *nomen dubium*.

Micronothosaurus Haas, 1963. The name proposed for a single, small skull from Wadi Ramon, Negev, Israel. Schultze (1970) has tentatively equated this genus with *Cymatosaurus* Fritsch, 1894 on the basis of similar postorbital region morphologies, a suggestion that is provisionally followed here. Ladinian.

Nachangosaurus Wang, 1959. A poorly known taxon represented by a single skeletal impression from the Scythian [not Permian (Young 1965a)] of Na-

chang, China. Sometimes considered a primitive sauropterygian (Kuhn 1961, 1964a, b; Wang 1959), Tatarinov and Novozhilov (in Orlov 1964) have suggested a possible close relationship of the fossil with thalattosaurs.

Namuncurania Rusconi, 1943. This taxon is not a sauropterygian, despite its questionable referral to the 'Nothosauria' by Kuhn (1964a). Rusconi (1943, 1948b) considered the fossil (vertebra and ribs) to be plesiosaurian but it may represent a marine crocodile. Jurassic of Argentina (Mendoza Province).

Neusticosaurus Seeley, 1882. A distinct taxon but one that has been difficult to distinguish from "*Pachypleurosaurus*" Broili, 1927. A relatively small humerus to femur ratio, narrow skull table, small size, and other characteristics were considered by Carroll and Gaskill (1985) to be distinctions separating *Neusticosaurus* from *Pachypleurosaurus*. Sander (1989), however, reasonably regards these two taxa as specific variants of the senior *Neusticosaurus*. Pachypleurosauria. Ladinian, southern Germany and the Italo-Swiss Alps [holotype (BMNH R53) from the Lettenkeuper Hoheneck Dolomite of Hoheneck, near Ludwigsburg, Baden-Württemberg, Germany].

Nothosauravus Kuhn, 1958a. *Nomen dubium* based upon a generically nondiagnostic, single sacral vertebra, possibly of a primitive sauropterygian, from the Kupferschiefer of Germany, lower Upper Permian.

Nothosauripus Kuhn, 1958b. The name given to an isolated pentadactyl print from the Ladinian shales of Besano, Italy, which was described by von Huene (1935) as belonging to a sauropterygian. It is a possible 'nothosaur' print but is not directly comparable to anatomical taxa.

Nothosaurops Leidy, 1870. Taxon based upon an isolated vertebral centrum from possibly Cretaceous rocks along the Moreau River, South Dakota. In 1873 Leidy labeled this specimen *Nothosaurops* in his plate 15 but referred to it as *Nothosaurus* in the text (pp. 287, 354). The centrum is actually that of a champsosaur.

Nothosaurus Münster, 1834. A very large, derived 'nothosaurid' commonly known from isolated and articulated material in the Germanic and western Tethyan provinces. The genus possesses a massive, longirostrine skull with very large, elongate, supratemporal fenestrae. Numerous genera based upon partial specimens are now generally considered to be equivalent, including *Conchiosaurus* v. Meyer, 1834; *Deirosaurus* Owen, 1854; *Dracosaurus* Münster, 1834; *Oligolycus* Fritsch, 1894; and others. However, *Nothosaurus* takes priority. Many species of *Nothosaurus* have been described and more than one genus may actually be represented by the total available material (such as *Paranothosaurus*). Nothosauriformes. Anisian (questionably uppermost Scythian)–uppermost Carnian.

Ocoyuntaia Rusconi, 1947. Although listed by Kuhn (1964a) as a questionable 'nothosaur,' this genus was described as a phytosaur and is most probably a 'thecodont' of uncertain status (Romer 1966). Triassic of Argentina.

Oligolycus Fritsch, 1894. Taxon based upon a lower jaw from the German lower Muschelkalk and now generally regarded as a junior synonym of *Nothosaurus* Münster, 1834.

Opeosaurus v. Meyer, 1847–55. Described from a single, fragmentary, lower jaw from the upper Muschelkalk of Ludwigsburg, Württemberg, this genus is perhaps a junior synonym of *Simosaurus* v. Meyer, 1842. The material cannot be considered diagnostic of a separate taxon and the genus is thus *nomen dubium*.

Pachypleura Cornalia, 1854 is a preoccupied synonym of *Pachypleurosaurus* Broili, 1927, and thus probably also of *Neusticosaurus* Seeley, 1882.

Pachypleurosaurus Broili, 1927. A famous but confused genus from the Middle Triassic shales of Monte San Giorgio, Switzerland, and adjacent areas. Originally described as *Pachypleura* Cornalia, 1854. Known from numerous articulated specimens and closely related to *Neusticosaurus* Seeley, 1882 and *Serpianosaurus* Rieppel, 1989. These genera are notable for their common exclusion of the postorbital from the very small supratemporal fenestrae. Sander (1989) reasonably considers *Pachypleurosaurus* to be a specific variant of *Neusticosaurus*. This interpretation is accepted here. Pachypleurosauria. Ladinian.

Palaeosaurus is an oft coined taxon name (synonym) by which various unrelated fossil reptiles have been known. The type specimen of *Lariosaurus* Curioni, 1847 was early referred to as *Palaeosaurus* by Balsamo-Crivelli (1839) (Arthaber 1924; Boulenger 1896; Rieppel 1987). Thus *Palaeosaurus* is also a synonym of *Lariosaurus* Curioni, 1847.

Paranothosaurus Peyer, 1939. This genus is recognized from a single complete skeleton from the Anisian/Ladinian boundary of Tessin, Switzerland. It is distinguishable from its close relative *Nothosaurus* Münster, 1834 primarily by its weakly developed pectrum and barlike interclavicle. Nothosauriformes. Anisian/Ladinian boundary.

Partanosaurus Skuphos, 1893a *emend.* 1893b. A problematic genus known from fragmentary remains from the Middle Triassic of Vorarlberg, western Austria. May be tentatively retained on the basis of its tall, ridged, neural spines; transversely ovate vertebral centra, distally expanded dorsal ribs, and slender scapular blade. Originally in the collection of the Austrian Geological Survey, the whereabouts of this material are now unknown.

Parthanosaurus Skuphos, 1893a is the incorrect original spelling of *Partanosaurus* Skuphos, 1893a *emend.* 1893b. This name appeared in the preliminary report of the fossil's discovery (Skuphos 1893a) in which the author stated that he was naming the genus after the geological horizon of its occurrence, the "Partnach-Schichten." As such this name is an incorrect original spelling under the *International Code of Zoological Nomenclature* [Third Ed., Ride et al. 1985, Article 32c (ii)] and subject to correction. The justified emendation was made by Skuphos (1893b) himself.

Phanerosaurus v. Meyer, 1860b. Based on vertebrae from the Lower Permian of Germany, Kuhn (1934) allied this taxon to *Nothosaurus* Münster, 1834. It is not sauropterygian but more likely belongs to the Anthracosauria (Romer 1966).

Philotrachelosaurus is an incorrect spelling in Nopsca (1928a) of *Psilotrachelosaurus* Nopsca, 1928b. The full description and designation of this fossil as a new genus appears in Nopsca (1928b) as *Psilotrachelosaurus. Philotrachelosaurus* is a *nomen nudum.*

Phygosaurus Arthaber, 1924. A problematic, intermediately-sized pachypleurosaur known only from the incomplete, headless, holotype from the Ladinian of Perledo, Italy. Originally described as a specimen of *Lariosaurus* Curioni, 1847 by Deecke (1886), Rieppel (1989) considers the material nondiagnostic at the generic level and a *nomen dubium.* The fossil is potentially part of the *Serpianosaurus* Rieppel, 1989 hypodigm. The type is now lost and may have been destroyed in a fire at the University of Strasbourg (Rieppel 1989).

Pistosaurus v. Meyer, 1839. A valid genus of Triassic sauropterygian belonging to the Plesiosauria. The nasals are vestigial and do not contact the nares; the interpterygoid vacuity is (secondarily?) present. Described on the basis of two skulls (v. Meyer 1847–55), the more complete of which is now lost

(fortunately after having been cast), several postcranial skeletons have since been assigned to the genus (Sanz 1983b; Sues 1987). Plesiosauria. Upper Muschelkalk (upper Anisian) of southern Germany.

Pontopus Nopsca, 1923b. This is an ichnogenus based on an apparently webbed track from the Upper Triassic of Cheshire, England, and first described as *Rhynchosauroides membranipes* Maidwell, 1911. Nopsca (1923b) suggested that the print was made by a pachypleurosaur such as *Neusticosaurus,* but *Pontopus* is now universally equated with *Rhynchosauroides* Beasly in Maidwell 1911 and is considered to represent a terrestrial or semiterrestrial lacertiloid.

Proneusticosaurus Volz, 1902. This genus appears to be valid but is poorly known. Only a few individuals have been assigned to it (Arthaber 1924). It is a large animal exhibiting greatly thickened ribs and presumably six distally narrow sacral ribs. The relatively large ischia and small thyroid fenestra of the type pelvis are remarkable. ?Nothosauriformes. Lower Anisian of Upper Silesia and possibly also upper Ladinian of Kärnten, Austria.

Psilotrachelosaurus Nopsca, 1928b. A possibly separate genus as evidenced primarily by a uniquely long and slender coracoid. However, only one headless specimen (from the Austrian Alpine Muschelkalk, probably 2 km west of Töplitsch) is known and the appearance of the coracoid may be a preservational artifact (Sues and Carroll 1985). Pachypleurosauria.

Purranisaurus Rusconi, 1948a. A taxon assigned to the 'Nothosauria' by Rusconi (1956) but actually representing a thalattosuchian (metriorhynchid) crocodile possibly equivalent to *Metriorhynchus* Meyer, 1830 (Gasparini 1980). Jurassic of Argentina (Mendoza).

Rhäticonia Broili, 1927. Problematic but seemingly unique taxon exhibiting pronounced "pachyostosis," stout humeri, and a short, conspicuously constricted rostrum. Known only from a very small, possibly juvenile, skeleton from the Albergschichten of Vorarlberg, Austria. This specimen was destroyed during World War II. Sauropterygia *incertae sedis.* Upper Ladinian.

Rhaeticonia is the anglicized version of *Rhäticonia* Broili, 1927, first used by Woodward in Zittel (1932). Current nomenclatural practice forbids the use of the umlaut in taxonomic names [*International Code of Zoological Nomenclature,* Third Ed., Ride et al. 1985, Article 32d (i, 2)].

Sanchiaosaurus Young, 1965a. A name proposed for a single, partial skeleton from near Kweiyang, Kweichou Province, China. The taxon is probably distinct and a member of the Nothosauriformes. Anisian.

Serpianosaurus Rieppel, 1989. Pachypleurosaur genus erected upon numerous specimens from the Grenzbitumen horizon of Monte San Giorgio, Kanton Tessin, Switzerland, and at one time informally referred to *Phygosaurus* Arthaber, 1924. Rieppel considers *Phygosaurus* to be a *nomen dubium* and unavailable for the inclusion of the Monte San Giorgio material. *Serpianosaurus* is characterized by a relatively large skull, elongate and straight dentary, and often non-thickened ribs. Pachypleurosauria. Anisian/Ladinian boundary.

Shyingyisaurus Young, 1965a. Based upon a poorly preserved skull and five anterior cervical vertebrae, *Shyingyisaurus* is from the Anisian of Kweichou Province, China. It is probably a distinct taxon and may be related to *Simosaurus.* Nothosauriformes. Anisian.

Silvestrosaurus Kuhn-Schnyder, 1990. Generic name recently proposed for the specimen described by Tschanz (1989) as *Lariosaurus buzzii.* It is a rather small nothosauriform from Monte San Giorgio with possible affinity to *No-*

thosaurus. If a distinct genus, it is not yet well characterized. Anisian/Ladinian boundary.

Simosaurus v. Meyer, 1842. An undoubtedly valid taxon from the Germanic Province and represented by numerous specimens, both crania and postcrania. Distinguished especially by a massive, brevirostrine skull with large, round, supratemporal fenestrae and short, squat teeth. Nothosauriformes. Ladinian–uppermost Carnian.

Sulmosaurus is an enigmatic name first appearing in von Huene (1956) but as an apparent corruption of *Sulmosuchus*. The latter name is itself supposedly the result of a verbal communication between O. Linck (Württemberg) and F. von Huene describing unpublished material (Kuhn 1964a); both genera are *nomina nuda*.

Sulmosuchus appears in von Huene (1952) [and in von Huene (1956) as *Sulmosaurus* (sic)] but is apparently based upon unpublished cranial material from the Keuper (Upper Triassic) of northwest Württemberg verbally described by O. Linck (Württemberg). The material has been considered primitively plesiosaurian but may represent *Nothosaurus* Münster, 1834. Without a proper description, *Sulmosuchus* is a *nomen nudum*.

APPENDIX C

SAUROPTERYGIAN CHARACTER STATES AND THEIR SIGNIFICANCE

Following previous 'nothosaur' classifications, a number of characters can be presumed to fulfill the requirement of variation having evolutionary (and taxonomic) significance. Each of these characters is discussed below along with some which are here recognized for the first time. Characters distinguishing the Sauropterygia from primitive outgroups are also examined, as well as those for each major monophyletic sauropterygian clade. Brief discussions can also be found, where relevant, of traditional characters which can now be discounted.

In general, the most useful features for phylogenetic analysis and classification are discrete characters such as the presence or absence of a particular structure. Discrete characters, where found, are perhaps less subject to reversals of evolution or to ontogenetic and individual (but not sexual) variation than the merely qualitative measure of the size and/or shape of a particular feature. Among pachypleurosaurs for example, Carroll and Gaskill (1985) and Sander (1989) report several individual variants of *Neusticosaurus* in which the size and form of the bones of the rostrum change, but in each case the same bones are present. In addition, discrete characters are more readily identified and coded for quantitative analysis. Meristic characters such as size and form can also be important, however, and often reinforce the indications of discrete characters and reflect phyletic trends. Care should nonetheless be exercised in coding meristic characters, and morphometric techniques applied whenever possible to insure that observed differences are statistically significant. These considerations are discussed below as necessary for the present analysis. Character numbers in the following discussion correspond to those of Table 2. A question mark in Table 2 indicates equivocal evidence or inapplicability of the character to a particular taxon.

1) Overall size. At first glance it might be imagined that a meristic character such as body size could not be accurately coded. However, examination of the sauropterygians and their "primitive" outgroups reveals a distinctly bimodal distribution between "small" and "large" forms. Phylogenetic analysis reveals that, with only the exception of *Lariosaurus* (and now possibly *Silvestrosaurus*), all known nothosauriforms were large animals (usually two m in length or larger). The pachypleurosaurs were, as far as is known, all considerably smaller (and like *Lariosaurus* only occasionally reaching one m in length). The plesiomorphic sister groups all contained small animals. *Lariosaurus* appears to have been secondarily reduced in length. 0—small, 1—large.

2) Length of the cervical region. A meristic character that in this case can be coded in the form of a ratio. Short necks are characteristic of the outgroups Captorhinomorpha, *Petrolacosaurus,* Younginiformes, and *Claudiosaurus,* as well as the sauropterygian placodonts. Their necks are less than half the length of their respective dorsal regions. All 'nothosaurs' and many plesiosaurs have cervical regions ranging from approximately half the length of their dorsal regions to an approximately equivalent length, while certain plesiosaurs have extremely long necks which are far longer than their bodies. Analysis suggests that the short neck of placodonts is an evolutionary reversal. 0—less than half the length of dorsal region, 1—half of, to approximately equal to, length of dorsal region, 2—far longer than length of dorsal region.

3) The presence or absence of cranial kinesis. Kinetic skulls are present in *Claudiosaurus,* the Younginiformes, and *Petrolacosaurus,* and although without

fenestration, the skulls of captorhinomorphs have movable basipterygoid articulations. The situation is unclear in the Pachypleurosauria, but the remaining sauropterygians have stoutly built, rigid crania. 0—kinetic, 1—akinetic.

4) The presence or absence of a subtemporal arch. This character is not applicable to the captorhinomorphs which exhibit no cranial fenestration. A subtemporal fenestra and arch are present in primitive diapsids, but the arch is likely to have been lost in *Claudiosaurus* and the Sauropterygia (Carroll 1981; Kuhn-Schnyder 1980). 0—present, 1—absent.

5) Size of the supratemporal fenestra. The size of the temporal openings has generally been agreed to be an important taxonomic character of 'nothosaurs.' Two general formats are observed: very large (larger than the orbits) as exemplified by *Nothosaurus,* and very small (smaller than the orbits) as in *Neusticosaurus.* The size of the openings is further correlated with postorbital skull length: short temporal region and wide skull table with small fenestrae, elongate temporal region and narrow skull table with large fenestrae. These features are relatively constant for the two skull types and seemingly represent the difference between two phyletic lines. Small fenestrae are clearly primitive for the Diapsida and are found in all relevant outgroups. Large fenestrae are present in the placodonts and plesiosaurs. 0—smaller than orbit, 1—larger than orbit.

6) The presence or absence of a temporal emargination. In *Claudiosaurus* and the Sauropterygia, where only a single temporal fenestra (the supratemporal) is present, the temporal arcade may be emarginated, most likely as a result of the loss of the lower arch (Carroll 1981; Kuhn-Schnyder 1980). Such an emargination is seen in the 'nothosaurs.' In the Placodontia and the Plesiosauria the cheek is not emarginated. The analysis suggests that this is a result of reversal. It is conceivable that the need for a strong bite for crushing or holding food items led to cranial akinesis and broad temporal arcades. 0—present, 1—absent.

7) The presence or absence of a quadratojugal. This is an important discrete variant found in the 'nothosaur' skull. Primitive diapsids, pachypleurosaurs, and placodonts seemingly retain a quadratojugal, although it appears to have been lost in the majority of nothosauriforms, i.e., most large 'nothosaurs' and the plesiosaurs. The loss of the quadratojugal can be used as a derived character uniting all sauropterygians with this trait. Reduction of both quadratojugal and jugal is probably primitive for the Sauropterygia, resulting from the presumed loss of the lower temporal arch of a truly diapsid ancestor. *Simosaurus,* however, sorts out with the plesiosaurs and 'nothosaurids' yet according to descriptions (von Huene 1921; Kuhn-Schnyder 1961, 1980) apparently retains a quadratojugal as a homoplasic character. If this is true, a redevelopment of this bone may be considered for this taxon. Conversely, *Corosaurus* may actually possess an unseen quadratojugal. If so, no reversal is required. 0—present, 1—absent.

8) The presence or absence of a quadrate notch. Primitively, a quadrate notch is absent in the reptiles and in early diapsids such as *Petrolacosaurus.* As, however, younginiforms, *Claudiosaurus,* probably all pachypleurosaurs, and placodonts have developed such a notch, its presence is primitive for the Sauropterygia and the loss of the notch in advanced nothosauriforms is apparently convergent to the condition in most plesiomorphic reptiles. 0—absent, 1—present.

9) The presence or absence of suborbital fenestrae. Suborbital fenestrae are present in *Petrolacosaurus,* younginiforms, *Claudiosaurus,* some pliosaurs, and possibly the placodonts (Rieppel 1989), but are unknown in 'nothosaurs' and plesiosaurs (senso stricto). Early descriptions (e.g., Boulenger 1896; Seeley 1882; and other authors) attributed large suborbital openings to some genera of 'nothosaurs' (e.g., *Lariosaurus* and *Neusticosaurus*) and many early classifications have

considered this to be a character of prime importance. Indeed, the family Lariosauridae has often been distinguished on this basis (e.g., Arthaber 1924; Nopcsa 1928a, b; and other authors). It is now known that these openings are merely preservational artifacts formed by the breakage of the thin palate, thus exposing the orbits from below (Carroll and Gaskill 1985; Peyer 1934; and other writers). This characteristic, therefore, has little taxonomic significance within the sauropterygian clade, although the loss of such fenestrae diagnoses it. The character seems to exhibit reversal in, e.g., *Pliosaurus* and perhaps also in the Placodontia. 0—present, 1—absent.

10) The relationship of the palatines to the pterygoids. In primitive reptiles and virtually all sauropterygians the palatines are separated in the palate by the union of the pterygoids. In placodonts, however, the palatines meet at the midline of the palate. This is apparently autapomorphous for the Placodontia. 0—palatines separated by pterygoids, 1— palatines meet at midline.

11) The presence or absence of an interpterygoid vacuity. This feature distinguishes the 'nothosaurs' from most sauropterygians. Primitive reptiles, *Claudiosaurus,* and plesiosaurs possess an interpterygoid opening, but the palate is closed in all known 'nothosaurs' and in the placodonts. Edinger (1935) was first to remove *Pistosaurus* from consideration as a 'nothosaur,' allying the genus instead with the Plesiosauria, largely on the basis of its open palate. Lacking direct evidence, *Corosaurus* is here coded as equivocal. The open palate of plesiosaurs represents an evolutionary reversal if strict parsimony analysis is applied. 0—present, 1—absent.

12) The presence or absence of the transverse flange of the pterygoid. The presence of such a flange is plesiomorphic while its loss seemingly unites *Claudiosaurus* with most sauropterygians. It may, however, have been redeveloped in the Placodontia and *Corosaurus.* 0—present, 1—absent.

13) The relationship of the premaxillae to the nasals. Primitively meeting each other at the rostral midline, the nasals of 'nothosaurs' are in many instances separated by extensions of the premaxillae to the frontals (as in, e.g., *Keichousaurus, Lariosaurus, Neusticosaurus, Simosaurus,* and other forms). This character, however, exhibits a great deal of homoplasy. For example, Kuhn-Schnyder (1963b, 1974), Carroll and Gaskill (1985), and Sander (1989) have demonstrated that individual variations occur in this relationship in *Neusticosaurus*: the nasals are sometimes separated; sometimes they meet at the midline suture. Additionally, separation of the nasals occurs in sauropterygians with small temporal openings and with large, and thus probably in two separate lineages. Reduction of the nasals may have been a general trend in the Sauropterygia and examples of convergence in the reduction (separation) of the nasals expected. The character is not applicable to most plesiosaurs which have lost their nasals. Only in the plesiomorphic plesiosaur *Pistosaurus* are nasals retained and these are also separated at the midline. 0—nasals meet at midline of rostrum, 1—nasals separated by the premaxillae.

14) The relationship of the nasals to the prefrontals. The nasals, when present, contact the prefrontals in most reptiles, including sauropterygians. Certain nothosauriform 'nothosaurs' lose this contact, however, as a derived feature. 0—nasal/prefrontal contact present, 1—nasal/prefrontal contact absent.

15) The presence or absence of a supratemporal. This bone is primitively present in the reptiles and is retained in *Claudiosaurus.* Its absence is a synapomorphy for the Sauropterygia. 0—present, 1—absent.

16) Shape of the supratemporal fenestra. Two distinct formats can be observed in the shape of this fenestra, whether "large" or "small." These can be identified

as either subcircular or elongate. Following parsimony analysis, a certain amount of homoplasy is evident in the distribution of the character. A subcircular shape is evidently plesiomorphic while lengthened openings appear derived. The latter shape dominates in the advanced nothosauriforms while *Corosaurus,* a conservative nothosauriform, is notable for its subcircular fenestrae. 0—subcircular, 1—elongate.

17) Contact of the postorbital with the temporal opening. In virtually all known Sauropterygia the postorbital forms part of the lateral border of the supratemporal fenestra. This is a primitive character that is found also in *Claudiosaurus,* the Younginiformes, etc. However, in "*Pachypleurosaurus,*" *Neusticosaurus,* and *Serpianosaurus* the postorbital is variably excluded from the margin of the temporal opening by extensions of the squamosal and postfrontal. Rarely does the bone enter the fenestra and then only just barely. These genera are closely related and such exclusion of the postorbital is a derived character which unites them. This situation is qualitatively different from the condition in most pachypleurosaurs. The very unusual *Elmosaurus* displays a similarly excluded postorbital but in this case, the squamosal is extremely large and excludes even the postfrontal and probably much of the parietal from the supratemporal fenestra. As noted above, the relationships of *Elmosaurus* are unclear, and the animal is certainly unique among known sauropterygians. In any event, it is not included in the present analysis. 0—postfrontal contacts fenestra, 1—postfrontal excluded from fenestra.

18) Shape of the postfrontal. Another meristic character, but again one that exhibits two distinct configurations. The plesiomorphic condition is one in which the postfrontal is tripartite with three recognizable processes. In the derived state, the postfrontal is subrectangular in shape, without any obvious projections. 0—tripartite, 1—subrectangular.

19) Contact of the postfrontal with the temporal opening. Primitively, the postfrontal is excluded from the supratemporal fenestra. An apparent autapomorphy for *Paranothosaurus* is the contact of this bone with the margin of the opening. 0—postfrontal excluded from fenestra, 1—postfrontal contacts fenestra.

20) The presence or absence of postparietals. Postparietals and tabulars are primitively present in reptiles, including *Claudiosaurus.* These bones are lost in all known sauropterygians and represent a derived character uniting the clade. *Simosaurus* has been described (Kuhn-Schnyder 1961, 1962) as possessing a postparietal and tabulars, but Schultze (1970) has demonstrated that this is an illusion created by the slight dorsoventral crushing of the skull in question. Kuhn-Schnyder (1966) indicated a questionable tabular in *Paranothosaurus,* but this may be part of the squamosal. No other occurrences of postparietal bones in sauropterygians have been reported. 0—present, 1—absent.

21) The presence or absence of tabulars. The discussion of character No. 20 above applies. 0—present, 1—absent.

22) The presence or absence of a lachrymal. Lachrymals, which are present in plesiomorphic outgroups, are apparently absent in sauropterygians. They have not been reported in most 'nothosaur' genera and only questionably so in others [e.g., "*Pachypleurosaurus*" (Carroll and Gaskill 1985)]. Kuhn-Schnyder (1964), however, identified a small element in the interior of the orbit of *Paranothosaurus* as a lachrymal and if this interpretation is correct, a bone in this position would be difficult to detect in most fossils. Young (1958) reported a large lachrymal for *Keichousaurus* but failed to distinguish it from the maxilla in his illustration of the skull. This now appears erroneous and lachrymals are seemingly not present in *Keichousaurus. Elmosaurus* apparently had large lachrymals (v. Huene 1957)

but is represented only by a fragmentary skull and is a possible sauropterygian of unknown relationships. 0—present, 1—absent.

23) Contact of the lachrymal with the external naris. As most sauropterygians seem not to have had lachrymals, this character only distinguishes Younginiformes and *Claudiosaurus* from *Petrolacosaurus* and the Captorhinomorpha. Only in the latter animals does the lachrymal contact the naris. 0—lachrymal contacts naris, 1—lachrymal excluded from naris.

24) Contact of the jugal with the orbit. In most of the reptiles analyzed, the jugal is relatively large and remains in contact with the margin of the orbit. Only in certain nothosauriform 'nothosaurs' is the jugal reduced and excluded from its border. *Lariosaurus* had been depicted as derived in this respect (Kuhn-Schnyder 1987) although Tschanz (1989) has suggested that it is primitive. Tschanz' (1989) figures are equivocal. Kuhn-Schnyder (1990) believes, probably correctly, that the animal examined by Tschanz (1989) was not *Lariosaurus*. 0—jugal contacts orbit, 1—jugal excluded from orbit.

25) Contact of the jugal with the quadratojugal. The meeting of these two bones is a plesiomorphic condition, whereas the loss of the quadratojugal in derived sauropterygians makes this character inapplicable for many taxa. In *Claudiosaurus* and those few 'nothosaurs' retaining a quadratojugal, this bone remains separate from the jugal. Both are seemingly reduced remnants of a lost subtemporal arch. The Placodontia are unusual among the sauropterygians in having a broad contact between these bones, but parsimony analysis suggests that this may be an autapomorphous result of reelaboration of the temporal arcade, perhaps in response to their mode of feeding. 0—jugal meets quadratojugal, 1—jugal does not meet quadratojugal.

26) Shape of the jugal. This meristic character can be readily categorized into three distinct formats. The plesiomorphic condition found in the three most primitive outgroups is that of a tripartite jugal with three equally long processes. A second format presents the maximum length of the jugal as bordering the orbit and without any posterior projection (probably reflecting the loss of this process as part of a previously existing lower temporal arch). This format is observed in *Claudiosaurus* and the Pachypleurosauria. Finally, the Nothosauriformes possess a jugal whose maximum length does not parallel the orbital margin, but rather extends posteriorly (perhaps as a reconfiguration) and nearly parallel to the tooth row. 0—jugal tripartite with no maximum length, 1—maximum length of jugal along orbital margin, 2—jugal maximum length caudad from orbit and approximately parallel to tooth row.

27) Character of the parietals. The obviously plesiomorphic condition of the parietals is for them to remain separate throughout ontogeny. This is observed in virtually all examined taxa save for the *Nothosaurus/Paranothosaurus* clade in which fused parietals are found. Tschanz (1989), however, describes an unusual form, called *Silvestrosaurus* by Kuhn-Schnyder (1990), with fused parietals. 0—parietals paired, 1—parietals fused.

28) The position of the parietal foramen. This trait is variable within the 'nothosaurs' from a central to a posterior positioning of the foramen between the parietals, although most genera exhibit the former condition. Central positioning is the plesiomorphic state. Caudad placement of the foramen seems to correlate with supratemporal fenestra elongation and could be related to cranial developmental rates within lineages. 0—parietal foramen centered on skull table, 1—parietal foramen shifted posteriad.

29) Character of the frontals. As in character No. 27 above, paired frontals

are found in most examined taxa and fused frontals in the derived *Nothosaurus/ Paranothosaurus* clade and possibly also in *Silvestrosaurus. Neusticosaurus* "*Pachypleurosaurus*" and *Serpianosaurus,* however, exhibit variable degrees of fusion (polymorphism) and the character may be of little value in such cases. 0—frontals paired, 1—frontals fused.

30) The shape of the frontals. A posterior extension of the frontals lateral to the parietals is present in 'eosuchians' and 'nothosaurs' with small supratemporal fenestrae. Apparently, only in *Corosaurus* is this extension fully developed in a large fenestra form. (See Fig. 7.) As such, this character may be primitive (plesiomorphic) for sauropterygians, and reduction of the frontal in other 'nothosaurs' and in plesiosaurs derived. However, the relatively plesiomorphic condition in captorhinomorphs is for no such process to be present. It is likely that this extension was developed in the Younginiformes and reversed in most nothosauriforms. 0—posterolateral process of frontal absent, 1—posterolateral process of frontal present.

31) Size of the prefrontal. This bone can be readily identified as being the same general size as the postfrontal in plesiomorphic outgroups, or rather distinctly smaller in the derived state observed in advanced nothosauriforms. 0—prefrontal not smaller than postfrontal, 1—prefrontal significantly smaller than postfrontal.

32) The presence or absence of palatal dentition. Palatal teeth are present in plesiomorphic reptiles and *Claudiosaurus* but absent in virtually all sauropterygians. The supposed palatal teeth of *Lariosaurus* described by Boulenger (1896) are the result of preservational distortion (palatal breakage and pyritization) (Peyer 1933). Only in placodonts do true palatal teeth appear in apparent sauropterygians. According to parsimony analysis, these teeth might have been regained in placodonts after their loss in the basal Sauropterygia. They are large and platelike, obviously related to the crushing of food items, and possibly linked to an elaboration of the palatines. As a Placodontia autapomorphy, it is perhaps unlikely that such teeth are homologous to the shagreen of the more primitive outgroups. 0—present, 1--absent.

33) The presence or absence of a rostral constriction. Certain 'nothosaurs' (e.g., *Nothosaurus*) possess a distinct constriction of the rostrum in the area of the premaxillary/maxillary suture. Present in only a few genera, this character is a derived one. It is not present in basal sauropterygians or more plesiomorphic groups. Some plesiosaurs and placodonts also possess constricted rostra and therefore some homoplasy is present in the distribution of this character. 0—absent, 1—present.

34) The presence or absence of nasals. The presence of nasal bones is a plesiomorphic condition that is found in all 'nothosaurs.' Only in plesiosaurs, with the exception of the primitive form *Pistosaurus,* is the derived loss of nasals found. 0—present, 1--absent.

35) The positioning of the external nares. Primitive reptiles exhibit terminally placed nostrils, whereas the nares of all sauropterygians are retracted. This is a typical aquatic adaptation seen also in other reptile lineages. 0—terminal, 1—retracted.

36) The presence or absence of a nasal/external naris contact. Primitively, the nasal bones of reptiles, including those of plesiomorphic Sauropterygia, contact the borders of the external nares. This relationship is apparently not present in *Ceresiosaurus* among the 'nothosaurs' and in *Pistosaurus.* The remaining plesiosaurs, having lost the nasals, cannot be evaluated for this character. 0—present, 1—absent.

37) The presence or absence of a diastema. Although some variation in the

size and positioning of the teeth is present in many advanced sauropterygians, only in the placodonts and some pliosaurs is a true diastema present. In the case of the placodonts this is most likely related to their presumably unique feeding style. 0—absent, 1—present.

38) The orientation of the dentition. Plesiomorphically, all teeth of the outgroups are positioned more or less vertically. All sauropterygians, however, exhibit a predominantly procumbent orientation of the anterior teeth. 0—vertical, 1—procumbent.

39) The nature of the dentition. The teeth of 'nothosaurs' are of two general types: isodont versus anisodont. This distinction has sometimes been used as a classificatory character, and indeed, anisodont dentition predominates amongst the nothosauriforms. Isodont dentition is found in the pachypleurosaurs, *Claudiosaurus,* and Younginiformes and is presumed relatively plesiomorphic for sauropterygians. Including captorhinomorphs and *Petrolacosaurus,* anisodont teeth are primitive, but an evolutionary reversal has probably taken place within the sauropterygian clade. 0—anisodont, 1—isodont.

40) Tooth shape. Four separate tooth-shape formats have been observed in sauropterygians. The plesiomorphic condition is that of smoothly conical, recurved teeth. The teeth of *Simosaurus,* however, were short and spatulate and the difference may be related to differing dietary and functional needs. This is certainly the case in placodonts where the teeth are polymorphic: short and squat incisorlike teeth, and platelike palatal "molars." 0—conical, 1—pointed and spatulate, 2—blunt and spatulate, 3—platelike.

41) The presence or absence or maxillary caniniforms. These teeth are present in the Captorhinomorpha and *Petrolacosaurus* and again in advanced 'nothosaurids.' Analysis using parsimony suggests that this is an evolutionary reversal. 0—present, 1—absent.

42) The presence or absence of premaxillary caniniforms. No pachypleurosaurs have enlarged premaxillary teeth and this is apparently the plesiomorphic condition. Such teeth are known in only three genera of 'nothosaurids.' 0—absent, 1—present.

43) The relative strength of the mandibular symphysis. A character perhaps related to function, mandible strength could be correlated with prey selection, as it is in crocodilians. However, genera with large supratemporal fenestrae consistently exhibit relatively long, stout symphyses. Other taxa possessed lightly braced dentaries. Such congruence between characters argues for an evolutionary (and taxonomic) significance for both. 0—weak, 1—robust.

44) The presence or absence of a retroarticular process. Primitive reptiles lack a retroarticular process. It is seemingly present in all sauropterygians (but in other groups as well). 0—absent, 1—present.

45) The presence or absence of trunk intercentra. Intercentra are primitive and found in the plesiomorphic groups of the present analysis. Some pachypleurosaurs are known to retain intercentra in the anterior cervical vertebrae, but all sauropterygians apparently lack them in the dorsal region. (The evidence is lacking for *Cymatosaurus.*) 0—present, 1—absent.

46) The form of the vertebral centrum. All sauropterygian vertebral centra are rather conservative in form. They are constricted cylinders that are plesiomorphically amphicoelous. Advanced 'nothosaurids' and plesiosaurs exhibit derived platycoelous centra. 0—amphicoelous, 1—platycoelous.

47) The presence or absence of foramina subcentralia. Ventral vertebral nutritive foramina are a uniquely derived feature of plesiosaurs and are not present in any 'nothosaurs' in the traditional sense. 0—absent, 1—present.

48) The form of the zygapophyses. Broad zygapophyses that are wider than the vertebral centrum are characteristic of all analyzed taxa other than the plesiosaurs minus *Pistosaurus*. 0—wider than centrum, 1—narrower than centrum.

49) The presence or absence of zygosphene/zygantrum articulations. These are absent in captorhinomorphs and *Petrolacosaurus* but developed in younginiforms, *Claudiosaurus,* and probably most sauropterygians. Plesiosaurs apparently lose such accessory articulations secondarily, whereas the nature of accessory articulations in the placodonts is distinctly different. (See character No. 50 below.) 0—absent, 1—present.

50) The presence or absence of hyposphene/hypantrum articulations. The presence of this character (Rieppel 1989) is an autapomorphy for the Placodontia relative to all other analyzed taxa. It may have been developed in this clade following its divergence from the 'nothosaurids' + plesiosaurs. 0—absent, 1—present.

51) The number of sacral vertebrae. This particular vertebral count is a discrete character which has sometimes been used for systematic purposes (e.g., Nopcsa 1928b; Peyer 1934; and other authors). The primitive reptilian sacral number is generally considered to be two (Romer 1956) and this condition is found in captorhinomorphs, primitive diapsids, and *Claudiosaurus*. The primitive 'nothosaurian' number appears to have been three as in *Corosaurus* and most pachypleurosaurs. Some other 'nothosaurs,' certainly, had increased this number to at least four (e.g., *Ceresiosaurus*), five (e.g., *Lariosaurus, Paranothosaurus,* and *Simosaurus*), and perhaps even six (*Proneusticosaurus*) (v. Huene 1952, 1959a; Peyer 1931; Sanz 1976; Schmidt 1986; Volz 1902; and other authors). *Ceresiosaurus, Nothosaurus,* and *Serpianosaurus* apparently exhibit polymorphism, whereas *Keichousaurus* seems to have reverted to only two sacrals. Known plesiosaurs and placodonts all possess three sacrals. Homoplasy is prevalent in the distribution of this character and a great deal of convergence seems evident. 0—two, 1—three, 2—four, 3—more than four.

52) The presence or absence of sacral rib distal expansions. Sacral ribs primitively have expanded distal ends for broad contact with the blade of the ilium, as in the Younginiformes, Captorhinomorpha, and comparable reptiles. In virtually all 'nothosaurs' with large temporal openings this morphology was retained, as it was in the Plesiosauria. Small fenestra forms (pachypleurosaurs), on the other hand, lost this expansion, making the sacral rib merely a strut of uniform thickness, or even one with its distal end narrower than its proximal. There appears to be a relatively consistent correlation between this latter condition, small size, and thickened ribs, perhaps due to the occupation of a particular environmental or structural niche by these small animals. The relatively small 'nothosaurid' *Lariosaurus* is similar to pachypleurosaurs in each of these ways. However, among large 'nothosaurs,' *Ceresiosaurus* and *Proneusticosaurus* also have thickened ribs and distally unexpanded sacral costae. A certain amount of homoplasy is therefore indicated for this character. 0—present, 1—absent.

53) The presence or absence of thickened ("pachyostotic") ribs. While plesiomorphic reptiles do not, some 'nothosaurs' exhibit pronounced "pachyostotic" thickening of their ribs, which has at times been used as a systematic character uniting them. Zangerl (1935) has shown that three grades of characteristic histologic differentiation occur within the variously thickened bones, particularly the ribs, of the Alpine pachypleurosaurs. These grades, identified as prepachyostosis, pachyostosis, and postpachyostosis, form a series paralleling younger stratigraphic occurrence, respectively (Zangerl 1935), and now seemingly reflect a phylogenetic trend. Most pachypleurosaurs have thickened ribs, but this may sometimes be

variably developed even for a particular genus (e.g., *Dactylosaurus*). Rieppel (1989) and Sander (1989) have further suggested the possibility of ontogenetic variation for this character. However, most nothosauriforms possess relatively slender, while nevertheless dense, ribs. The degree of 'nothosaur' rib expansion and/or "pachyostosis" may be related to overall adult size and functional needs in the aquatic environment, but also appears relatively consistent within lineages. 0—absent, 1—present.

54) The number of elements comprising each gastral segment. Although this character was rejected as useful by Peyer (1934), all utilized taxa have five elements per segment (the plesiomorphic condition) except for *Neusticosaurus* and "*Pachypleurosaurus,*" which Carroll and Gaskill (1985) and Sander (1989) describe as having only three. 0—five, 1—three.

55) The presence or absence of dermal armor. Among the taxa analyzed, only certain placodonts possess such armor as an obviously derived character (synapomorphy?). 0—absent, 1—present.

56) The nature or absence of a sternum. Character polarity is here equivocal as the Captorhinomorpha and *Petrolacosaurus* cannot be coded. The Younginiformes, however, possess an ossified sternum; Carroll (1981) indicates an unossified sternum for *Claudiosaurus,* while all sauropterygians lack this element. Progressive loss of the sternum is suggested. 0—ossified, 1—unossified, 2—absent.

57) The presence or absence of a cleithrum. This bone is primitively present but lost in all sauropterygians, *Claudiosaurus* and some younginiforms. 0—present, 1—absent.

58) The presence or absence of a posterior process of the interclavicle. The presence of such a process is a plesiomorphic state for the reptiles examined, whereas it is lost in some advanced sauropterygians. 0—present, 1—absent.

59) The length of the interclavicular posterior process. Although a meristic character, a bimodal distribution between long and short processes (where present) is apparent, and its reduction is presumably derived. 0—elongate, 1—short.

60) The presence or absence of a clavicular "corner." 'Nothosaurs' and placodonts usually have a sharply pronounced anterolateral corner to each clavicle. (See, e.g., Figs. 36 and 37.) Plesiomorphic reptiles are characterized by clavicles whose anterolateral margins are smoothly rounded. The reduced clavicles of plesiosaurs also lack "corners." 0—absent, 1—present.

61) The nature of the scapulocoracoid. Plesiomorphic reptiles possess an undivided scapulocoracoid. A separate scapula and coracoid are present in the Sauropterygia. 0—undivided, 1—divided.

62) The position of the scapula. A notable synapomorphy of the Sauropterygia is the superficial placement of the scapula relative to the clavicle. Other reptiles have the scapula lying medial to the clavicle. Rieppel (1989) has discussed the controversy regarding the condition in the Placodontia and the apomorphic condition is here accepted for them. 0—medial to the clavicle, 1—superficial to the clavicle.

63) The presence or absence of a posterior extension of the coracoid. A stout median coracoid symphysis is present in all sauropterygians except placodonts, but only in the Plesiosauria is an elongate posterior extension beyond the thickest point of this symphysis (the transverse pectoral bar) present. Plesiomorphic reptiles have neither pectoral fenestration nor separate coracoids and the character is here not applicable. 0—absent, 1—present.

64) The presence or absence of a supracoracoid foramen or notch. Primitively present, a supracoracoid foramen is absent in *Corosaurus,* certain pachypleurosaurs, and the Plesiosauria. These absences are convergent. 0—present, 1—absent.

65) The presence or absence of pectoral fenestration. Sauropterygians are distinguished from their outgroups by central fenestration of their pectoral girdle. The placodont condition is apparently homologous, although the reduced coracoids no longer meet at the body midline. 0—absent, 1—present.

66) The presence or absence of a longitudinal pectoral bar. Not applicable to the nonfenestrated pectra of the plesiomorphic taxa, no bar is present in most sauropterygians, but is found in some advanced plesiosaurs. 0—absent, 1—present.

67) The nature or absence of a posterior ramus of the iliac blade. A large iliac blade ramus is primitively present, whereas most 'nothosaurs' exhibit a statistically significant reduction in this ramus. *Corosaurus* and *Simosaurus* are conservative in this regard. The plesiosaurs have no posterior blade ramus; this is presumably lost as the most derived state. 0—prominent, 1—small, 2—absent.

68) The presence or absence of an ilio-pubic contact. The lack of a contact between the ilium and pubis is a well known synapomorphy of advanced plesiosaurs. *Pistosaurus* is plesiomorphic in maintaining such a contact, as do all other analyzed taxa. 0—present, 1—absent.

69) The nature of the anterior border of the pubis. This border is concave in most test taxa. Only in *Corosaurus* and most plesiosaurs is the bone known to be expanded and the anterior border convex. This is seemingly a convergence. The pubis is expanded in placodonts, but the border remains concave. 0—concave, 1—convex.

70) The presence or absence of an obturator foramen. An obturator foramen or notch is plesiomorphic and apparently present in all examined taxa save the Plesiosauria (the state in *Pistosaurus* is unknown). Its loss is another plesiosaur synapomorphy. 0—present, 1—absent.

71) The presence or absence of thyroid fenestration. The distribution of this character mirrors that of character No. 65 above. All sauropterygians exhibit fenestrated pelves, although the fenestration appears very much reduced in placodonts. 0—absent, 1—present.

72) The nature of the forelimb. This is a feature that is apparently autapomorphic for *Ceresiosaurus*. Most test taxa have fore- and hindlimbs that are approximately equivalent in build (excepting length). In *Ceresiosaurus* the forelimb, and most notably the humerus, is far stouter and more robust than the hind (femur). 0—forelimb not significantly more robust than hindlimb, 1—forelimb far stouter than hindlimb.

73) The shape of the humerus. The curvature of the humerus has often been regarded as a significant character for 'nothosaurs': there is a correlation between temporal-opening size and humerus form. 'Nothosaurs' with small supratemporal fenestrae (pachypleurosaurs) all display rather straight humeri with relatively slender shafts and significant distal expansions. Other 'nothosaurs' possess robust, strongly curved, probably derived humeri. This is true also for the Placodontia. Advanced plesiosaurs have straight but very robust propodials that could conceivably be derived from the 'nothosaurid' format. 0—straight and slender, 1—strongly curved and robust, 2—straight and robust.

74) The nature of the humeral epicondyles. Although a meristic character, a significant reduction in the size of the epicondyles can be recognized in *Claudiosaurus* and the Sauropterygia. Plesiomorphic forms have large condyles. 0—prominent, 1—reduced or absent.

75) The nature or absence of an ectepicondylar foramen. Captorhinomorphs and *Petrolacosaurus* lack this foramen as the presumably plesiomorphic state, whereas it is developed in Younginiformes. *Claudiosaurus* and the sauropterygians

minus the Plesiosauria possess an ectepicondylar notch that is presumably transformed from the younginiform foramen. The lack of any foramen in plesiosaurs is an obvious reversal. 0—absent, 1—present, 2—transformed to notch.

76) The presence or absence of an entepicondylar foramen. Plesiomorphically present, the entepicondylar foramen is absent in plesiosaurs and convergently absent in some placodonts. 0—present, 1—absent.

77) The presence or absence of a spatium interosseum. This character is another synapomorphy for the Plesiosauria as they alone have lost the interosseal space of the epipodia. (*Pistosaurus* as a plesiomorphic plesiosaur retains it.) 0—present, 1—absent.

78) The radius-to-ulna-length ratio. Epipodial shapes and relative lengths, although possibly varying ontogenetically, may have some significance. One consistency is that in all pachypleurosaurs in which the forearm is known, as in some Younginiformes, the radius is significantly longer than the ulna; they are approximately equal in length in the nothosauriforms. The pachypleurosaur state is seemingly a synapomorphy uniting the clade. Plesiomorphic reptiles that retain a large olecranon process have a significantly longer ulna than radius. 0—ulna significantly longer than radius, 1—radius significantly longer than ulna, 2—ulna and radius approximately equal in length.

79) The presence or absence of a midlimb joint. Because of the extreme shortening and flattening of their epipodials, plesiosaurs (minus *Pistosaurus*) lost their ability to flex their limbs at the propodial/epipodial joints. Articulated 'nothosaur' skeletons indicate some slight ability for plesiomorphic flexion. 0—present, 1—absent.

80) The nature or absence of hyperphalangy. Plesiomorphic taxa possess the primitive reptile phalangeal formula; this characteristic is apparently retained in some pachypleurosaurs. Other pachypleurosaurs and some 'nothosaurids' increase this number very slightly. Plesiosaurs increase the number of phalanges by an order of magnitude, and can be coded separately. Phalangeal formula is, however, difficult to determine in a number of taxa. 0—absent, 1—slight, 2—extreme.

81) Nature of the carpus and tarsus. Although variable with ontogeny, the carpus and tarsus are well ossified in adult plesiomorphic reptiles. Most sauropterygians exhibit a pronounced reduction in the degree of ossification although plesiosaurs, with their highly modified limbs, display a reelaboration of the carpal and tarsal elements in the adult condition. 0—well ossified, 1—poorly ossified.

82) The hindlimb to forelimb ratio. In most analyzed taxa, the hindlimb is relatively longer than the forelimb, but the reverse is sometimes true and polymorphism is occasionally present. The relative lengths of the limbs appear to have varied ontogenetically (see Carroll and Gaskill 1985; Rieppel 1989; Zangerl 1935, 1963), but this is not well quantified. The presumed adult condition is used in the analysis and a significant amount of homoplasy is evident. 0—hindlimb longer than fore, 1—forelimb longer than hind.

83) The breadth of the ulna. Generally, the ulna is approximately as broad as is the radius. However, as a derived state, the ulna is nearly twice as broad as the radius in *Keichousaurus, Ceresiosaurus,* and *Lariosaurus.* These seem to be convergences. Although the radius and ulna are approximately equivalent in breadth in advanced plesiosaurs, both elements are far broader relatively than plesiomorphic epipodials and the ulna is here coded as derived. 0—narrow, 1—broad.

84) The presence or absence of a pisiform. Primitively, a pisiform is present in the carpus of the test taxa. Most sauropterygians lost this element although it was apparently variably regained in some forms. 0—present, 1—absent.