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THE NOTHOSAUR *PACHYPLEUROSAURUS* AND THE ORIGIN OF PLESIOSAURS

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CONTENTS

Description of *Pachypleurosaurus edwardsi*, from the middle Triassic of Italy and Switzerland, provides a basis for establishing the pattern of aquatic locomotion within the Nothosauria and for determining their relations with more primitive terrestrial reptiles and fully aquatic plesiosaurs.

Judging by the proportions of the trunk, limbs and tail, nothosaurs, like modern crocodiles and marine iguanids, relied mainly on lateral undulation of the trunk and tail for aquatic propulsion. The rear limbs probably acted mainly as rudders. Differences in the structure of the pectoral girdles and forelimbs among nothosaurs and the elaboration of the coracoids suggest that the forelimbs were becoming important in propulsion, with emphasis on the back stroke. *Pachypleurosaurus* has the greatest degree of development of the anterior portion of the shoulder girdle, suggesting that the recovery stroke was of considerable importance. In this feature *Pachypleurosaurus* approaches the pattern seen in plesiosaurs.

It is concluded that the transition between primitive terrestrial diapsids and plesiosaurs occurred via a succession of changes in patterns of aquatic locomotion. Early sauropterygians would have used almost exclusively the axial skeleton and its musculature in swimming. As in the majority of secondarily aquatic reptiles, stereotyped behaviour patterns of terrestrial locomotion would have rendered use of the forelimbs disadvantageous in the water, and they were progressively reduced to limit drag. The hind limbs were also reduced and initially functioned to control changes in depth and direction.

The relations of the dermal and endochondral elements of the shoulder girdle in nothosaurs and plesiosaurs differ from those of the majority of early reptiles in having the scapulae superficial to the clavicles and the interclavicle superficial to the clavicles. This may be attributed to a redevelopment of the endochondral and dermal elements subsequent to a period of reduction associated with an early stage in aquatic adaptation.

Nothosaurs and plesiosaurs are unique among secondarily aquatic diapsids in the emphasis on the forelimbs for propulsion. In plesiosaurs, both the fore and hind limbs are greatly enlarged and the significance of the tail for propulsion is much reduced. Both limbs may have served in a mode of swimming similar to that practised by the modern sea lions.

Although individual vertebrae and bones of the limbs and girdles appear to show a transition from nothosaurs through primitive to advanced plesiosaurs, major differences in the proportions of the trunk, girdles and limbs clearly distinguish nothosaurs and plesiosaurs. This may be attributed to a marked reduction in the amount of lateral undulation of the trunk region and elaboration of the rear limbs as paddles in the immediate ancestors of plesiosaurs.

Introduction

During the Mesozoic, while the dinosaurs dominated the land, the seas were occupied by a host of reptiles that had secondarily returned to the water. Among the most diverse and widespread of Mesozoic marine reptiles were the plesiosaurs. They had large paddle-shaped limbs, short tails and long necks. Their general appearance would have matched the popular concept of the sea serpent. Most were large, with some genera reaching a length of more than 15 m (Saint-Seine 1955; Romer 1956; Brown 1982). In *Kronosaurus*, the skull alone exceeded 3 m in length (Romer & Lewis 1959).

Plesiosaurs became dominant in the early Jurassic and continued to the end of the Mesozoic. It has long been assumed that their closest relatives and putative ancestors were a group of less highly specialized aquatic reptiles from the middle Triassic, the nothosaurs. The nothosaurs are generally smaller than plesiosaurs and the structure of their limbs shows clearly their descent from terrestrial ancestors.

Nothosaurs and plesiosaurs share a number of derived characters which differentiate them from more primitive diapsid reptiles, and support the assumption that they shared a unique common ancestry. In contrast to most secondarily aquatic reptiles, the limbs are large, suggesting that they played a major role in locomotion. The lower temporal bar is lost, but the quadrate remains rigid. In contrast to the vast majority of tetrapods, the scapulae lie superficial to the clavicles.

Among more primitive diapsid reptiles, *Claudiosaurus* shares with the nothosaurs the loss of the lower temporal bar, partial closure of the palate and elongation of the neck, and shows reduced ossification of the limbs and changes in their proportions that are suggestive of an incipient stage in the evolution of aquatic locomotion. In other features of the skeleton, *Claudiosaurus* closely resembles primitive terrestrial diapsids including *Youngina* and *Thadeosaurus* (Carroll 1981).

Claudiosaurus and nothosaurs appear to represent intermediate stages in the transition from terrestrial ancestors to the fully aquatic plesiosaurs. This transition has the potential for serving as an important example of the patterns of evolution associated with major changes in habitat and skeletal anatomy. Much yet remains to be known to elucidate this sequence, however. The transition is by no means continuous; *Claudiosaurus* is far more primitive than any nothosaurs and might have given rise to the plesiosaurs directly.

Although their general body shape and pattern of aquatic adaptation suggest that nothosaurs may have given rise to plesiosaurs, some specific features of their anatomy indicate that the known genera are too specialized for this role. In most nothosaurs the pterygoids meet ventrally at the midline beneath the base of the braincase, completely occluding the interpterygoid vacuities. These openings are small but still evident in plesiosaurs. Nothosaurs also exhibit a highly specialized pattern of the shoulder girdle which appears very distinct from that of plesiosaurs; this may imply that the two groups had divergent locomotor patterns. These differences suggest that nothosaurs and plesiosaurs may share a common ancestry rather than exhibiting an ancestor–descendant relationship.

No genera have been described as showing a transition in the structure of the postcranial skeleton between the pattern typical of nothosaurs and that characteristic of plesiosaurs. The genus *Pistosaurus* from the Middle Triassic appears to show a combination of an essentially nothosaurian postcranial skeleton together with a skull pattern which is close to that of Jurassic plesiosaurs. Unfortunately, it is not certain that the skull and postcranial skeleton are correctly associated (Edinger 1935; von Huene 1948).

Even if the known nothosaurs are not specifically ancestral to plesiosaurs, knowledge of their anatomy may yet provide information regarding the possible evolutionary pathway toward the pattern of swimming employed by the plesiosaurs. This paper will concentrate on the anatomy of a single nothosaur genus as a basis for comparison with plesiosaurs and for evaluating the different patterns of swimming that characterize these two groups.

Classification of nothosaurs

Nothosaurs may be divided into two large groups, the pachypleurosaurids and the nothosaurids. The nothosaurids are of larger size, typically exceeding 2 m in length, with a proportionally larger skull in which the upper temporal openings are substantially larger than the orbits. The pachypleurosaurids are all of smaller size, with the largest specimens little more than 1 m in length. The skulls are relatively smaller, with the upper temporal opening much smaller than the orbit. Further justification for the recognition of these groups is provided in a recent review by Sanz (1984).

Among the well-known genera, *Nothosaurus*, *Paranothosaurus*, *Lariosaurus*, *Ceresiosaurus*, *Corosaurus* and *Simosaurus* may be assigned to the Nothosauridae. The pachypleurosaurids include *Pachypleurosaurus*, *Dactylosaurus*, *Anarosaurus* and *Neusticosaurus* and perhaps the less completely known genera *Phygosaurus*, *Psilotrachelosaurus* and *Elmosaurus*. The skull and general body form of the Chinese genus *Keichousaurus* also accord with the pachypleurosaurid pattern.

Although nothosaurs are known from hundreds of specimens (mostly from the Middle Triassic of Europe) assigned to about 20 genera, few species are known from well-preserved specimens including both the skull and postcranial material, and none have been completely described and restored so as to provide a solid basis for establishing their taxonomic position or pattern of locomotion.

The largest and most diverse collection of nothosaurs is in the Institute for Palaeontology at the University of Zürich. This collection, almost exclusively from the region of Monte San Giorgio in the southern Alps, includes at least four genera. The most common nothosaur, represented by hundreds of specimens, is attributed to the genus *Pachypleurosaurus*. Included in this material are several larger skeletons that have been referred to informally as 'Grosser Pachypleurosaurus'. Examination of these specimens reveals several important differences from the bulk of the *Pachypleurosaurus* material. These larger animals have not previously been described and provide a very good basis for establishing anatomical comparisons with plesiosaurs (figures 1–6, 12–20).

The general resemblance of these larger specimens to those attributed to *Pachypleurosaurus* by Peyer (1932, 1933) and Zangerl (1935) is sufficiently close that it was necessary to make comparisons with the type of *Pachypleurosaurus* (*Pachypleura*) *edwardsi* (Cornalia 1854) to establish which more closely approaches the pattern of the originally described material. The type of this species (figure 1), described from the Italian Alps, proved to resemble much more closely the animals termed 'Grosser Pachypleurosaurus', rather than the very numerous smaller specimens long attributed to *Pachypleurosaurus*.

The most striking feature is the structure of the manus and pes. The specimens of 'Grosser Pachypleurosaurus' show a phalangeal count of 1, 2, 3, 4, 2 in the manus, and 1, 2, 3, 4, 3 in the pes. Other specimens attributed to *Pachypleurosaurus* always have two phalanges in the first digit and three phalanges in the second, and approach a typically reptilian count in the lateral digits (figure 5). In both forms, the number of phalanges of digits 3, 4 and 5 is somewhat variable, but the number in digits 1 and 2 is constant. Although neither the manus nor the pes is completely articulated in the type specimen, the first digit of both definitely has only a single phalanx and the second only two.

Numerous other differences, which are consistent in all specimens examined, are listed in table 1. These clearly demonstrate that there are two distinct taxa of pachypleurosaurid nothosaurs in the fauna of the southern Alps. Only a relatively small number of specimens, belonging to a species which reaches a body size of over 1 m, can be included in *Pachypleurosaurus edwardsi*.

The type specimen of *Pachypleurosaurus edwardsi* comes from near Besano in northern Italy, approximately 5 km from the locality of Alla Cascina at Monte San Giorgio from which have come most of the specimens of 'Grosser Pachypleurosaurus'. The fossil-bearing beds can be traced without break between the two localities. The exact equivalence of the horizons has not been established, however, and their lithology is different. Both are considered lower Ladinian in age (Kuhn-Schnyder 1974).

Detailed comparison of the larger specimens from Alla Cascina (figures 2, 3 and 4) with the type is complicated by its relative immaturity. It is approximately 30 cm in length to the tip of the tail. The ends of the bones are ill-defined and most have the surface marked by many fine pits and grooves that are the hallmark of immature tetrapods. The head is relatively much larger than in more mature specimens. Fortunately, comparison can be extended to other, small specimens from Alla Cascina from which have come a great range of sizes (table 2) including individuals only slightly larger than the type. There is also one specimen from the Besano locality which is considerably larger than the type. Specimen number 2466 in the Zürich collection (figure 6) consists of the sacral and proximal caudal region and much of the rear limbs of a skeleton which is as large as the larger specimens from Alla Cascina; it agrees with them in most anatomical and proportional features.

FIGURE 1. Pachypleurosaurids (*a*) Type of *Pachypleurosaurus edwardsi* (Cornalia) Museo Civico di Storia Naturale, Milano (natural size). Primarily dorsal view; because of the great length of the neural spines the proximal caudal vertebrae are displayed in lateral view. (*b*) Dorsal view of *Neusticosaurus* sp., specimen 3604 in the collection of the Institute of Palaeontology, Zürich. Neural spines are short throughout the column (natural size). (*c*) Ventral view of *Neusticosaurus* sp., specimen 1057, Museum of Comparative Zoology, Harvard (natural size).

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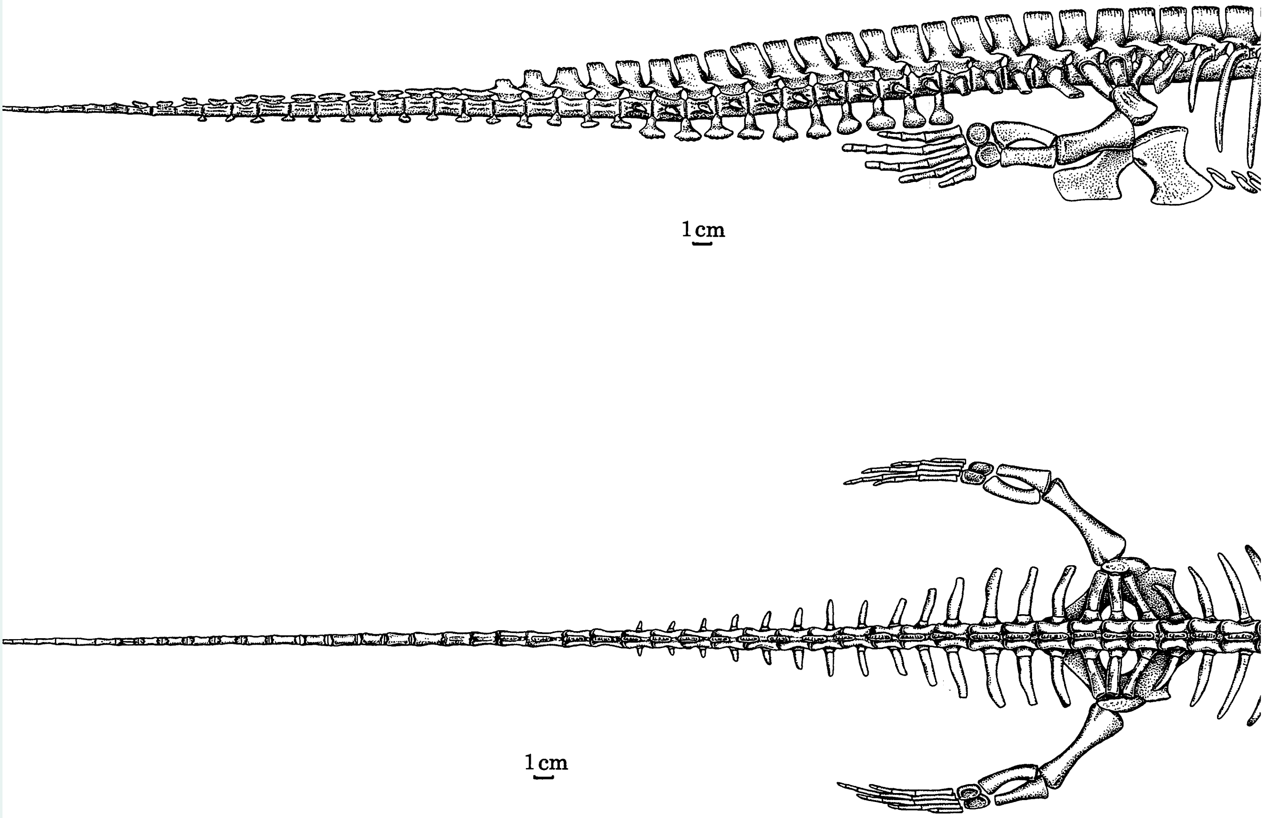
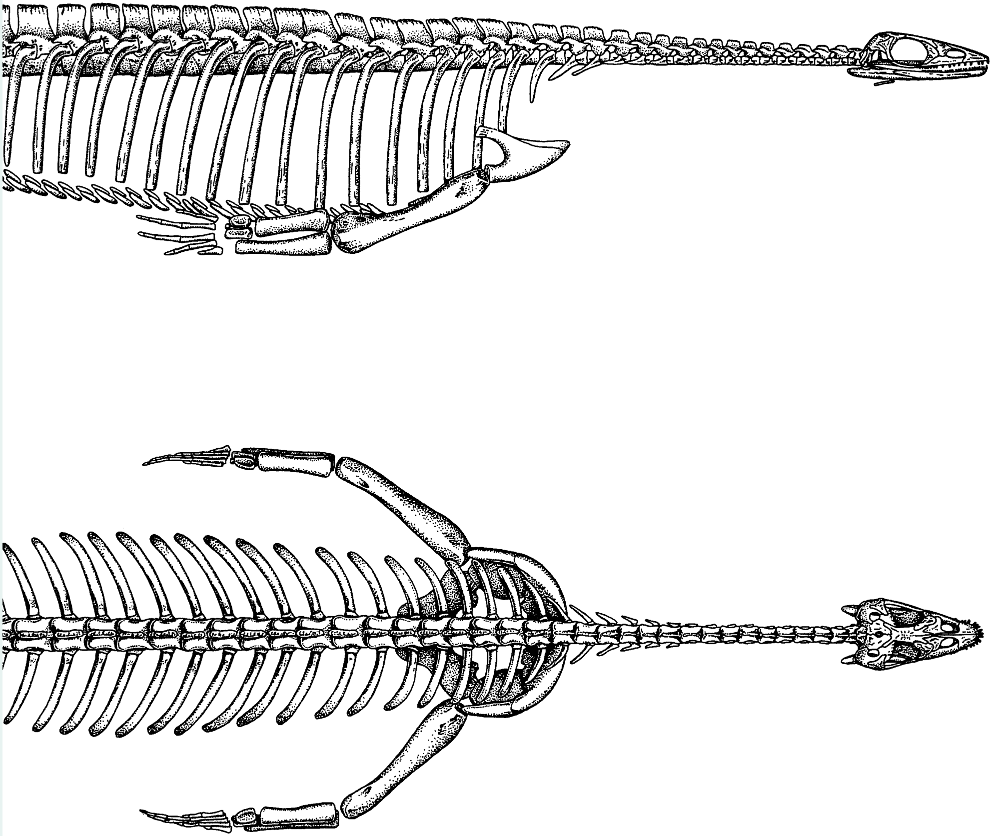
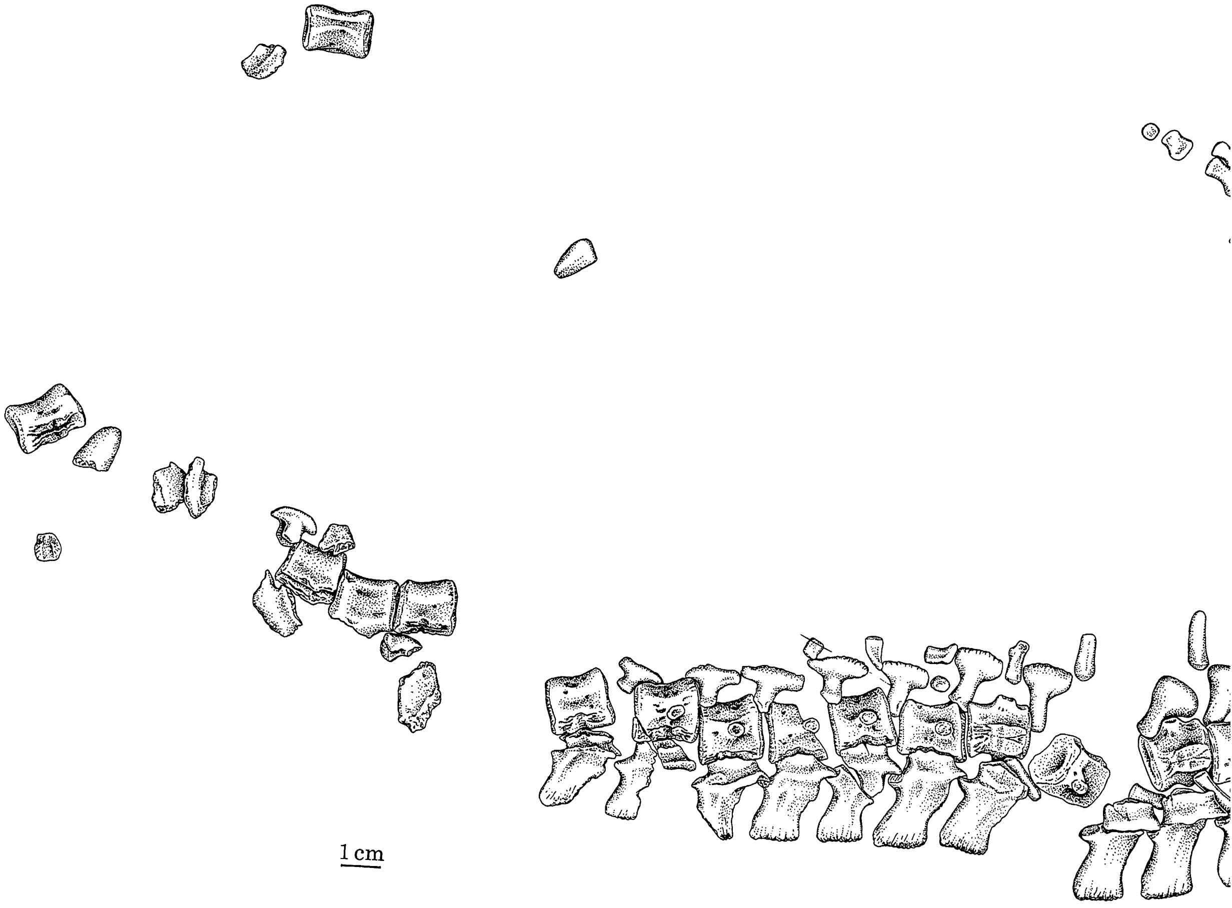


FIGURE 4. *Pachypleurosaurus edwardsi*. Restorations of skeleton in latera



ral and dorsal views, based on adult proportions.



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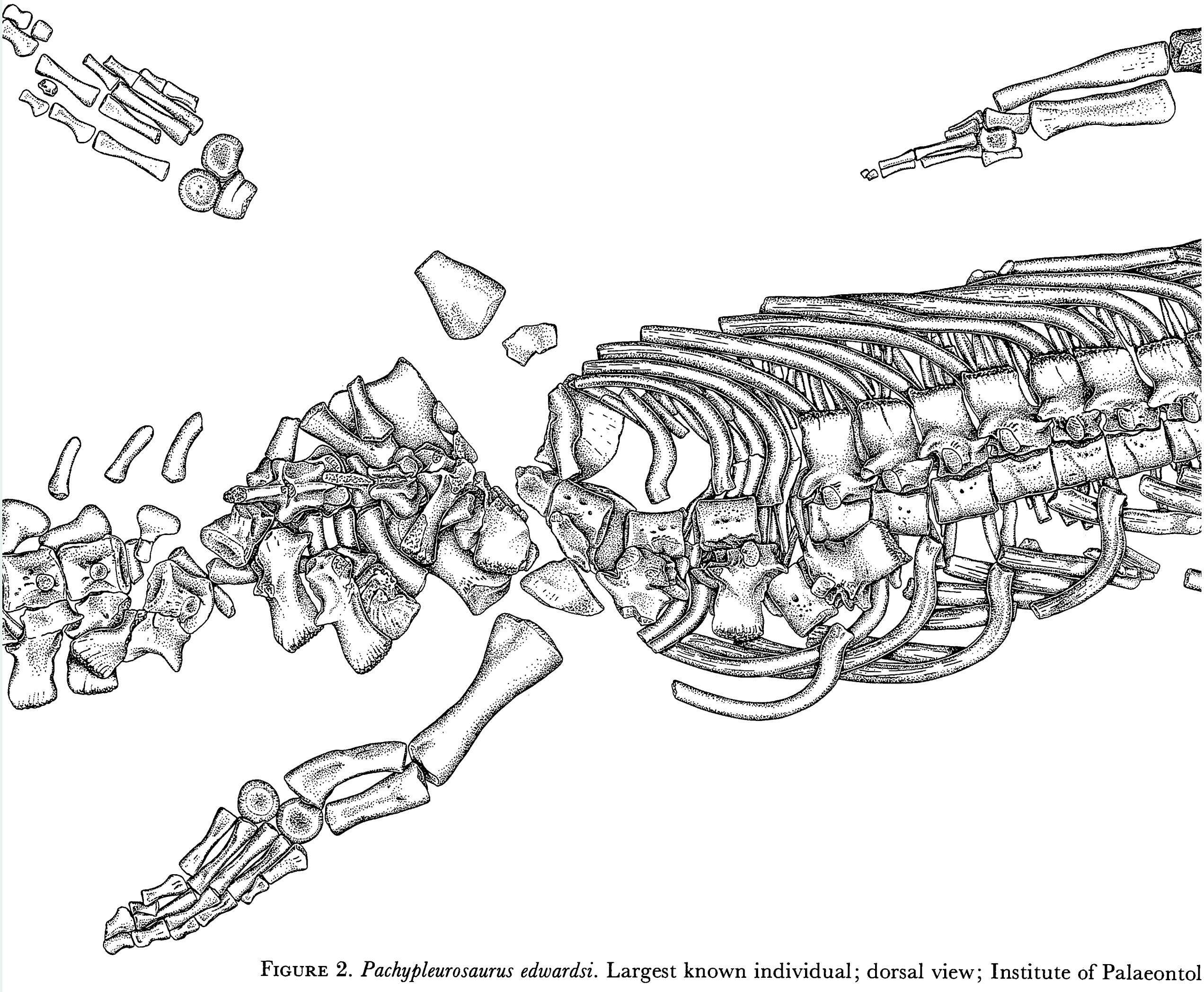
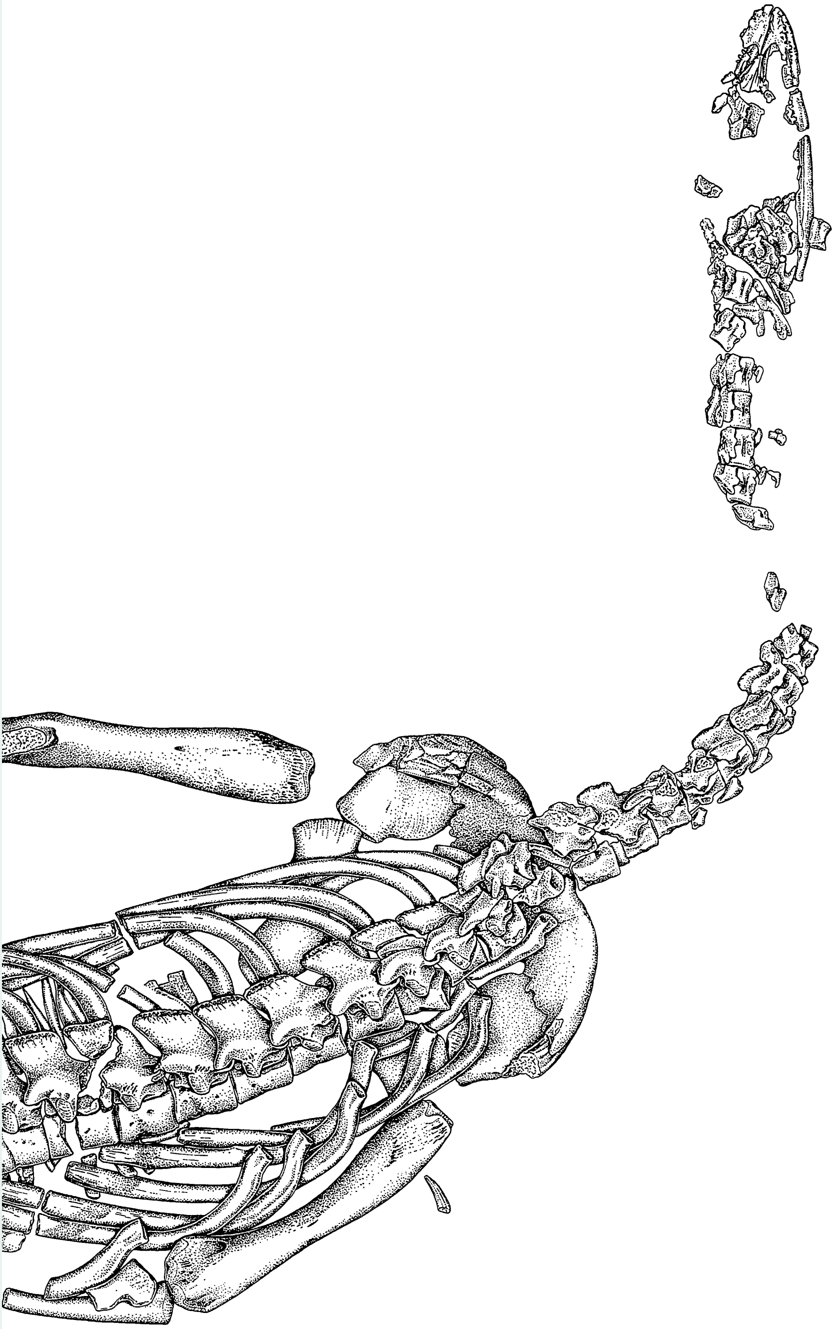


FIGURE 2. *Pachypleurosaurus edwardsi*. Largest known individual; dorsal view; Institute of Palaeontol



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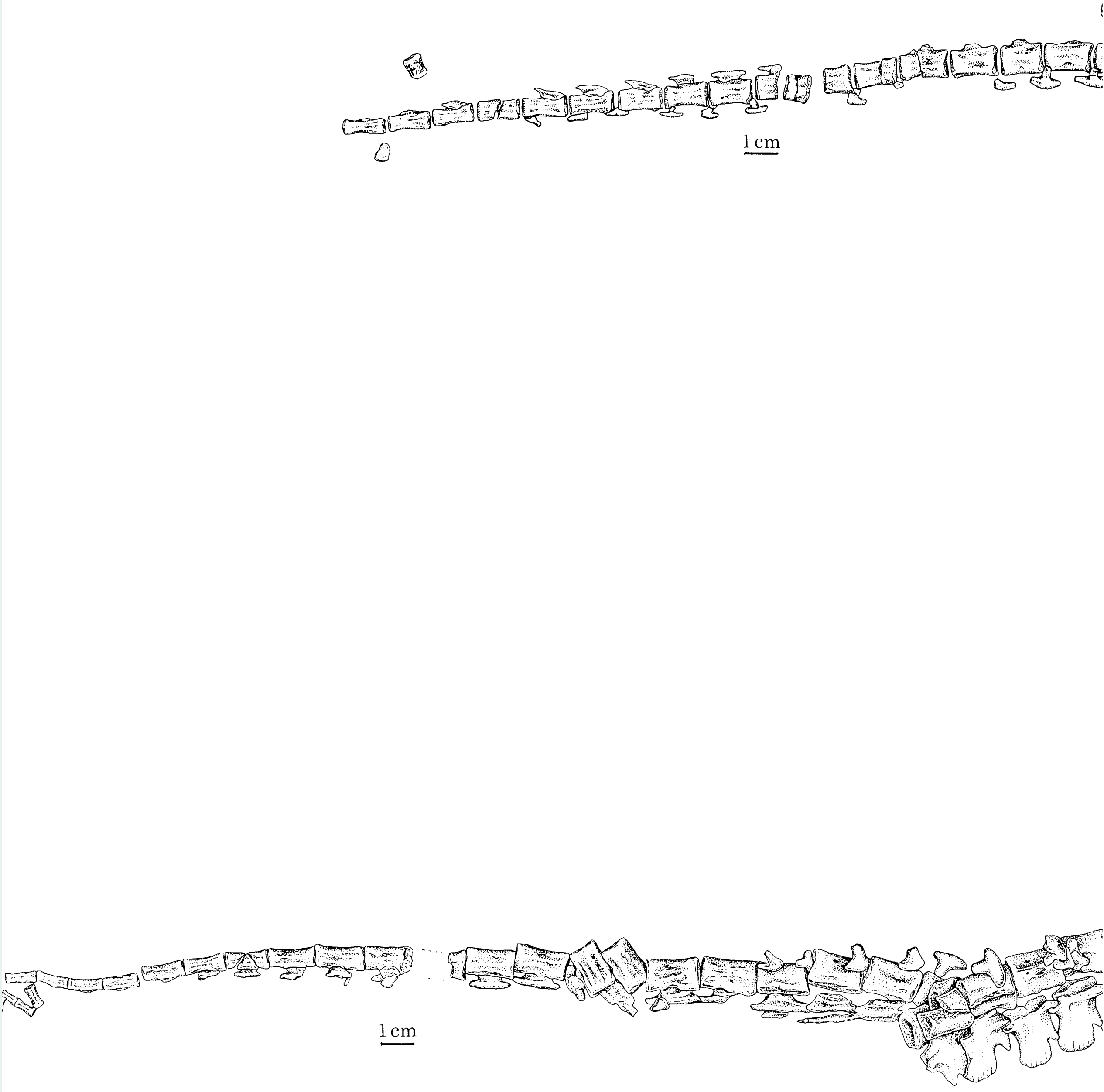
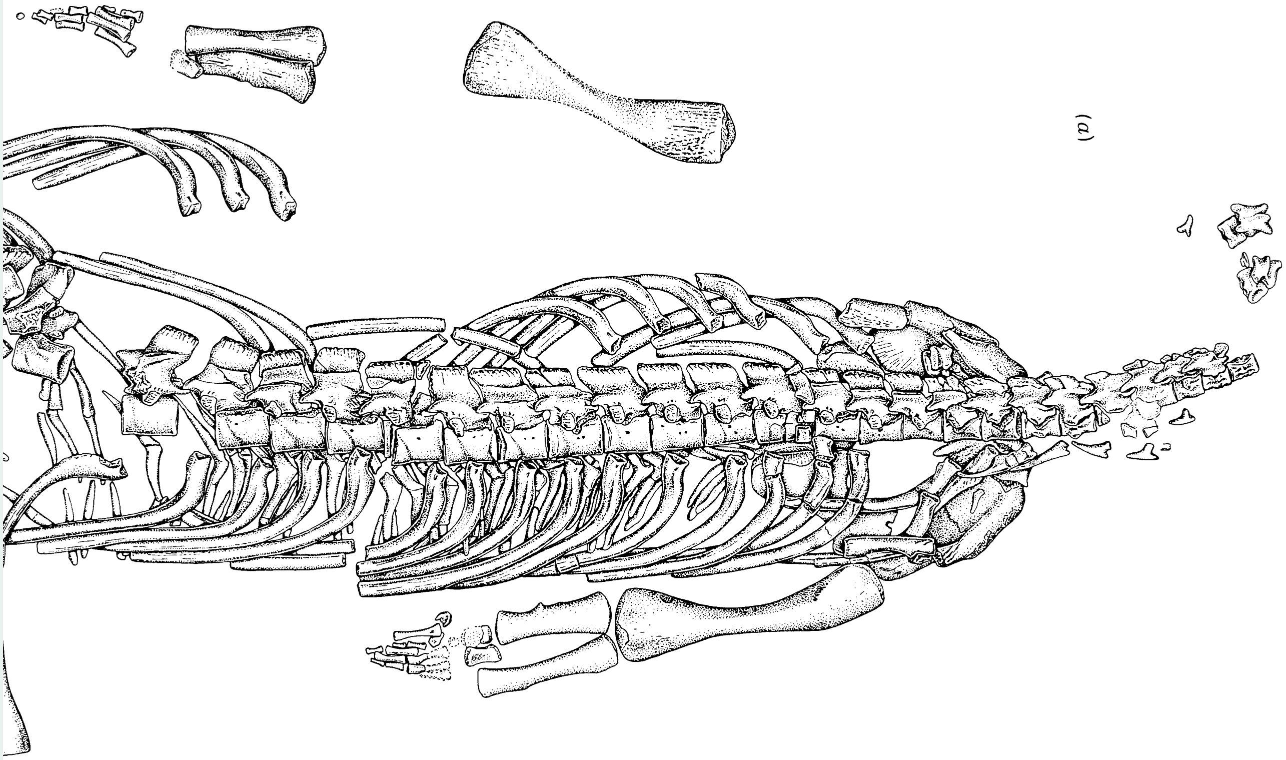


FIGURE 3. *Pachypleurosaurus edwardsi*. (*a*) Institute of Palaeontology, Zürich, 3806. (*b*) Adult individual in ventral vie
Institute of Palaeontology, Zürich, 3460.

view,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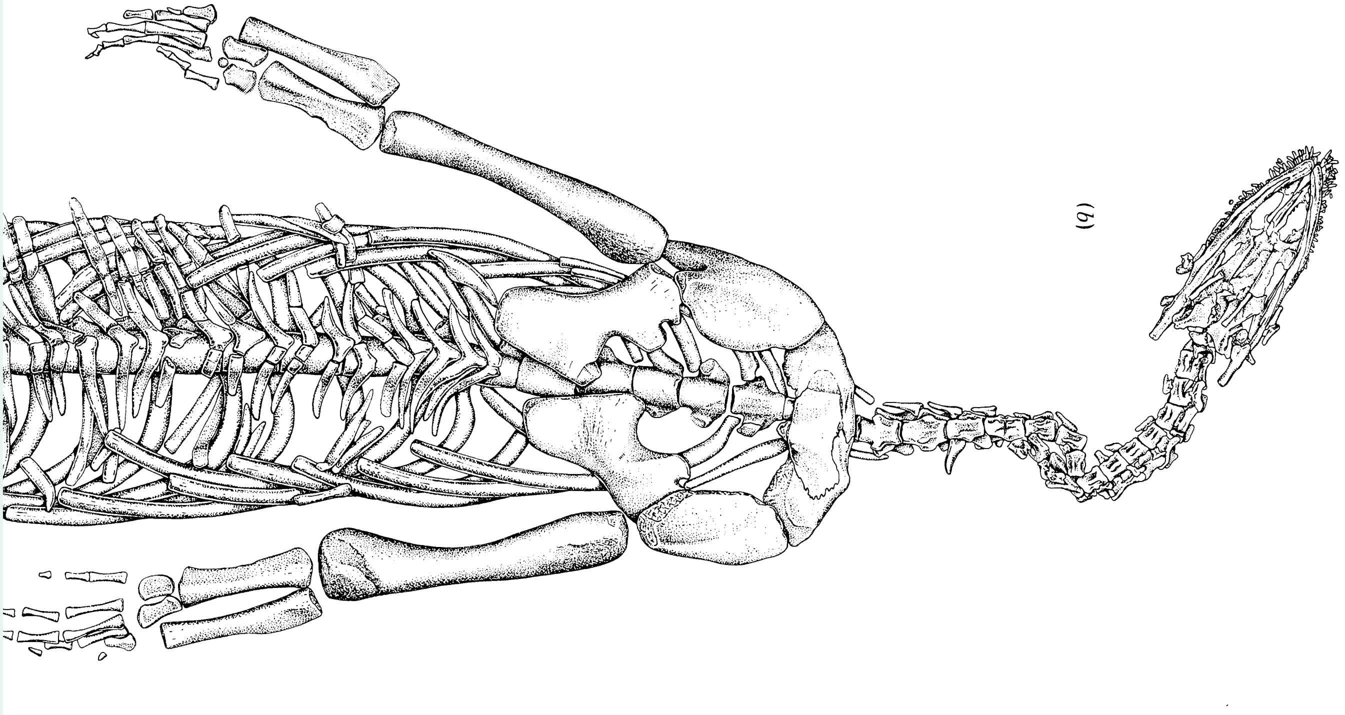
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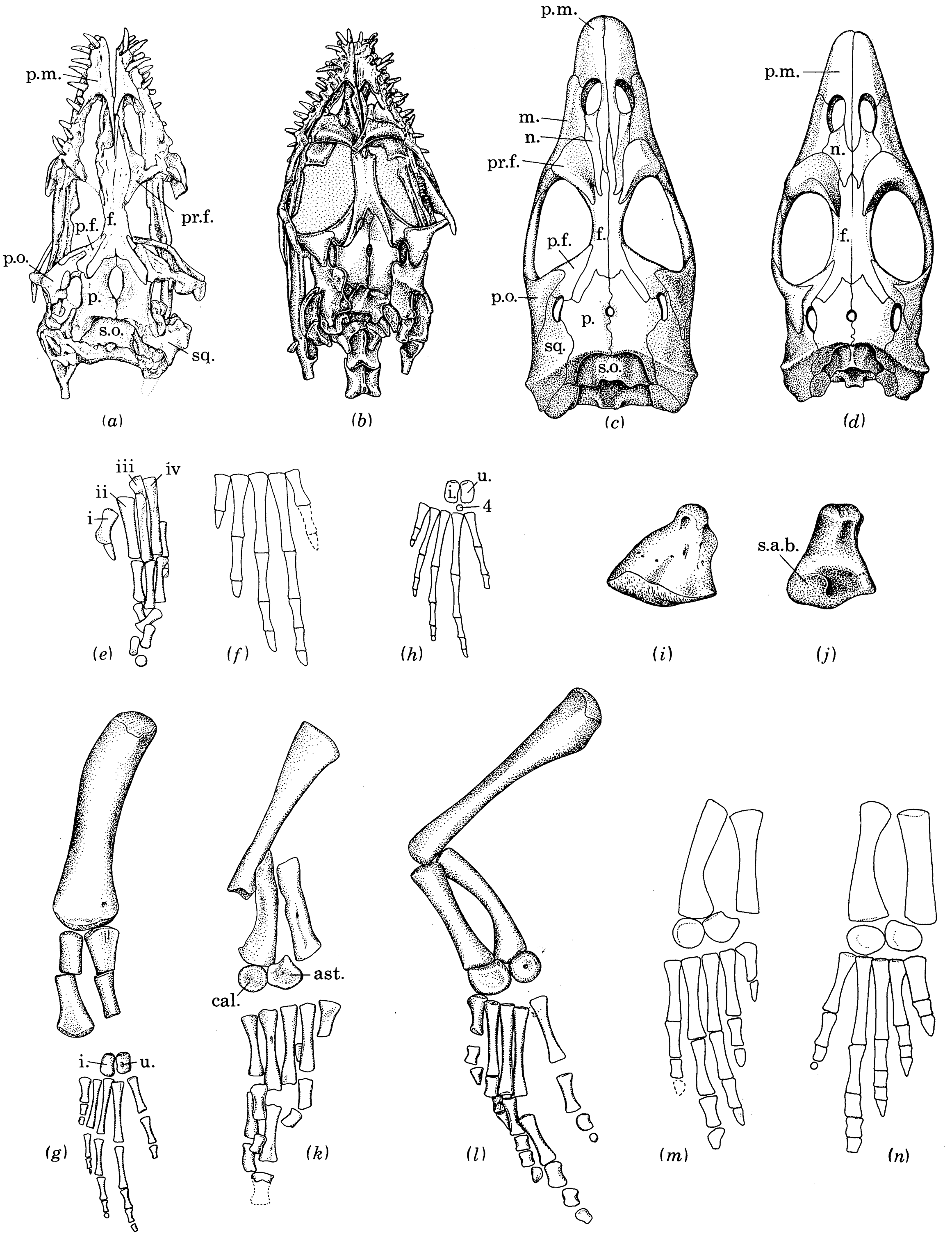


FIGURE 5. Pachypleurosaurids. (*a*) Skull of the type of *Pachypleurosaurus edwardsi* (magn. × 2). (*b*) Skull of *Neusticosaurus* sp., 3604 (magn. × 2). (*c* and *d*) Restorations of the skull of *Neusticosaurus*, showing different patterns of the frontals, nasals and premaxillae. In (*c*) the frontals meet the premaxillae and exclude the nasals from the midline. In (*d*) the nasals meet at the midline and separate the frontals from the premaxillae. This is but one of many variable features evident in this species (from Kuhn-Schnyder 1963). (*e*) Left manus of the type of *Pachypleurosaurus edwardsi* (magn. × 3). (*f*) Reconstruction of the manus of *Pachypleurosaurus edwardsi*, based on the type. (*g*) Left forelimb of *Neusticosaurus* sp. in dorsal view (magn. × 2), Institute of Palaeontology, Zürich, 3530. (*h*) Reconstruction of the manus of *Neusticosaurus* sp. (*i*) Lateral view of left ilium of *Pachypleurosaurus edwardsi*, Institute of Palaeontology, Zürich, 3758 (magn. × 2). (*j*) Lateral view of left ilium of *Neusticosaurus* sp., Institute of Palaeontology, Zürich, 3739 (magn. × 3). (*k*) Left rear limb of the type of *Pachypleurosaurus edwardsi* (magn. × 2). (*l*) Rear limb of *Neusticosaurus* sp., Institute of Palaeontology, Zürich, 3530 (magn. × 2). (*m*) Reconstruction of the lower rear limb of *Pachypleurosaurus edwardsi* based on the type. Manus and pes of adult specimen of *Pachypleurosaurus edwardsi* illustrated in figures 17 and 20. (*n*) Reconstruction of the lower rear limb of *Neusticosaurus* sp. Abbreviations used in figures follow text.

TABLE 1. FEATURES DISTINGUISHING *PACHYPLEUROSAURUS EDWARDSI* FROM *NEUSTICOSAURUS*

Pachypleurosaurus edwardsi	*Neusticosaurus* sp.
skull:	
width of the upper temporal openings approximately one-sixth the longitudinal diameter of the orbit	width of the upper temporal openings approximately one-tenth the longitudinal diameter of the orbit
antorbital distance approximately twice the postorbital distance	antorbital distance less than 50% greater than the postorbital distance
skull table extends beyond the lower jaws, emargination of cheek not visible dorsally	skull table relatively narrow, emargination of cheek visible dorsally
appendicular skeleton:	
width of clavicular blade more than half the length of the median fenestra of the pectoral girdle	width of clavicular blade approximately one quarter the length of the median fenestra of the pectoral girdle
length of humerus ranges from 128 to 185% of the femur	length of humerus ranges from 67 to 129% of the femur
third metacarpal longer than fourth metacarpal	third metacarpal shorter than fourth metacarpal
one phalanx on digit 1, and two phalanges on digit 2 of both manus and pes. Phalangeal count of digits 3, 4 and 5 typically 3, 4 and 3 in manus and pes	two phalanges on digit 1, and three phalanges on digit 2 of both manus and pes. Phalangeal count of digits 3, 4 and 5 typically 4, 5, 3
first phalanx of digits 2, 3 and 4 of manus and pes nearly as long as corresponding metacarpals and metatarsals	first phalanx of digits 1 and 2 of manus, and all of tarsal digits much shorter than corresponding metacarpals and metatarsals
ilium lacks clearly defined acetabulum and supra-acetabular buttress	acetabulum and supra-acetabular buttress clearly defined
astragalus slightly wider than calcaneum	astragalus considerably wider than calcaneum
size:	
total length to end of tail ranges from 30 to 120 cm. Length of humerus ranges from 17 to 85 mm	total length ranges from 9 to 58 cm. Length of humerus ranges from 4.3 to 30 mm

Most individuals of *Pachypleurosaurus* are further differentiated from *Neusticosaurus* by proportional changes associated with larger size. These include the greater length of the neural spines and the relatively smaller size of the skull. The greater length of the neural spines, even in relatively small individuals of *Pachypleurosaurus* results in the proximal caudal vertebrae being exposed in primarily lateral view, whereas they are nearly always exposed in dorsoventral view in *Neusticosaurus*. Among specimens of similar size, those of *Pachypleurosaurus* are consistently less fully ossified than those of *Neusticosaurus*.

The differences between *Pachypleurosaurus edwardsi* and the majority of smaller nothosaur specimens from the Alpine region are sufficiently great to support generic distinction between the two forms. Unfortunately, it is difficult to establish the proper name and type for the smaller form. Despite the suspicion expressed by both Zangerl (1935) and Kuhn-Schnyder (1959) that more than a single species is represented among the pachypleurosaurid material from Monte San Giorgio, no other species within this family has been named from this locality. A second pachypleurosaurid species was named by Kuhn-Schnyder (1959) from a locality in eastern Switzerland, however. *Pachypleurosaurus staubi* was based on a single specimen from near Bergrün in the canton of Graubünden (Number A/III 254 in the Zürich collection). This specimen (figure 7) consists of the trunk region, girdles and limbs. What is preserved resembles closely the multitude of small pachypleurosaurid specimens from Monte San Giorgio and it would certainly be placed in the same species if it had been found at that locality. The proportions of the humerus and femur and the number and proportions of the phalanges of the manus differentiate it clearly from the type of *Pachypleurosaurus edwardsi*. Further information on the smaller pachypleurosaurids has been provided by Mateer (1976) in a carefully illustrated description of specimens from northern Italy that he referred to as *Pachypleurosaurus* cf. *staubi*. This work reinforces the distinction between this species and *P. edwardsi*.

Among other species that have been assigned to the Pachypleurosauridae, most can be distinguished from the taxa in question by one or more anatomical differences. *Psilotrachelosaurus töplitschi* Nopcsa (1928) – the type and only specimen of which also lacks the skull – apparently differs from all other nothosaurs in having a long, narrow coracoid and in having all the metacarpals and metatarsals of approximately the same length. In the specimen described by Kuhn-Schnyder, and in other pachypleurosaurids, the extremities of the coracoid are widely expanded and the first metacarpal is much shorter than the second. *Anarosaurus* is clearly distinguished from other pachypleurosaurids by the significantly greater length of the femur relative to the humerus. In the specimen described by Nopcsa (1928), the length of the femur exceeds that of the humerus by almost 30%. In *P. staubi*, the femur is between 4 and 5% longer than the humerus. *Dactylosaurus gracilis* Gürich (1884) is known from only the anterior end of the skeleton, but the forelimb, especially the ulna and radius, are much slimmer than those of *P. staubi*. To judge by the high degree of ossification of the carpals in this specimen, *D. gracilis* reached an adult degree of ossification at a much smaller size than did any of the pachypleurosaurids in the Zürich collection. *Dactylosaurus schroederi* Nopcsa (1928), also achieved a high degree of ossification at a relatively small size, and the radius and ulna are very slender compared with those of *P. staubi*. According to Nopcsa's description, *D. schroederi* has four carpals, including a pisiform. This bone is not present in other pachypleurosaurids.

Phygosaurus perledicus Arthaber (1924) is known only from a headless trunk together with the pectoral girdle, incomplete forelimb and anterior portion of the pelvis. The glenoid–acetabular distance is approximately 20 cm, which is greater than that of most specimens of the smaller pachypleurosaurid species in the Zürich collection, yet the distal end of the humerus and proximal end of the ulna and radius appear relatively incompletely ossified. The ribs and vertebrae, especially well seen in X-ray (Peyer 1933), do not exhibit pachyostosis, which is particularly well pronounced in the larger specimens in the Zürich collection.

Numerous nothosaurs have been described from China in the last three decades. In his recent review, Sanz (1984) suggests that most genera are closely related to *Nothosaurus*. He is uncertain about the position of *Keichousaurus* (Young 1958). In most features it appears typical of pachypleurosaurids, but the ulna is a massive element, quite unlike that of any of the European genera.

One remaining European nothosaur, *Neusticosaurus pusillus* (Fraas) does show many similarities with the smaller pachypleurosaurid from the alpine region (figure 8). This animal, from the Lettenkohle (Lower Keuper) near Ludwigsburg, 14 km north of Stuttgart, was first described by Oscar Fraas (1881) as a new species of *Simosaurus*. Seeley (1882) recognized that the skull was very distinct from the type of that genus and placed it in a new taxon, *Neusticosaurus*. Eberhard Fraas (1896) later described a host of smaller specimens from Ludwigsburg as members of a second species, *N. pygmaeus*, on the basis of their smaller size. These are almost certainly juvenile specimens of *N. pusillus*.

The description and illustration of *Neusticosaurus* by Seeley and Eberhard Fraas are adequate in most respects to demonstrate the similarity of this material with the smaller Alpine species. None of the specimens from Ludwigsburg are as well preserved, but what can be seen of the skeleton shows no clearly distinguishing features. All proportions fall within the limits of the

TABLE 2. DIMENSIONS OF THE NOTHOSAURS *PACHYPLEUROSAURUS EDWARDSI* AND *NEUSTICOSAURUS*

	Pachypleurosaurus edwardsi																		*Neusticosaurus*					
specimen numbers	3935	3460	3437	3806	3458	2811	2810	3758	3452	3453	3456	3454	3708	3407	3440	3447	3439	Type	3629	3556	3604	3789	3409	Type
skull length at midline	65	56.8	59.6	—	—	53.5	52.4	42	37.6	32	—	33	33.6	33.1	32.6	25.6	28.8	26	23.2	25.2	21.6	12.7	13.2	30
lower jaw from symphysis to end of retroarticular process	74	63.5	62.4	—	—	63.1	55.9	45	43.5	—	—	40	37.3	38.1	37.6	27.6	30.3	29	27.7	29.5	26.9	13.3	13.6	
total length to tip of tail	1200	1140	—	—	—	—	910	—	—	—	—	—	—	440	—	296	—	301	318	314	—	96	90	—
neck, to front of dermal shoulder girdle	—	127	—	—	—	143	110	72	—	—	—	70	52.5	—	—	37.1	44.1	42	53	51	40.8	15.3	14	65
trunk, front of shoulder girdle to base of tail	405	368	315	315	—	305	274	182	153	150	135	—	—	127	—	94.6	87.4	85	95	88.9	91	28.9	24.1	125
tail	—	587	—	—	544	—	474	—	—	—	200	—	—	219	—	138	—	150	147	150	117	39.1	38.4	—
glenoid–acetabulum	295	280	260	246	240	230	208	133	116	110	110	—	103	92.5	—	72	64.5	59	72.8	70.5	70	21.8	19.1	92
l. cervical vertebrae, just	12	11	10	10	—	—	7.8	5.2	—	—	—	4	—	—	—	2.7	2.5	—	—	3	—	1	0.8	—
v.d. anterior to pectoral	8	—	—	7	—	—	—	—	—	—	—	3.5	—	—	—	1.7	1.7	—	—	—	—	—	—	—
h.d. girdle	—	6	5	—	—	—	5.3	3	—	—	—	—	—	—	—	—	—	—	—	1.8	—	—	—	—
l. anterior trunk vertebrae	15	14	13.1	11	—	—	10.3	6	—	—	—	—	—	—	—	3.5	—	—	—	3.1	—	1	0.8	—
v.d.	9	—	8.5	7	—	—	6.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
h.d.	—	8.2	8.5	—	—	—	—	4	—	—	—	—	—	—	—	2.4	—	—	—	2	—	—	—	—
l. posterior trunk vertebrae	18	15.8	15.2	15	14	—	—	7.3	7.8	6.7	—	6.5	5.5	—	—	4.3	—	—	—	3.8	—	1.4	—	4.2
v.d.	13	—	10.3	10	7.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
h.d.	—	10.3	—	—	—	—	—	4.6	—	—	—	—	—	—	—	3	—	—	—	2.6	—	—	—	—
l. sacral vertebrae	—	14.3	14	14	—	—	—	7	6.9	—	—	—	5.1	—	—	—	—	—	—	3.7	—	—	—	—
v.d.	—	—	—	10	—	—	—	5	—	—	—	—	4.2	—	—	—	—	—	—	—	—	—	3	—
h.d.	—	10.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.4	—	—	—	—
l. anterior caudal vertebrae	16	16	13.8	14	13.7	14.9	11.9	7.1	7.4	6.7	6	—	5.6	6.1	—	4	3.6	4	—	3.5	—	1.3	3.2	—
v.d.	16	13	11.5	13	11.5	—	9	5.3	—	4	5	—	—	4	—	3.2	3.2	—	—	—	—	—	—	—
h.d.	16	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.3	—	—	—	—

humerus	85	80	83	72	69.7	55.9	56.4	34.9	39.4	31.1	31.3	29	25	35.2	31.7	20.2	17.7	17	16.5	17.4	16.9	4.2	4.3	22
ulna	40	34.9	36.4	32	30.4	27.3	26.7	16.3	17.2	13.7	13.4	14	11.7	15.2	14.4	8.2	7.4	7	8	8.4	7.6	2.2	2.1	11
radius	50	43.1	41.2	38	38.6	31.8	31.2	19	20.7	15.8	16.5	16	13.5	18.3	17.4	11.2	9.5	9.5	9.2	9.6	9.2	2.5	—	12
ulnare	10	9.5	9.2	8	7.7	6.1	—	3.1	—	3.3	2.8	—	2.5	2.6	—	—	1.3	1.5	1.2	1.3	1.4	0.4	—	—
intermedium	13	11.9	11.5	9	10.2	6.8	—	3.9	—	—	3.7	—	3.3	3.7	—	—	2.1	—	2	2.1	1.6	0.5	—	—
1 metacarpals	12	8	—	6	—	6.2	6.1	3.3	—	3.1	2.8	3	2.8	2.5	2.5	2	2	1.5	2	2.1	1.6	—	—	—
2	17	14	—	11	—	12.1	11.7	5.9	—	5.6	5.5	6	5.2	5.6	5.5	—	3.4	3	3.6	3.7	3	—	—	—
3	18	16.3	—	13	13.2	13.6	13.1	6.9	—	7.2	6.4	6.5	5.3	6.3	6.1	—	3.9	3.7	4	4.2	3.4	—	—	—
4	—	15.5	15.1	13	—	10.2	12.2	7.9	—	6.2	—	—	4.9	5.9	5.5	—	3.2	3.2	—	4.3	3.7	—	—	—
5	—	9.9	—	—	—	7.5	7.5	—	—	3.7	—	—	3.4	3.3	4.4	—	2.5	2	—	3.1	2.2	—	—	—
1 digits as restored	—	4	—	4	—	—	—	—	—	—	1.8	1.5	—	—	1.6	—	—	0.7	1.2	1.7	1.3	—	—	—
2 (excluding metacarpals)	—	11	—	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.1	—	—	—	—
3	—	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.7	—	—	—	—
4	—	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.5	—	—	—	—
5	—	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.4	—	—	—	—
femur	51	49.2	45.5	39	41.2	45.1	37.9	23.3	24.9	20	18.6	18	17	19.3	17.7	12.6	12.2	15	18.1	17.4	16.1	5.9	6.5	26
tibia	30	28.2	27.2	—	25.1	24.9	21.2	13	14.8	11.1	10.8	11	9.6	11.3	—	6.8	6.9	9	8.5	8.4	7.9	2.8	2.4	11
fibula	35	32.3	28.1	27	29.2	26.4	24.7	14.5	16.5	12.2	12.4	13	11.3	12.8	—	8	8.3	10	9.6	—	8.4	3.3	2.5	11
proximodistal axis of calcaneum	12	11	9.1	—	8.9	7	—	3.9	4.6	3.8	3.3	4	2.6	3.2	—	1.7	—	2	1.9	1.9	1.8	0.5	—	—
1 metatarsals	15	12.5	11.9	10	12	10.1	—	5.2	—	5	4.8	4.5	4.3	4.4	—	3.1	—	3	3.3	3.5	2.5	0.8	0.8	—
2	23	18.7	18.2	16	—	17.7	—	8.6	—	7.2	7.5	7.5	7	7.6	—	5	—	5.5	5.1	—	4.3	1.8	1.5	—
3	25	21.4	20.7	17	19.8	19.8	—	10.9	—	8.8	—	8.5	7.7	8.8	—	5.6	—	7	6.3	—	5.5	2.2	1.9	—
4	26	22.2	20.8	18	20	20.5	—	11.5	—	9.8	9	9	8.2	9.4	—	6.1	—	7	6.8	—	5.8	2.5	2.1	—
5	21	17.9	16.6	14	16.4	16	—	9.1	—	7.5	6.9	7	6.3	7.2	—	4.6	—	5	4.9	—	4.3	1.7	1.4	—
1 digits as restored	9	16.4	6.8	6	—	5.7	—	2.7	—	2.8	—	2.5	2.4	2.8	—	1.9	—	1.5	2.8	—	2.2	0.7	1	—
2 (excluding metatarsals)	21	18	16.5	13	—	—	—	—	—	7.2	—	—	6	6.4	—	4.1	—	4.5	4	—	2.9	1.1	1.5	—
3	35	31	—	—	—	24.3	—	—	—	13	—	—	10.5	—	—	6.6	—	7.5	5.8	—	4.9	1.9	—	—
4	43	41	—	—	—	33.1	—	—	—	15.3	—	—	12.5	—	—	8.2	—	—	7.5	—	6.5	2.5	—	—
5	28	26	—	—	—	19.1	—	—	—	—	—	—	6.3	—	—	5.2	—	—	5	—	3.9	1.2	—	—

Except for the types, all the specimens are from the Institute of Palaeontology, Zürich. Measurements in millimetres. l., Length of centrum; v.d., vertical diameter of centrum; h.d., horizontal diameter of centrum.

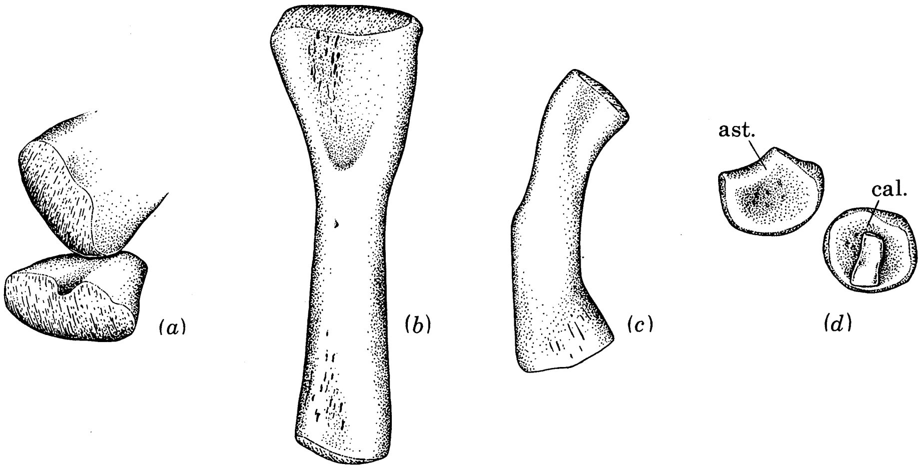


FIGURE 6. Elements of the rear limb of *Pachypleurosaurus edwardsi*, Institute of Palaeontology, Zürich, 2466. (*a*) Base of ilium and head of femur. (*b*) Femur in ventral view. (*c*) Fibula. (*d*) Astragalus, calcaneum and terminal phalanx (magn. × 1.45).

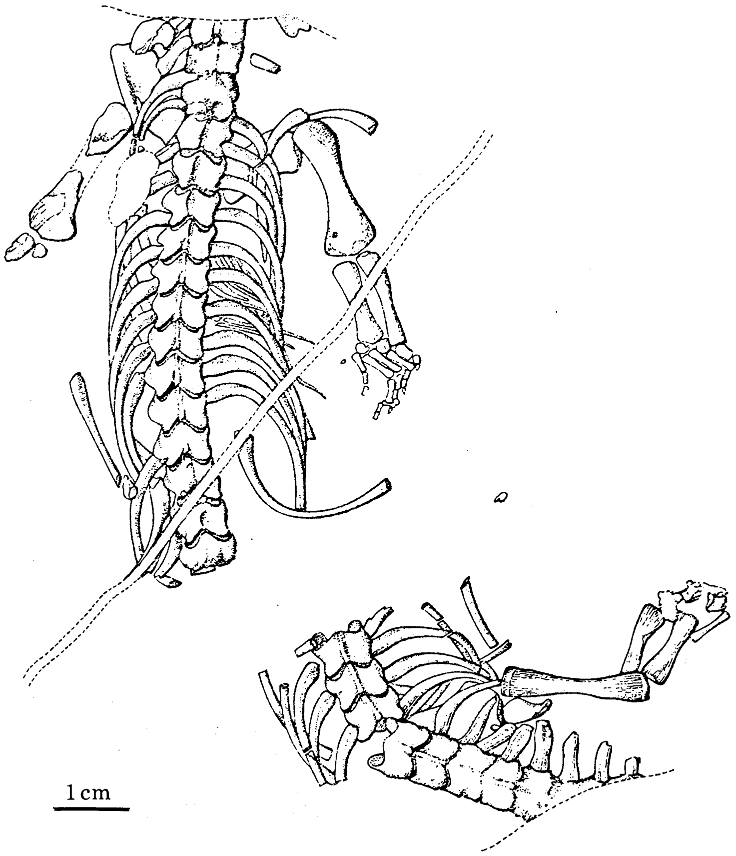


FIGURE 7. Type of '*Pachypleurosaurus*' *staubi*, no. A/III 254, Institute of Palaeontology, Zürich (natural size), from Kuhn-Schnyder (1959, figure 1).

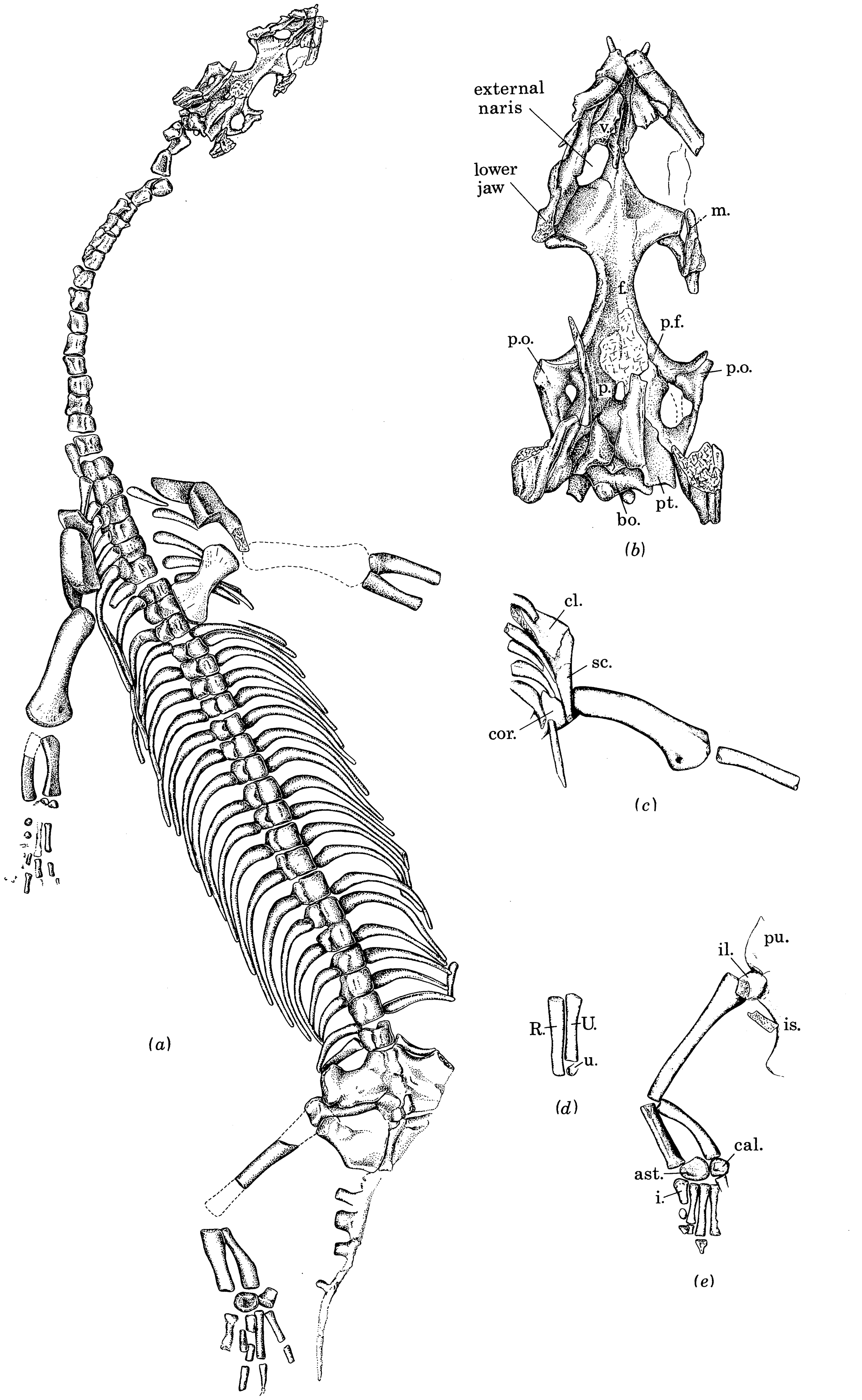


FIGURE 8. Type specimens of *Neusticosaurus pusillus*. (*a*) Holotype in primarily ventral view (natural size). (*b*) Skull of holotype, approximately 2.5 times natural size. (*c*, *d* and *e*) Fore and hind limbs of paratype, approximately 1.2 times natural size. British Museum (Natural History) specimen numbers 53 and 54.

Alpine species. There are two phalanges evident in the first digit of the pes, and the astragalus is far larger than the calcaneum. In contrast with all specimens of *Pachypleurosaurus* the femur is longer than the humerus.

There is, however, one very conspicuous difference from both pachypleurosaurids and all other nothosaurs which appears in the earlier descriptions of *Neusticosaurus*: the structure of the palate. Seeley described very large suborbital vacuities, in contrast to the condition in all other nothosaurs in which the palate forms an almost unbroken sheet of bone. In fact, as might be guessed from the illustrations, and was confirmed by examination of the specimen, the palate is largely missing and the large openings are the orbits seen in ventral view.

As described by Seeley, traces of the front and back of the lower jaws are preserved, as well as the back of the palate. Most of what can be seen is the under-surface of the skull roof. Unfortunately, the bone surface is not well preserved and few sutures are clearly evident. In general, the pattern resembles that of the Alpine species. The right upper temporal opening appears quite small. The left is broken on the lateral margin, but appears nearly as large as that of *Pachypleurosaurus edwardsi*. In contrast with that species, but in common with the smaller form from Switzerland, the skull table is narrow and the lower temporal embayment would be visible in dorsal view.

A further feature that appears distinctive in Seeley's illustration is the relative length of the metatarsals. The first appears almost as long as the second. Preparation shows that he had included the first phalanx with the metatarsal. As now distinguished, the first metatarsal, like that of both Alpine species, is less than half the length of the second.

To the degree that comparisons are possible, the material from Ludwigsburg closely resembles the smaller alpine species, but can be distinguished from *Pachypleurosaurus*. The name *Neusticosaurus* may thus be used in reference to the numerous pachypleurosaurid specimens that do not belong to *Pachypleurosaurus*. '*Pachypleurosaurus*' *staubi* may be included in the genus *Neusticosaurus*, but in the absence of a skull, it is uncertain whether or not it belongs to the same species. In view of this uncertainty, and the relatively poor preservation of the material from Ludwigsburg, the smaller Alpine form will be referred to as *Neusticosaurus* sp.

The two genera may be distinguished as follows:

Class Reptilia
Order Sauropterygia
Suborder Nothosauria
Family Pachypleurosauridae

Neusticosaurus Seeley 1882

Type species. *Neusticosaurus pusillus*.

Diagnosis. Pachypleurosaurid nothosaur distinguished from *Pachypleurosaurus* in the lesser width of the skull table, in having two phalanges in the first digit and three in the second, the lesser width of the clavicles and the shorter antorbital length. Differentiated from *Dactylosaurus* by the greater thickness of the ulna and radius, from *Anarosaurus* in the greater length of the humerus relative to the femur, from *Phygosaurus* by the greater degree of pachyostosis and lesser size at maturity, and from *Psilotrachelosaurus* by the greater width of the extremities of the coracoids. Ulna less massive than that of *Keichousaurus*. Known distribution: Middle and Upper Triassic (Ladinian and Lower Carnian) of Central Europe.

Pachypleurosaurus (*Pachypleura*) (Cornalia) 1854

Type species. Pachypleurosaurus edwardsi.

Diagnosis. Nothosaur reaching a total length of at least 120 cm. Distinguished from all other described species by reduction of phalangeal count of manus and pes to 1, 2, 3, 4, 2 and 1, 2, 3, 4, 3. Humerus from 130 to 180% the length of the femur. Ilium lacks supra-acetabular buttress and well-defined acetabulum. Relatively small dorsal temporal openings identify this genus as a member of the Pachypleurosauridae and distinguish it clearly from the assemblage including *Lariosaurus*, *Ceresiosaurus*, *Nothosaurus*, *Paranothosaurus* and *Simosaurus* in which the upper temporal openings are much larger than the orbits. Neural spines of trunk and tail tall and rectangular. Three pairs of sacral ribs. Carpus consists of elongate ulnare and intermedium and tiny distal carpal. Only the astragalus and calcaneum of the tarsus are ossified.

Holotype. Complete skeleton in the Museo Civico di Storia Naturale in Milano. It was collected from Ca'del Frate, near Besano, Italy.

The following specimens in the collection of the Institute of Palaeontology, Zürich may be assigned to the genus *Pachypleurosaurus*: the majority come from Alla Cascina at Monte San Giorgio, these include 2811, 3407, 3425, 3427, 3428, 3430, 3435, 3436, 3437, 3439, 3440, 3447, 3452, 3453, 3454, 3456, 3458, 3459, 3460, 3702, 3708, 3758, 3759, 3769, 3775, 3776, 3797, 3806, 3935. Zangerl listed two specimens as being from an uncertain horizon below that of Alla Cascina; 3450 is now indicated as coming from Crocefisso-Serpiano and 3438 as from Val Serrata-Cava Inferiore. Four specimens found since Zangerl's study are recorded as coming from localities other than Alla Cascina, but within the area of Monte San Giorgio; 3711 from Valle Serrata, 3719 from Acqua de Ghiffo, and 3749 and 3778 from Val Porina, Cava Inferiore. Number 2466 comes from the same locality as the type; number 2810 also comes from northern Italy, from a locality referred to as Pra dei Spirit.

The geological horizon of the localities for which there is adequate stratigraphic data are indicated in figure 10.

The stratigraphic ranges of *Pachypleurosaurus* and *Neusticosaurus* overlap in the area of Monte San Giorgio, but they are common in different localities, suggesting that they normally inhabited different environments. No material of *Neusticosaurus* has been described from Alla Cascina, from which came most of the specimens of *Pachypleurosaurus*. On the other hand, only a single specimen of *Pachypleurosaurus* has come from Acqua del Ghiffo which has yielded hundreds of specimens of *Neusticosaurus*. The locality of Aqua Ferruginosa has produced no specimens of *Pachypleurosaurus*, but the localities of Val Porina and Valle Serrata, from which a few specimens of that genus have been found, may include beds of equivalent age.

Growth and body proportions

Measurements of the material of *Pachypleurosaurus* are shown in table 2; various ratios are indicated in table 3. The animals are listed in sequence of overall body size or the size of large, readily measured units. Body length, to the end of the tail, in *Pachypleurosaurus* shows a four-fold increase, from approximately 30 to 120 cm. Proportions of most skeletal elements, measured relative to the distance between the glenoid and acetabulum, remain relatively constant, regardless of body size. Exceptions include the proportionately greater size of the rear limb in the type, and the large forelimb of 3407.

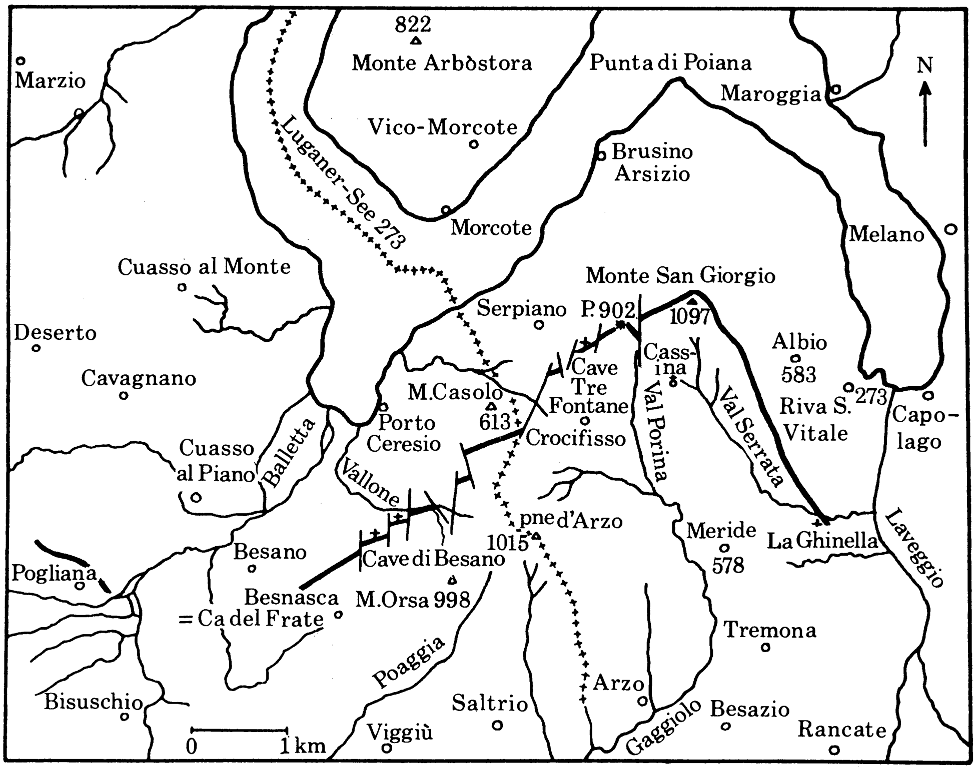


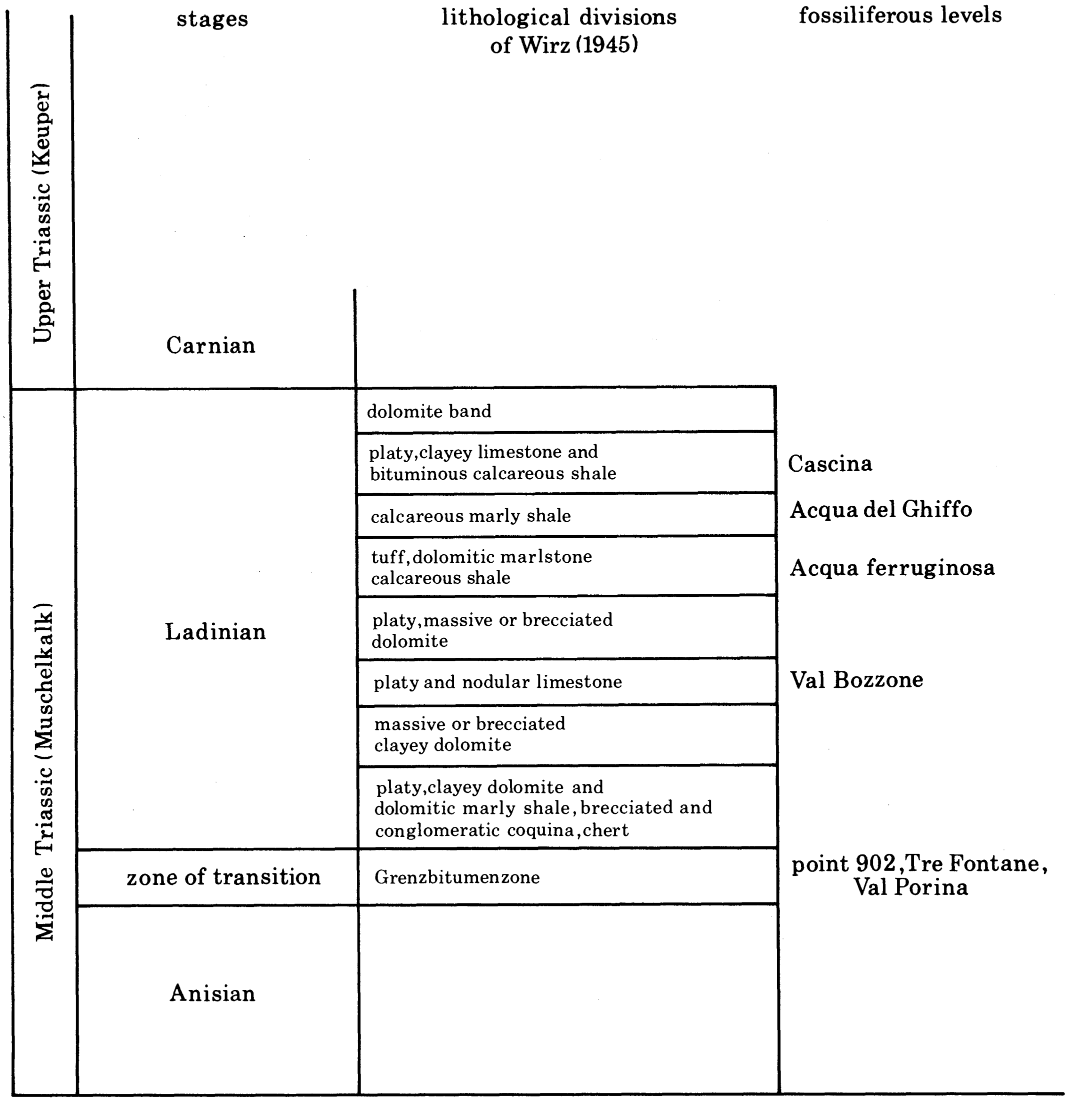
Figure 9. Map of the area in southern Switzerland and northern Italy from which have come the specimens described in this paper (from Kuhn-Schnyder 1974).

The length of the tail varies widely among the few animals in which it appears complete, despite the similarity in vertebral count. The length of the neck and trunk are also somewhat variable, at least partly because the margin of the shoulder girdle may be displaced a considerable distance during burial. The anterior cervical vertebrae may also be telescoped under the skull.

Romer & Price (1940) and Currie (1978, 1981 *b*) have used vertebral dimensions as a basis for comparison between species, and in growth studies of single species among pelycosaurs and eosuchians. The diameter of the centra may be a particularly significant measure of the bulk in terrestrial animals. In nothosaurs, which were presumably supported largely by the water, it might not be expected to have the same significance, but it would still be a useful basis for comparison if it could be readily measured in most specimens. Unfortunately, vertebral diameter is difficult to measure accurately, particularly in the smaller animals. Currie (1981 *b*) has demonstrated that vertebral length also provides an effective basis for comparison, but even this dimension can only be accurately measured in specimens that are exposed in ventral view.

If either the dimensions of individual vertebrae or the entire glenoid–acetabular distance is used as a standard, there is no evidence of allometric change in any of the limb measurements over the four-fold increase in body size shown by these specimens. In marked contrast, the skull and jaws show a continuous decrease from approximately 45% of the glenoid–acetabulum length in the smallest specimens, to a little over 20% in the largest.

The change in the relative size of the skull and the constancy of other major body proportions can be seen by comparison of one of the smallest specimens (3447) and the largest (3935). The



	stages	lithological divisions of Wirz (1945)	fossiliferous levels
Upper Triassic (Keuper)	Carnian		
Middle Triassic (Muschelkalk)	Ladinian	dolomite band	
		platy, clayey limestone and bituminous calcareous shale	Cascina
		calcareous marly shale	Acqua del Ghiffo
		tuff, dolomitic marlstone calcareous shale	Acqua ferruginosa
		platy, massive or brecciated dolomite	
		platy and nodular limestone	Val Bozzone
		massive or brecciated clayey dolomite	
		platy, clayey dolomite and dolomitic marly shale, brecciated and conglomeratic coquina, chert	
	zone of transition	Grenzbitumenzone	point 902, Tre Fontane, Val Porina
	Anisian		

FIGURE 10. Stratigraphic section showing levels within the Middle Triassic from which *Pachypleurosaurus edwardsi* and *Neusticosaurus* have been collected (from Rieber & Sorbini 1983).

length of the trunk, the glenoid–acetabular distance, and all of the major limb elements in 3447 range from 22 to 26% of their length in 3935. In contrast, the skull in 3447 is 41% as long as that of 3935 (as estimated from the length of the lower jaws). The width of the arches of the cervical vertebrae shows a corresponding decrease in larger individuals. In contrast, the length of the neural spines of the trunk and tail show positive allometry relative to other vertebral measures.

Only a small number of specimens are preserved in their entirety, permitting measure of total body length. Evaluation of size can also be made on the basis of acetabular–glenoid distance, and an even larger number of specimens can be considered if only a single bone, such as the femur or humerus, is measured. Size distribution of humeri is shown graphically in figure 11. Compared with that of *Neusticosaurus* the size range is very great. Rather than showing a normal

Table 3. Proportions of the nothosaurs *Pachypleurosaurus edwardsi* and *Neusticosaurus*

	Pachypleurosaurus edwardsi																		*Neusticosaurus*					
specimen numbers	3935	3460	3437	3806	3458	2811	2810	3758	3452	3453	3456	3454	3708	3407	3440	3447	3439	Type	3629	3556	3604	3789	3409	Type
skull/glenoid–acetabulum	22%	20%	23%	—	—	23%	25%	32%	33%	30%	—	—	33%	32%	—	36%	45%	44%	32%	35%	31%	58%	69%	33%
skull + neck/trunk	—	50%	—	—	—	65%	60%	63%	—	—	—	—	—	—	—	66%	84%	80%	80%	85%	70%	97%	113%	76%
skull/p.t.c.	3.6	3.6	4	—	—	—	—	5.8	—	4.8	—	5.1	6.1	—	—	6.0	—	—	—	6.6	—	9.1	—	7.1
skull/humerus	76%	71%	72%	—	—	96%	93%	120%	97%	103%	—	114%	136%	94%	103%	130%	161%	153%	141%	145%	128%	302%	307%	136%
glenoid–acetabulum/p.t.c.	16.4	17.7	17.1	16.4	17.1	—	—	18.2	14.9	16.4	—	—	18.7	—	—	16.7	—	—	—	18.6	—	15.6	—	21.9
glenoid–acetabulum/total	25%	25%	—	—	—	—	23%	—	—	—	—	—	—	21%	—	24%	—	20%	23%	23%	—	23%	21%	—
tail/glenoid–acetabulum	—	2.10	—	—	2.27	—	2.28	—	—	—	1.8	—	—	2.37	—	1.92	—	2.54	2.01	2.11	1.67	1.79	2.01	—
humerus/glenoid–acetabulum	29%	29%	32%	29%	29%	24%	27%	26%	34%	28%	28%	—	24%	38%	—	28%	28%	29%	23%	25%	24%	19%	23%	24%
humerus/p.t.c.	4.7	5.1	5.5	4.8	5.0	—	—	4.8	5.1	4.6	—	4.5	4.5	—	—	4.7	—	—	—	4.6	—	3.0	—	5.2
ulna/humerus	47%	44%	43%	44%	44%	49%	47%	47%	44%	44%	43%	48%	47%	43%	45%	41%	42%	41%	48%	48%	45%	52%	49%	50%
radius/humerus	58%	54%	50%	53%	55%	57%	55%	54%	53%	51%	53%	55%	54%	52%	55%	55%	54%	56%	56%	55%	54%	60%	—	55%
metacarpal 3/humerus	21%	20%	—	18%	19%	24%	23%	20%	—	23%	20%	22%	21%	18%	19%	—	22%	22%	24%	24%	20%	—	—	—
humerus/femur	167%	163%	182%	185%	169%	124%	149%	150%	158%	156%	168%	161%	147%	182%	179%	160%	145%	113%	91%	100%	105%	71%	66%	85%
radius/tibia	167%	153%	151%	—	154%	128%	147%	146%	140%	142%	153%	145%	140%	162%	—	165%	138%	105%	108%	114%	116%	89%	—	109%
femur/glenoid–acetabulum	17%	18%	18%	16%	17%	20%	18%	18%	21%	18%	17%	—	17%	21%	—	18%	19%	25%	25%	25%	23%	27%	34%	28%
femur/p.t.c.	2.8	3.1	3.0	2.6	2.9	—	—	3.2	3.2	3.0	—	2.8	3.1	—	—	2.9	—	—	—	4.6	—	4.2	—	6.2
tibia/femur	59%	57%	60%	—	61%	56%	56%	56%	59%	56%	58%	61%	56%	59%	—	54%	57%	60%	47%	48%	49%	47%	37%	42%
fibula/femur	69%	66%	62%	69%	71%	59%	65%	62%	66%	61%	67%	72%	66%	66%	—	63%	68%	67%	53%	—	52%	56%	38%	42%
metatarsal 4/femur	51%	45%	46%	46%	49%	45%	—	49%	—	49%	48%	50%	48%	49%	—	48%	—	47%	38%	—	36%	42%	32%	—

p.t.c., Length of posterior trunk centrum.

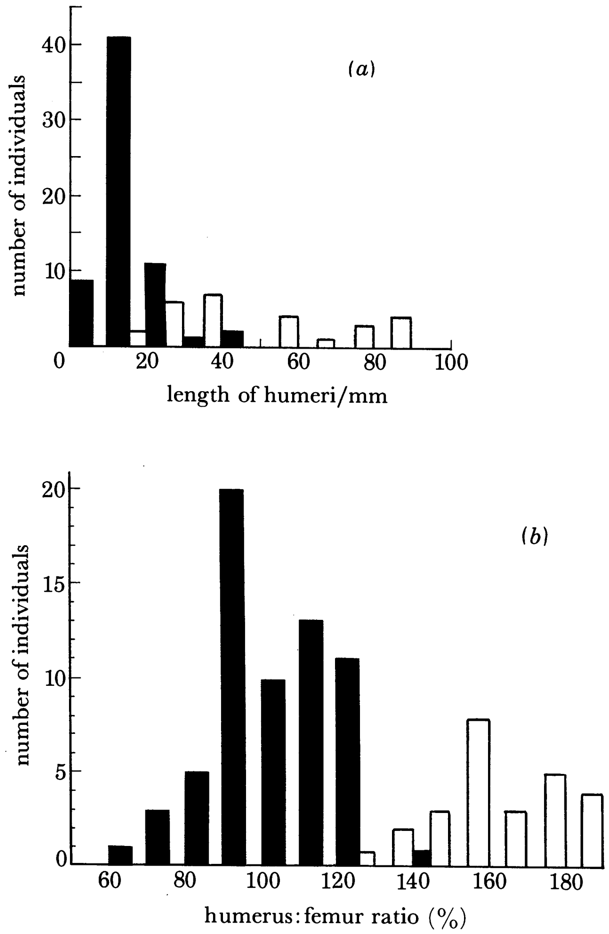


FIGURE 11. Distribution of humeral size in *Pachypleurosaurus edwardsi* and *Neusticosaurus* sp. (*a*) Distribution of humeral length. Solid bars, *Neusticosaurus* sp., open bars *Pachypleurosaurus edwardsi*. (*b*) Distribution of humerus/femur ratios in *Pachypleurosaurus edwardsi* (solid bars) and *Neusticosaurus* sp. (open bars). Data of *Neusticosaurus* sp. primarily from Zangerl (1935).

distribution, it appears weakly bimodal, with a gap in the middle of the series. This is in very strong contrast with the size distribution of *Neusticosaurus* which is sharply unimodal. The pattern exhibited by *Pachypleurosaurus* is that expected in large, relatively long-lived animals, in which several age classes are represented.

ANATOMY OF *PACHYPLEUROSAURUS*

Axial skeleton

Description of the skull is based on the following specimens: the type and 3454, showing mainly the dorsal surface: 3407 and 3437, exposed primarily in lateral view; 3460, 2810 and 3439, showing the palate; elements of the braincase are seen in the largest specimen, 3935 (figures 12–14).

All the specimens are considerably flattened, revealing most of their structures in essentially a single plane. The reconstructions (figure 14) are of necessity composites and only the dorsal view is based primarily on a single specimen, 3454. There are apparently no significant changes

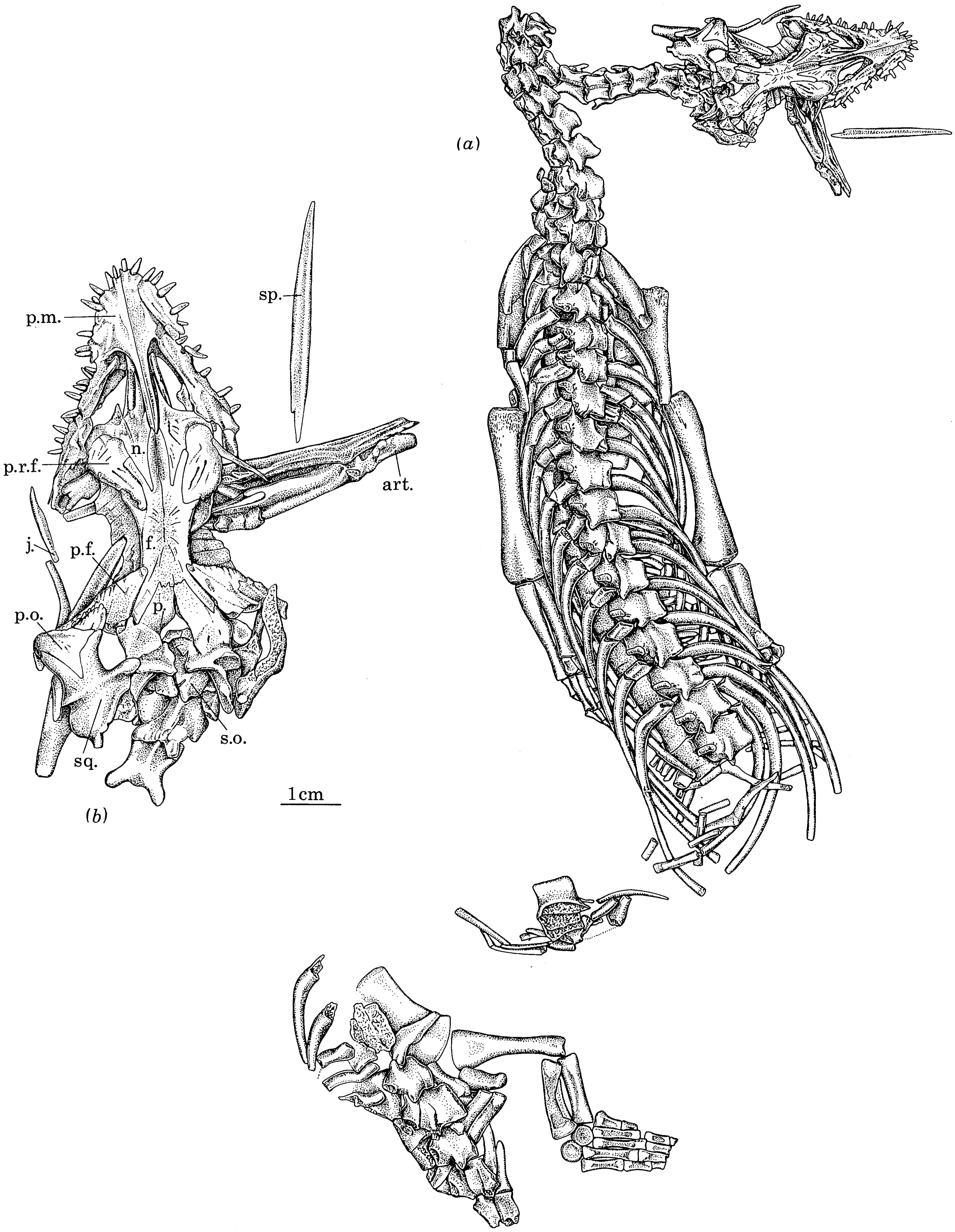


FIGURE 12. *Pachypleurosaurus edwardsi*, Institute of Palaeontology, Zürich, 3454. (*a*) Skeleton (natural size). (*b*) Skull (magn. ×2).

in proportions within the skull over the size range represented here (the length of the lower jaw ranges from 31 to 73 mm).

One of the most striking features of the skull is its small size in the adult (figure 4). This may be associated with aquatic feeding, in which the small head can be readily moved through the water. Such negative allometry may also have made it more practical to feed on a particular food source over a wide range of body size.

In general, the skull structure and proportions are similar to those of the small pachypleurosaurid genera *Neusticosaurus*, *Anarosaurus* and *Dactylosaurus*. As in all nothosaurs, there is no lower temporal bar. The braincase is covered ventrally by the confluence of the pterygoids and the interpterygoid and suborbital vacuities are both closed. As in other pachypleurosaurids, the upper temporal opening is much smaller than the orbit, in contrast with its large size in *Nothosaurus*, *Paranothosaurus*, *Simosaurus*, *Ceresiosaurus* and *Lariosaurus*, and the postorbital portion of the skull is relatively narrow and short. In these features the smaller nothosaurs much more closely resemble primitive eosuchians such as *Youngina*. This is plausibly the primitive condition for nothosaurs in general. The most striking difference from previous descriptions of small nothosaurs that is revealed by this study is the posterior embayment of the quadrate in the form of an otic notch. The surface of the dermal bones is marked with longitudinal striations. The orbital margin of the postfrontal is more conspicuously grooved. The maxillae and premaxillae are irregularly pitted.

In dorsal view, the skull of *Pachypleurosaurus* resembles that of *Neusticosaurus* (figure 5) in most respects except for the relatively larger size of the upper temporal opening and the greater length of the antorbital region relative to the postorbital. In these proportions, *Pachypleurosaurus* is closer to the pattern of *Youngina* and *Claudiosaurus*. The skull table is broad, arching out beyond the lower jaw. In contrast to *Anarosaurus*, *Dactylosaurus* and *Neusticosaurus*, the cheek emargination is not evident dorsally. The orbits are large, making up nearly 30% of the skull's length, and located substantially posterior to the middle. The jugal forms an extremely narrow ventral margin of the orbit. The pineal opening appears large, its diameter at least half that of the upper temporal opening. The external nares are elongate, extending for about one third of the antorbital distance. As in most other aquatic reptiles they are set well back from the anterior margin of the skull.

No specimen shows any evidence of retention of the postparietals, supratemporals or tabular bones which are present in more primitive diapsid reptiles. Both the squamosal and parietal extend lappets onto the occipital surface. The squamosal also forms the lateral and posterior margin of the upper temporal opening and the dorsal margin of the lower temporal embayment. Anteriorly, the squamosal is covered by the postorbital, a triangular bone whose posterior apex extends toward the occipital margin nearly separating the lateral exposure of the squamosal into dorsal and ventral portions. As in *Neusticosaurus* but in contrast with *Anarosaurus*, the postorbital does not contribute to the margin of the upper temporal opening, but is separated from it by contact between the squamosal and postfrontal. The jugal has a slightly broadened area of contact beneath the postorbital, and extends forward nearly to the front of the orbit.

The parietal does not show a ventral extension medial to the temporal opening such as is evident in *Youngina* and *Claudiosaurus* where it would have served to increase the area of origin for the adductor jaw musculature. The bone is deeply notched behind the temporal opening for the attachment of the squamosal, and is thickened medially to form a transverse ridge which divides the skull table from the occipital surface.

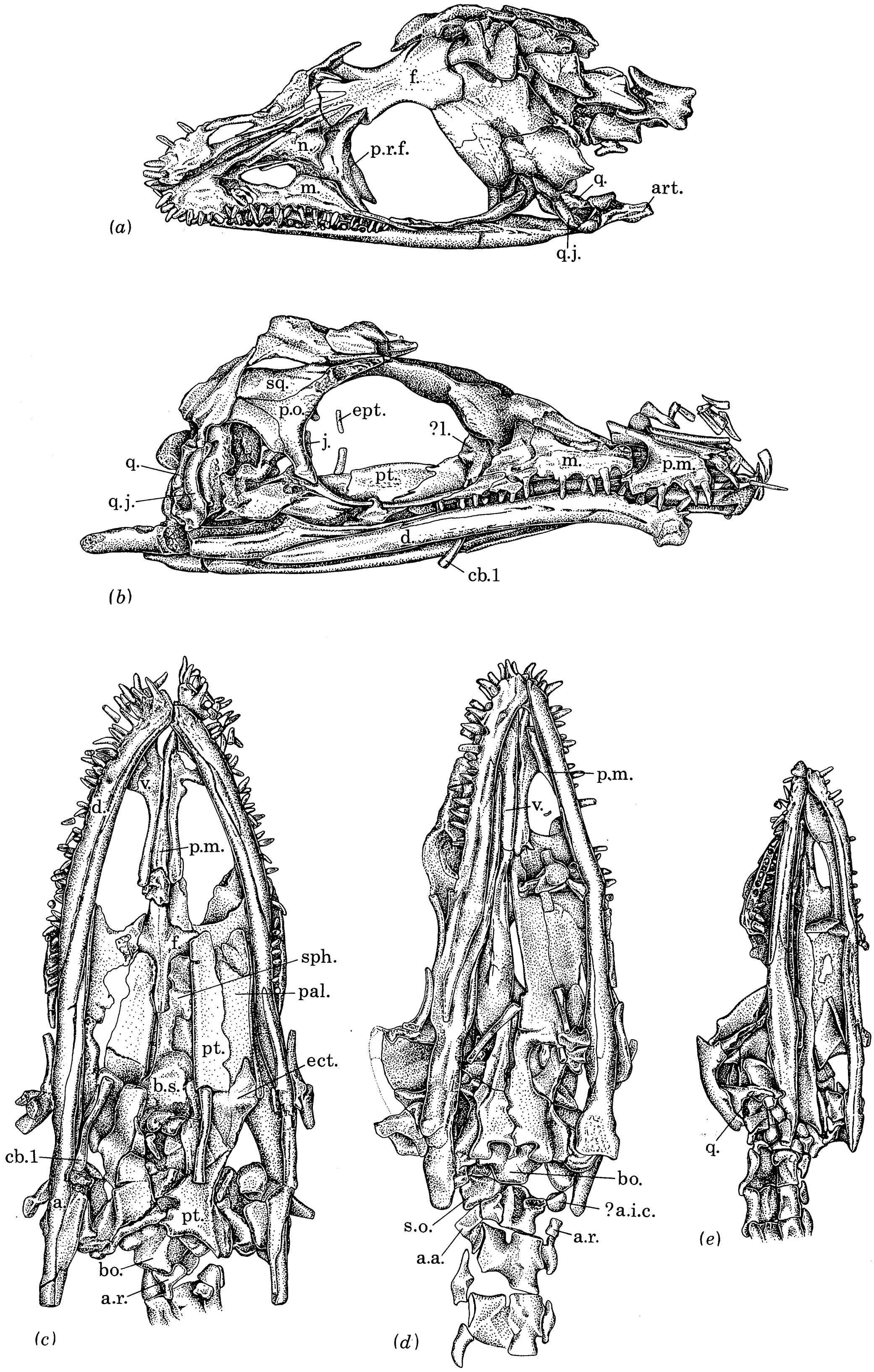


FIGURE 13. Skulls of *Pachypleurosaurus edwardsi*. (*a*) 3407 (magn. × 2), (*b*) 3437 (magn. × 1.45), (*c*) 3460 (magn. × 1.45), (*d*) 2810 (magn. × 1.45), (*e*) 3439 (magn. × 2); all from the Institute of Palaeontology, Zürich.

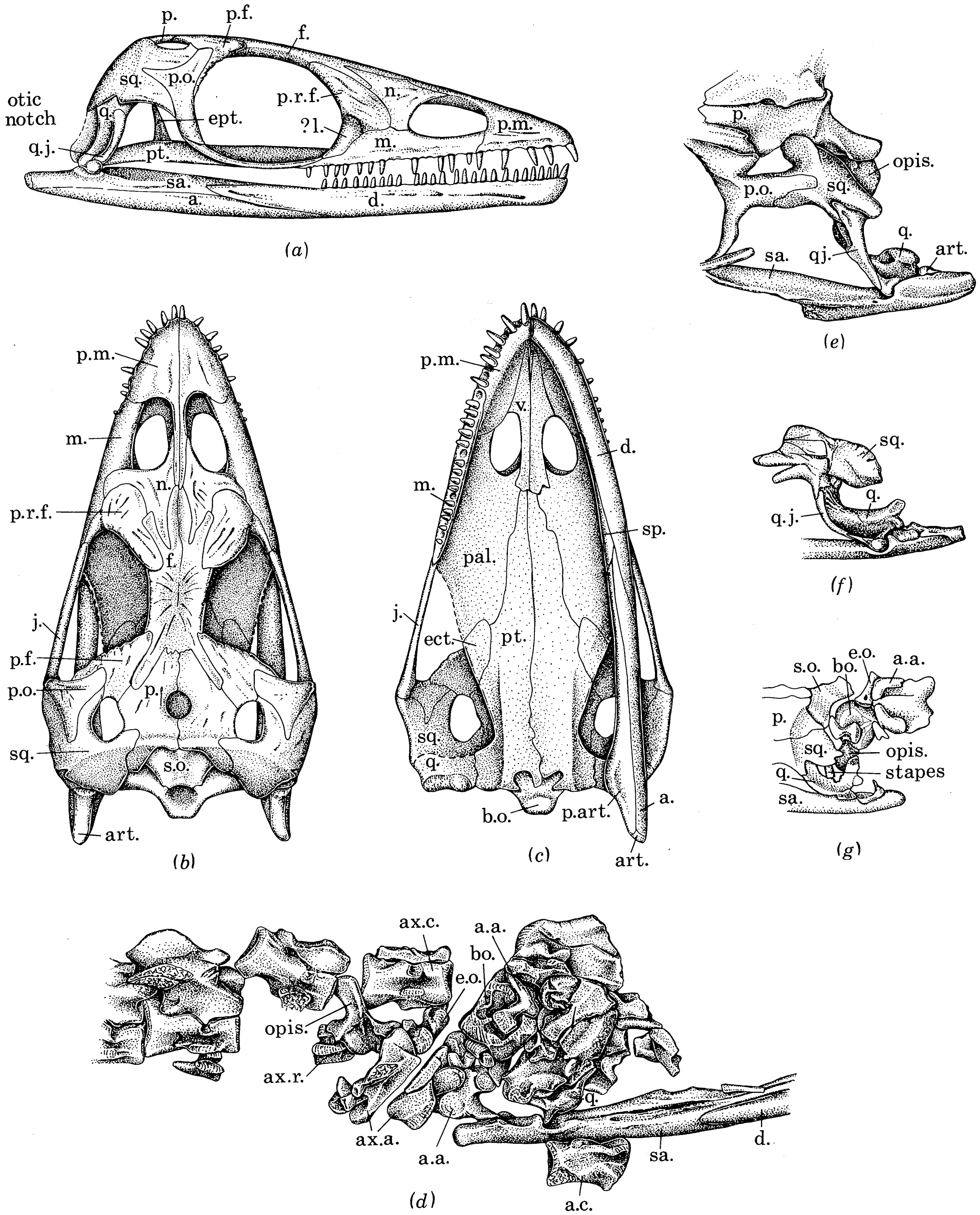


FIGURE 14. (*a*, *b*, *c*) Restorations of the skull of *Pachypleurosaurus edwardsi* in lateral, dorsal and palatal views. Proportions based primarily on 3454 (magn. × 2) with details from skulls illustrated in figure 13. (*d*) Anterior cervical vertebrae and elements of braincase of *Pachypleurosaurus edwardsi*, 3935 (magn. × 1.45). (*e*) Detail of quadrate and adjacent bones of *Neusticosaurus* sp. Institute of Palaeontology, Zürich, 3678 (magn. × 2). (*f*) Detail of quadrate region in *Neusticosaurus* sp., 3747, Institute of Palaeontology, Zürich (magn. × 3). (*g*) Detail of quadrate and stapes of *Neusticosaurus* sp., Institute of Palaeontology, Zürich, 3740 (magn. × 2).

The pre- and postfrontals are relatively massive bones forming arching elements anterior and posterior to the orbit, suggesting the presence of a large, bulging eyeball. A large number of sclerotic plates are evident in both orbits of 3454. The prefrontal curves down towards the palate. In none of the specimens is the lower anterior margin of the orbit well preserved, and it is difficult to establish whether there was a separate lacrimal bone or whether this area is formed entirely by the maxilla and prefrontal.

The fused frontals form a narrow girder between the orbits. The degree of fusion between the paired precursors differs from specimen to specimen. In the type there is a short sutural separation remaining posteriorly. In 3454 the division is still evident along the anterior half of the bone. Little, if any, trace of sutural division is evident in 3407. A similar variation in the degree of fusion of the frontal is evident in *Neusticosaurus*. Long processes of the frontal extend posteriorly between the parietals and postfrontals and similar extensions reach anteriorly between the nasals and prefrontals. The nasal bones, which are lost in plesiosaurs, are large elements in nothosaurs. In *Pachypleurosaurus* they are consistently separated at the midline by the contact between the frontals and premaxillae. They each extend a long curving process anterior to the prefrontal to reach the maxilla. An anterior process runs along the medial margin of the narial opening.

The long posterior processes of the premaxillae form a deep subdivision between the external nares. Anteriorly, the bones expand to form a broad snout. Ventrally, the premaxilla extends a wide shelf toward the vomer. In 3407, where the dentition is especially well exposed, there are six teeth and five intervening gaps for replacement teeth in the left premaxilla. Only four teeth are present on the right side. In 3437, where the teeth have broken from their sockets, they can be seen to have long roots. This genus clearly shares the thecodont implantation common to plesiosaurs. The teeth also show a similar pattern of ridges and grooves. The left maxilla of 3407 shows 14 teeth in place, with space for five more. Like those of the premaxilla, the anterior teeth are long and somewhat procumbent. They become shorter and more vertical in orientation posteriorly. The maxilla has only a short and very narrow extension beneath the orbit, where it is overlapped by the jugal.

The lower cheek region is distorted in all specimens, but its general proportions can be seen in 3449, 3407 and 3437. All show the quadrate as having a relatively narrow, vertically oriented lateral exposure, which is covered above the area of the condyle by a narrow quadratojugal. The quadrate is recessed posteriorly and forms (together with the quadratojugal) a conch-shaped structure resembling in shape and proportions the quadrate of primitive lizards. This area is much more clearly exposed in some specimens of *Neusticosaurus* (figure 14*e*–*g*). If the lateral margin of the quadrate–quadratojugal supported a tympanum in the manner of lizards, it would have been large enough to provide a comparable impedance-matching function. It might be considered surprising that a basically aquatic group such as the nothosaurs should have a middle ear well developed to detect airborne vibrations. This may represent a primitive condition retained from a more terrestrial ancestor, or nothosaurs may have continued to make use of airborne sounds as is common among modern aquatic anurans. The implied presence of a middle ear cavity might militate against deep diving abilities, although a quadrate of essentially similar proportions is retained in the modern marine iguana. Brown (1981, p. 339) cites the probable absence of a stapes as a diagnostic feature of plesiosaurs.

Dorsally, the quadrate extends underneath the squamosal which is notched at its margin to provide a specific area of attachment. The dorsal surface of the quadrate is not well exposed in any specimen, but it is unlikely that any significant degree of mobility was possible to judge from the nature of the ventral contact between the quadrate and the pterygoid. In palatal view it can be seen that these bones have an extensive, somewhat interdigitating contact, precluding any but the most limited movement.

As in all nothosaurs, the pterygoids extend medially and posteriorly to cover ventrally all but the very back of the braincase. Posteriorly these bones meet one another along a wavy suture line and dorsally they are solidly attached to the basioccipital, precluding any movement relative to the braincase. Ventrally, the pterygoids appear almost completely flat, without the distinction in orientation that differentiates the transverse flange and the quadrate ramus in more primitive reptiles. As in other nothosaurs, there are distinct ridges, running parasagittally just medial to the subtemporal fenestrae, marking off the base of the short quadrate processes. These ridges probably mark the medial limit of the pterygoideus muscle. Anteriorly the pterygoids extend as narrowing processes to the vomers.

In all specimens showing the palate, the ectopterygoid appears as a small triangular element forming a short portion of the margin of the subtemporal fenestra. In contrast with most primitive diapsids, it forms no part in securing the palate to the cheek. In plesiosaurs and the nothosaurs *Simosaurus* and *Nothosaurus*, the ectopterygoid extends laterally to the jugal or maxilla, or both, but it is apparently separated from the margin of the skull by a broad stretch of the palatine in *Pachypleurosaurus*.

Although the posterior margin of the palatine is covered by the lower jaws in all of the skulls that are exposed ventrally, it is clearly a very large, essentially flat bone. It appears very thin and is not always complete laterally, but it is doubtful that a well-defined suborbital opening was retained. This opening is not substantiated in any nothosaurs, but it has been illustrated in the plesiosaur *Pliosaurus*. The palatine forms a long suture with the pterygoid, and a shorter contact with the vomer. The internal nares are nearly circular openings. The vomers are narrow paired bones which expand somewhat anterior to the internal nares. They are not strongly attached to one another and are typically separated by the posterior processes of the premaxillae in crushed specimens.

Elements of the braincase are for the most part covered by the very extensive palate and the occipital surface is usually covered by the cervical vertebrae. As in other early diapsids, the supraoccipital is an arched plate of bone which extends beneath the margin of the parietals, but is not suturally connected. Lateral to it there persisted posttemporal fenestrae. In the type, the otic capsule can be seen to form a stout lateral rod that extends to the top of the cheek region. Laterally it was strongly supported by the extensive occipital portion of the squamosal. A disarticulated element that is apparently the opisthotic is visible in 3945, but it is not possible to reconstruct its normal orientation. The anterior portion of the otic capsule is partly visible through the temporal emargination in 3437, but it is so badly crushed that no significant details are visible. The stapes has not been identified in *Pachypleurosaurus*, but in the other genus from Monte San Giorgio it is in the form of a short cylindrical rod (figure 14*g*).

Elements that can be recognized as the exoccipitals are visible in several specimens, but they are either badly damaged or partly covered by other bones. They appear very small and to contribute little to the occipital condyle. They are recessed anteriorly for the jugular foramen and pierced by a single opening for the XIIth nerve. The basioccipital is exposed dorsally in 3935, showing the area for attachment to the exoccipitals and opisthotics and a deep median recess. Crushed fragments of the basisphenoid are visible in 3460 between the disarticulated pterygoids, revealing the retention of the articulating surfaces of the basipterygoid processes. More anteriorly in the same specimen, thin plates of bone are evident between the palate and skull roof which are probably remains of the sphenethmoid.

In 3437 and 3439 the epipterygoid can be seen as a narrow rod of bone extending from the back of the pterygoid toward the skull roof. It is somewhat expanded at its base, but is much narrower than the epipterygoid of *Nothosaurus* (Schroeder 1914).

The hyoid apparatus is represented in several of the skulls by two rod-shaped first ceratobranchials, resembling those of *Claudiosaurus* and other primitive diapsid reptiles.

The lower jaws are slender and only weakly attached at the symphysis in contrast with the stoutly built jaws of *Nothosaurus* and *Ceresiosaurus*. Their occlusal surface is typically closely appressed to the skull, although in 3407 the dorsal surface is exposed, revealing space for 28 socketed teeth, all but two of which are in place.

An important feature is a recess along the dorsolateral surface of the surangular which may have provided a specialized area of insertion for the lateral portion of the adductor jaw musculature. Laterally, the dentary forms most of the jaw surface. It bears a deep longitudinal groove, occasionally interrupted anteriorly, extending from the back of the tooth row nearly to the symphysis. The loss of the lower temporal bar and the arching of the skull table beyond the level of the lower jaw would have enabled a portion of the adductor musculature to attach to the lateral surface of the lower jaw, as in cynodont therapsids (Barghusen 1968). The main force of the jaw muscles, primitively in a dorsomedial direction, could have had a partly balancing lateral component in this genus.

While the lateral component of the jaw muscles may have been amplified in the nothosaurs with the loss of the lower temporal bar (Rieppel & Gronowski 1981), the more medial muscles seem to have been limited by the great extent of the posterior part of the palate. The transverse flange of the pterygoid, which in modern crocodiles and lizards forms the main area for insertion of the pterygoideus, is lost. Although this muscle may have continued to originate along the margin of the subtemporal fossa, its mechanical advantage would not have been as great as in primitive reptiles.

The posterior ventral margin of the jaw was made up of the long narrow angular, extending nearly half the length of the mandible. The inner surface was formed by the prearticular posteriorly and the splenial anteriorly; the outline of the former bone is nowhere clear, but the splenial is displaced and fully exposed in 3454. The articulating surface of the articular is in the form of a transverse groove, behind which the bone extends as a long retroarticular process, supported by the angular and prearticular.

Detailed knowledge of the postcranial skeleton has come mainly from the large, presumably adult specimens 3935, 3460 and 3806 (figures 2, 3 and 4). This is supplemented by information from the type and other smaller animals. Even in the largest specimens, neurocentral sutures are evident throughout the column and most specimens show some degree of separation of the elements. This is a common feature of aquatic reptiles. The sutural connection is complex and precise, assuring tight attachment in life, but once the soft tissue decays separation is precluded only by the consolidation of the surrounding sediments. Only in the caudal region and possibly anterior to the first cervical are intercentral elements present. The centra are shallowly amphicoelous throughout the column.

In the most completely articulated skeleton, 3460, which shows the entire vertebral column, there are 36 presacrals, three sacrals and 42 caudals. In the slightly larger specimen, 3935, in which the neck vertebrae are disarticulated and one or more elements may have been lost, there are 37 presacrals. An accurate count of the entire column is difficult to establish in other specimens. None can be demonstrated to have a count that departs significantly from these figures. In contrast, the number of presacral vertebrae in well-articulated specimens of the smaller form from Monte San Giorgio range from 35 or 36 (3464, 3431, 3412) to 43 (3604, 3629) or 44 (3556), with a full spectrum of intermediate counts (Zangerl (1935) and subsequent observations).

There are approximately 17 cervical vertebrae and 19 or 20 in the trunk. The division between the cervical and trunk vertebrae can be established by a shift in rib articulation, but this area is frequently obscured by the shoulder girdle in specimens exposed in ventral view, making an exact count difficult. As preserved, there are 15 vertebrae exposed anterior to the margin of the pectoral girdle in 3460. In 3835 the number is 16. The first 13 or 14 vertebrae bear small ribs that extend almost directly posteriorly. Ribs 15, 16 and 17 are somewhat intermediate in character while rib 18 in both specimens is similar to, but slightly shorter than, the typical trunk ribs.

Specimen 3806 lacks the head and the anterior cervical vertebrae. The trunk vertebrae, in contrast, are relatively well articulated and 20 can be accounted for. In this specimen a change in the nature of the surface for rib articulation is clearly noted between the neck and the trunk. All the typical trunk ribs are clearly single headed. In contrast, the posterior cervical ribs, through the 16th, are clearly double headed. The 18th appears to be essentially single headed. This will be considered the first trunk vertebra. It lies dorsal to the anterior margin of the shoulder girdle. A rib with a slight division of the head accompanies the vertebra in this position in 3935.

The neck tapers anteriorly and the length of the centra decreases progressively to about one-half that of the anterior trunk vertebrae. The length of the neural spines also decreases progressively anterior to the base of the neck. Compared with primitive terrestrial diapsids such as *Youngina* and *Thadeosaurus*, the neck is long and appears quite flexible, but it is far shorter in proportion to the trunk than that of even the most primitive plesiosaur. *Plesiosaurus hawkinsii* from Street, at the base of the British Liassic, has approximately 19 cervical vertebrae and the neck and head constitute 55% of the precaudal skeleton. In adult specimens of *Pachypleurosaurus*, they account for only 33 to 39%.

The cervical centra do not show any specializations to facilitate sharp bending. The angles of the zygapophyses are nowhere readily measured, but those of the neck appear to be tilted at roughly 5–10°. In 3806, the arches of the posterior cervical vertebrae are particularly well exposed and show that the anterior margin of the neural spine extends well anteriorly between the arches of the next vertebra. This would seem to limit twisting of the neck and dorsal flexion, but might not greatly reduce lateral flexion.

The anterior cervical vertebrae are not well preserved and clearly exposed in any of the specimens. The manner in which they are crushed makes it difficult to make consistent reconstructions in dorsal, lateral and ventral views. The centra are preserved in articulation in 2810, 3407, 3439 and 3460. Disarticulated elements of the atlas and axis can be identified in 3935 where they show more anatomical detail. In most primitive diapsids, the axis is the largest of the cervical vertebrae, and the atlas centrum is much smaller. In *Pachypleurosaurus*, the length of the first three cervicals shortens progressively anteriorly, with that of the atlas only slightly shorter than the axis or the third. The axis arch is not clearly distinguished from those more posterior in position. The atlas arch is paired with the dorsal portion closely resembling the more posterior arches. The medial surface of this arch is exposed in 3935, showing a large surface for articulation with the centrum. The lateral surface is broken or obscured in all specimens. Several show a tiny rib in association with the atlas, but its mode of attachment to the arch is not evident.

The atlas centrum is bevelled on its anterior ventral margin, possibly, as in *Neusticosaurus* for a small intercentrum. A bone is present adjacent to this area in 2810, but the surface is broken, precluding positive identification as a vertebral element. The atlas centrum bears a longitudinal groove for the vertebral artery between the ventral parapophysis at the anterior end of the bone and a more dorsal articulating facet which may have accommodated the capitulum of the first cervical rib as well as the arch. Dorsally, the centrum is notched to form long surfaces for attachment of the arch. The axis centrum has a similar longitudinal groove for the artery, separating the two surfaces for attachment of the rib heads which are here midway in the length of the centrum.

The atlas–axis complex shows no significant similarities to those of advanced plesiosaurs, to judge by Andrews' description of *Muraenosaurus* and *Cryptocleidus* (1910).

The vertebrae just behind the atlas do not differ from it significantly. Toward the base of the neck the parapophyses become more prominent. Ventrally, they can be seen to extend laterally well beyond the base of the centrum from near its midpoint. The parapophyses are abruptly lost in the trunk region where the articulation of the rib is assumed entirely by the arch. In the posterior portion of the neck the transverse processes become correspondingly larger.

The number of trunk vertebrae corresponds well with that seen in primitive eosuchians, including *Thadeosaurus* and *Kenyasaurus* (Currie 1981*b*). This may indicate retention of a primitive condition. *Claudiosaurus*, which has been described as being close to the ancestry of nothosaurs, has only 16 trunk vertebrae, but this might be a specialization related to a shift in body proportions associated with a preliminary stage in aquatic adaptation. *Claudiosaurus* has, in effect, achieved a long neck by posterior displacement of the shoulder girdle while retaining a primitive number of presacral vertebrae, all of which have become elongated. Nothosaurs have increased the total number of presacral vertebrae, but the increase appears to be concentrated in the cervical region, while the trunk retains (or has returned to) the number common to primitive diapsids. Primitive plesiosaurs also have approximately 20 trunk vertebrae.

The cervical and caudal centra are somewhat constricted medially and bear variably developed longitudinal grooves. In contrast, those of the trunk region have a swollen appearance like the fleshy limbs of a chubby baby. Most are marked posteriorly by a pair of grooves running ventrally from beneath the zygapophyses which probably mark the course of the segmental spinal nerves. The lateral surface of the centra is marked by a scattering of small pits. The surface for attachment of the neural arch runs almost the entire length of the dorsal surface of the centra. The length of the centra increases gradually over the first seven trunk vertebrae and remains more or less constant back to the sacral region. The vertical diameter of the centra shows a corresponding increase (figure 15).

The neural arches have a very long pedicle, extending nearly the length of the centrum at the base, but narrowing dorsally. Throughout the trunk, the transverse processes are formed entirely by the arch except for the most posterior two vertebrae in which the centrum contributes as well.

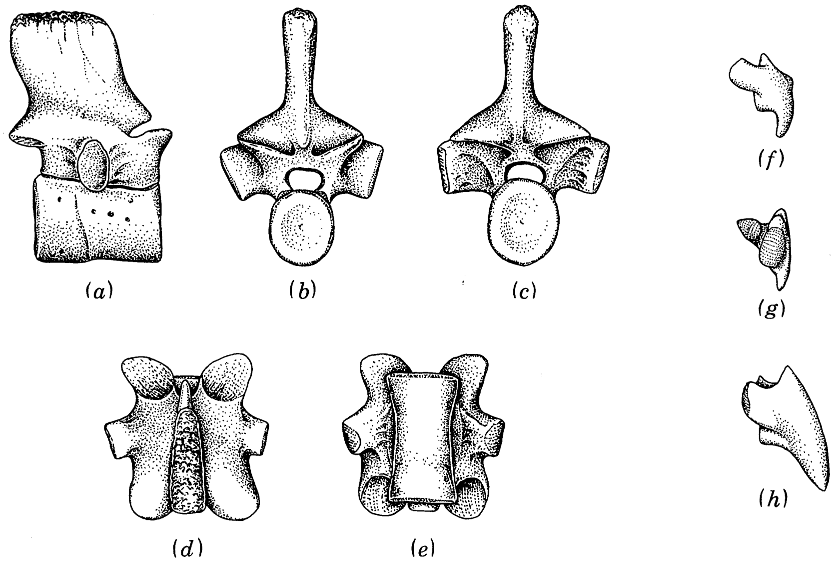


FIGURE 15. *Pachypleurosaurus edwardsi*. (*a*–*e*) Trunk vertebra in lateral, anterior, posterior, dorsal and ventral views, based largely on vertebra 28 in 3935, with details from 3769 (natural size). (*f*–*h*) Cervical ribs; rib number 7 in dorsal and medial views; number 12 in dorsal view, specimen 3935 (magn. × 2), both from the Institute of Palaeontology, Zürich.

The zygapophyses are broad and appear relatively flat; their inclination appears to be limited to between 5 and 10°, but this is difficult to measure accurately in closely articulated specimens. In addition, although they are generally well preserved, the arches are somewhat distorted. The neural spines are tall and rhomboidal; the dorsal margin is flat, but most, except those close to the sacrum, tilt posteriorly. The dorsal surface is broad and rugose, like that of *Claudiosaurus*, presumably for the attachment of interspinous ligaments. There is only a narrow gap between successive neural spines, strongly limiting dorsoflection.

A very important feature of these vertebrae is the presence of extra articulating surfaces. For most of the column in most of the specimens, the vertebrae are so closely articulated that these are difficult to see, but nearly all of the vertebrae in the neck region, trunk and anterior portion of the tail have the anterior margin of the base of the neural spine fitting into the posterior margin of the more anterior vertebrae between the zygapophyses. A somewhat similar condition has been described by Currie (1981*a*, *b*) for both the terrestrial eosuchian *Youngina* and the specialized aquatic genus *Hovasaurus*.

In addition, and even harder to see, are paired processes extending posteriorly below the level of the zygapophyses of the posterior trunk vertebrae, so as to fit between the bases of the anterior zygapophyses of the next vertebra. These accessory articulating structures would presumably have made rotation of the vertebrae around the long axis nearly impossible, and might also have restricted lateral flection of the trunk. Except where the vertebrae have become disarticulated from one another, the trunk region appears ramrod straight in these specimens. It appears to have formed an almost rigid structure in the living animal.

In the otherwise well-articulated specimens, 3935 and 3806, the vertebrae of the posterior trunk and sacral region have become separated. This region retains nearly its normal configuration in 3454, however. The structure of the neural spines continues the pattern seen in the posterior trunk vertebrae. The transverse processes of the sacral vertebrae are expanded and formed from projections of the centra as well as the neural arches. The transverse processes are not fused to the ribs as they are in eosuchians. The 'swollen' appearance of the trunk centra is not evident in the sacral region, and the edges of the anterior and posterior articulating surfaces are conspicuously raised.

The anterior caudal vertebrae continue the pattern of the sacrals, with the centrum contributing progressively more to the transverse processes. Posterior to the third caudal, the arches no longer reach the level of the rib. There is considerable variability in the position of the last centrum to bear a transverse process. It ranges from the tenth caudal in 3438 to the 14th in 3806. The anterior neural spines of the tail resemble those more anterior in position, but the zygapophyses in the area of the eighth through the 14th vertebra are more sharply tilted, reaching perhaps 20° from the horizontal. The zygapophyses of the caiman are similarly angled in this region.

Among the anterior caudal centra that are exposed in dorsal view, the area for attachment to the arch is very narrow relative to that in the trunk region. Narrow arches in the caudal region would allow for more massive epaxial musculature to flex the tail.

The neural spines of the caudal vertebrae continue large through the 17th, and then over four segments diminish rapidly in size. Abbreviated arches, resembling the cleat on a boat to which a rope is attached, continue through the 31st caudal, and they are missing altogether on the last 11 caudals. The 42 caudals in 3460 appear to represent the entire tail. The same number is present in the type.

In 3806 and 3935, the most anterior haemal arch follows the fourth caudal vertebra. In 3407, 3438, 3456 and 3460 the first fully developed haemal arch follows the third vertebra. In 3460, fragments that may represent a rudimentary arch follow caudal two. This centrum is notched for an arch in 3711 as well. No haemal arch in which the dorsal portion is exposed shows a cross piece.

Distally, the haemal spine is flattened laterally and expanded anteroposteriorly to form a structure that is nearly comparable to the neural spines in length and breadth, and like them, is rugose distally. The size of the haemal arches diminishes markedly after that associated with the 14th caudal vertebra, but they continue posteriorly, with the last observed between the 28th and 29th caudal centra.

The great extent of the neural and haemal spines from the fifth through the 15th segment would form a significant swimming surface.

Ribs are associated with all presacral vertebrae. In 2810, 3439 and 3460 small ribs lie adjacent to the atlas and axis. The two heads are linked by a short arch which forms the passage for the vertebral artery. From this, short horizontal processes extend both anteriorly and posteriorly just lateral to the centrum. The ribs of the next eight cervical vertebrae are of similar configuration and extent, with the tuberculum attached to the arch and the capitulum to the parapophyses of the centrum. At the base of the neck, the shaft of the rib increases in length and extends more laterally. Ribs 15 and 16 angle ventrally as well. All are sharply pointed. The ribs on the 17th vertebra are intermediate in character between those of the neck and trunk with a relatively short shaft and still a trace of a double head, but more posteriorly the ribs are much longer, oriented in a mainly transverse plane and are strictly single-headed.

Among the anterior trunk ribs, especially well exposed in 3806, the dorsal surface of the shaft in the area of maximum curvature is relatively flat anteroposteriorly, and overhangs the posterior surface. Most of the trunk ribs end flatly, but the three or four anterior to the last presacral are bluntly pointed.

The length of the trunk ribs gradually increases from the 18th to reach a maximum at about the 26th, and then decreases gradually through the 35th or 36th. The rib associated with the last trunk vertebra is much shorter, flattened at the end and angled toward the ilium. In isolation, it appears like an additional sacral rib, but it cannot have reached the ilium (figure 18).

Only three pairs of ribs can be unequivocally termed sacrals. The first has a relatively narrow shaft, but the distal end is expanded vertically to provide more extensive attachment to the ilium and the distal end of the second sacral rib. It does not have a very large area of attachment however, and would have provided much less support than the next two. The second and third sacral ribs are presumably homologous with the two pairs in eosuchians and other primitive diapsids. They have thick shafts, and the ends are broad. They are not expanded to form a plate-like structure however, as are the articulating surfaces in eosuchians and crocodiles. Even though the ends of these ribs are not greatly expanded, they more than occupy the restricted medial surface of the ilium.

There are from 10 to 14 pairs of caudal ribs. The first two are nearly as stout as the sacrals, with extensive surfaces for attachment for the vertebrae. They are angled anteriorly and at least the first pair might have reached the ilium if that bone had the broad dorsal expansion common to most early reptiles. As it is, they can have had no direct role in supporting the girdle. The length of the ribs diminishes rapidly posterior to the fifth caudal, and the last few are but tiny nubbins of bone. Unlike the eosuchians, lepidosaurs and archosaurs, the caudal ribs are not fused to the centra. The extensive and complex articulating surfaces suggest that they were tightly attached during life, however.

In contrast to the ribs of the more common nothosaur at Monte San Giorgio, those of *Pachypleurosaurus* show little pachyostosis.

Appendicular skeleton

The pectoral girdle (figure 16) is one of the most striking features of nothosaurs. *Pachypleurosaurus* follows the pattern that is typical of the group. The scapula and coracoid are separately ossified. The cleithrum is lost, and the clavicles and interclavicle form a solid bar of bone anteriorly and ventrally, behind which there is a large opening between the medial surfaces of the scapulae and coracoids. The function of this large opening eludes analysis.

Another curious feature is the relation between the dermal and endochondral bones. In all primitive tetrapods, the blade of the clavicle is a superficial element (reflecting its dermal origin) that underlies the anterior ventral portion of the scapula. In nothosaurs, the relation is reversed, with the anterior ventral margin of the scapula broadly underlying the posterior portion of the clavicular blade. The same peculiar relation also occurs in plesiosaurs. The relation of the clavicle and interclavicle is also reversed. Primitively, the edges of the clavicular blades lie superficial to the anterior margin of the interclavicle. In *Pachypleurosaurus* and other nothosaurs the interclavicle is much smaller and lies essentially ventral to the clavicular blades. This relation is particularly evident in the immature specimen 3447 (figure 16*b*).

The peculiar relation of the clavicles and scapula among the sauropterygians must indicate a significant change in developmental processes. At least, it is very difficult to envisage how normal dermal ossification of the posterior margin of the clavicle could occur when this bone lies internal to the anterior margin of the scapula. It seems more likely that the clavicle is formed, at least partly, in the manner of endochondral bone. This may also explain its strictly medial position relative to the interclavicle.

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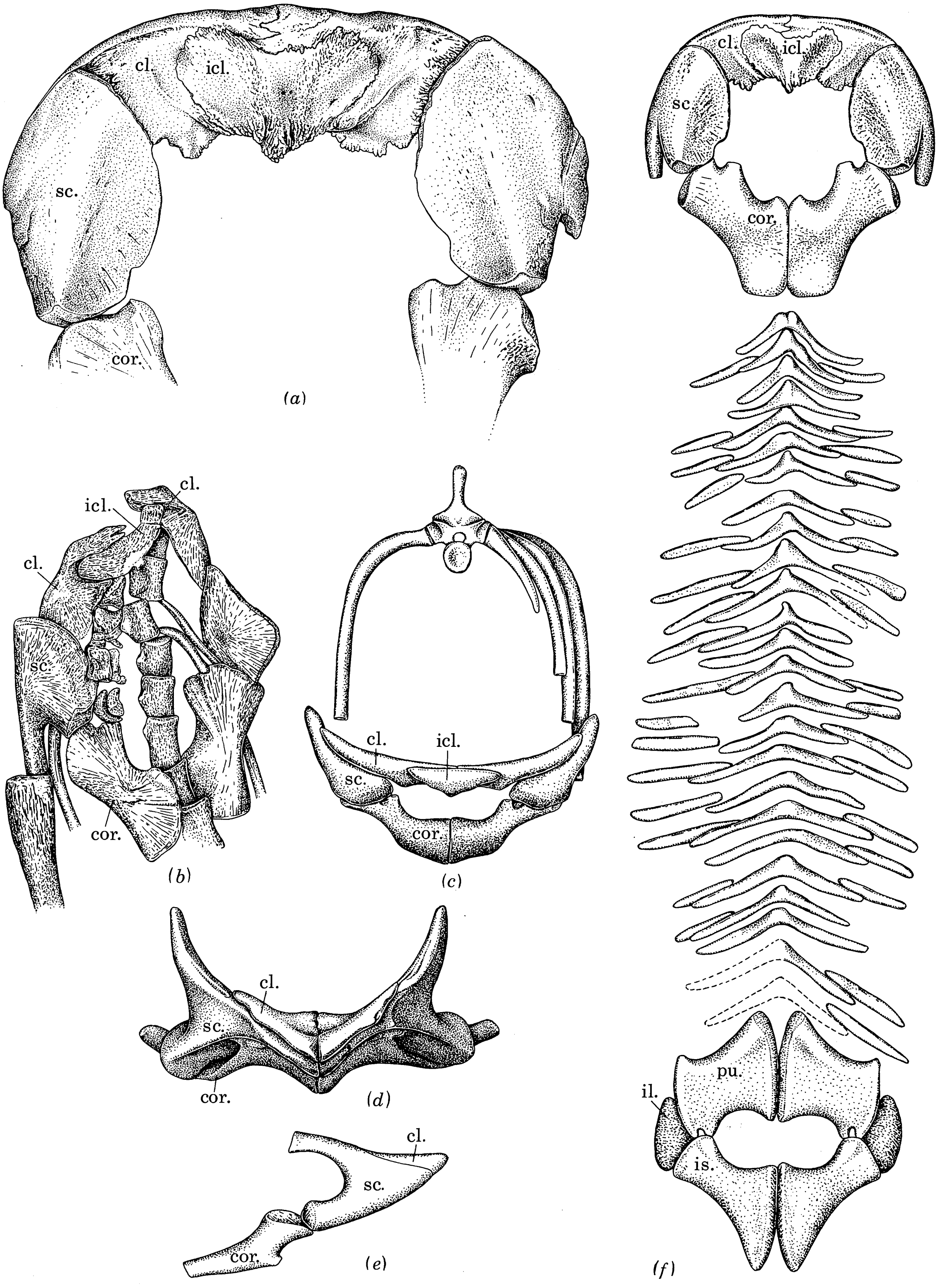

FIGURE 16. Shoulder girdle of *Pachypleurosaurus edwardsi*. (*a*) Ventral view from **3935** (natural size). (*b*) Ventral view from immature specimen **3447** (magn. ×2). (*c*) Reconstruction of shoulder girdle in anterior view with associated vertebrae and ribs. (*d*) Reconstruction of the shoulder girdle of the plesiosaur *Cryptocleidus oxoniensis* in anterior view (from Andrews 1910). (*e*) Reconstruction of shoulder girdle of *Pachypleurosaurus edwardsi* in lateral view. (*f*) Ventral view of pectoral and pelvic girdles with gastralia. Pectoral girdle based on **3935**, gastralia from **3460** (only minimally restored), pelvic girdle from **3459**. Scale of gastralia and pelvic girdle enlarged to match that of the pectoral girdle (approximately half natural size).

It is difficult to restore the original three-dimensional configuration of the shoulder girdle in *Pachypleurosaurus* or its position relative to the trunk. There is no fixed relation to the axial skeleton longitudinally or vertically. As preserved, the anterior margin of the clavicle typically lies behind the 15th or 16th cervical centrum. The anterior, dermal margin of the shoulder girdle appears almost horizontal in anterior view. To fit appropriately with the scapulae, the coracoids would have had to be angled ventrally at the midline, about 12° from the horizontal. The orientation of the girdle as viewed laterally has been restored to follow the probable outline of the body as it thins from the trunk to the narrowing base of the neck.

In the larger specimens of *Pachypleurosaurus* the girdle is preserved almost strictly in dorsal and ventral view. The anterior elements maintain their natural associations, but the coracoids are always somewhat displaced. The clavicles and interclavicle are solidly attached to one another, and the scapulae closely integrated with the clavicles. The left and right coracoids are only weakly attached to the scapulae, and although they abut against one another via a relatively long midline suture posteriorly, they are usually disarticulated. The clavicle has a short stem and a broad ventral plate. Except in the immature specimen 3456, the stem is so closely integrated with the anterior margin of the scapular blade that the division between the bones is very difficult to establish. In smaller specimens, the stem is short, narrow and pointed distally. The blades of the clavicles are broad, thick and strongly attached to one another via a midline suture. The ventral surface is generally flat. A rugose line near the anterior margin may mark the limit of origin of the clavicular deltoid laterally, and an extensive pectoralis medially. This line extends posteriorly and medially over the surface of the interclavicle to approach the midline.

The interclavicle is a thin plate of bone, superficial to the ventral surface of the clavicle. It has a very short stem, barely extending beyond the margin of the clavicles, which is extremely rugose ventrally and posteriorly, possibly for attachment of a ligament comparable to the acromiocoracoid ligament in turtles (Walker 1973) which extends along the midline to the coracoid symphysis.

The scapula and coracoid develop as distinct areas of ossification. Compared with primitive captorhinomorph reptiles (Holmes 1977, figure 4), the scapula incorporates most of the area occupied by the anterior coracoid. The coracoid of nothosaurs and the posterior coracoid in captorhinids lie posterior to the anterior surface of the glenoid. In immature eosuchians in contrast, the single coracoid lies more anterior in position, and surrounds the coracoid foramen (Currie 1981*b*; Currie & Carroll 1984).

The scapula is broadly curved with the large ventral portion essentially horizontal in orientation while the narrow blade extends in a parasagittal plane. Compared with primitive reptiles, the blade is very short and narrow. Rather than extending mainly vertically, it angles posteriorly at about a 45° angle. The exact angle is difficult to establish since no specimens are exposed in strictly lateral view. The blade resembles that of plesiosaurs in having the base narrow and well anterior to the glenoid. The blade is rounded at the base and laterally compressed dorsally. There would be little area for attachment for muscles such as the serratus, cucullaris and levator scapulae that support the shoulder girdle on the trunk in terrestrial vertebrates, reflecting the aquatic nature of this animal whose mass would have been supported primarily by the buoyancy of the water. There is no evidence for the presence of a suprascapular cartilage, an important element in most primitive reptiles.

A variably sharp demarcation is evident ventrally between the smooth area of curvature extending downward from the base of the blade and the shallowly concave ventral surface of the scapula. This may mark the geneal line of division between the laterally originating scapulohumeralis and scapular deltoid muscles and the ventral supracoracoideus. The ventral surface of the scapula thins medially, but the margin remains well demarcated. Posteriorly, it curves laterally where it borders the coracoid foramen.

The posteroventral margin of the scapula forms the thickened anterior surface of the glenoid. Medially, the bone thins progressively and angles anteromedially where it forms a smooth contact with the coracoid. The surface of the bone lateral to the glenoid is roughened, and may mark the area of attachment of the joint capsule or the origin of short fibres of the subcoracoscapularis.

The coracoids, as in all other nothosaurs, are widely separated anteriorly. They make contact with the scapulae along a short border between the surface of the glenoid and the lateral margin of the coracoid foramen. The two bones form the lateral margin of this foramen as in plesiosaurs, but the medial border which would be formed by the scapula is not ossified. Each coracoid extends a well-developed process medial to the coracoid foramen toward the extensive unossified area between the scapulae.

The anterolateral border of the coracoid forms the posterior surface of the glenoid. It is thickened to about one-half the width of the corresponding portion of the scapula. The surface of unfinished bone is essentially flat and faces anterolaterally. The bone angles posteromedially, thins and is flat ventrally. As it approaches the midline it expands and thickens to form a long symphysial contact.

The glenoid surface is made up approximately equally by the scapula and coracoid. Considerable cartilage must have been present in the living animals to define the surface of articulation since the bones in the fossil meet at nearly right angles. As ossified, the glenoid surface of the scapula faces primarily posteriorly, and that of the coracoid, slightly anterior of lateral. Both face slightly ventrally rather than straight laterally, suggesting a primarily ventral to horizontal excursion of the humerus, with little movement above the horizontal. The articulating surface of the scapula extends laterally beyond that of the coracoid, which together with its posteriorly facing articulating surface suggests that the humerus was typically restricted in its anterior excursion. As preserved, all the specimens show the humerus extending posteriorly to lie close to the body wall.

Romer (1956, p. 304) has suggested that the shoulder girdle of nothosaurs was reinforced to counteract the thrust of the limb paddles. Compared with that of plesiosaurs, however, it seems particularly ill-suited for this role. The scapulae and coracoids of plesiosaurs meet solidly at the midline throughout their length and are thickened medial to the glenoid. In contrast, the central portion of the nothosaur girdle is completely unossified. This is not a primitive condition but a specialization, for the medial portion of the scapulocoracoids are much more completely ossified medially in captorhinomorphs and primitive eosuchians.

Whether or not the central area of the girdle was ossified, major ventral muscles including the pectoralis and supracoracoideus, as in lizards, turtles and crocodiles, would have originated near the midline and acted across the unossified area to move the humerus. In sea turtles in which the major swimming movements are produced by the forelimbs, the central portion of the girdle is also unossified, but the surrounding bones are solidly fused to one another in contrast to the apparently weak coraco-scapular joint in nothosaurs.

There is no trace of a sternum in nothosaurs, nor is there any room for this bone between the coracoids and the gastralia.

The description of the humerus is based mainly on a superably preserved, three-dimensional bone in 3935 (figure 17). It is relatively long and slim. The general pattern retains the features of its terrestrial forebears with the extremities expanded and twisted relative to each other at an angle of 50–60°. The bone is bowed posteriorly. The proximal end is not appreciably flattened, as it is in primitive terrestrial reptiles and *Claudiosaurus*, but broadly oval. The proximal surface provides little information regarding the limitations of its movements in the glenoid. The end is depressed at the centre and surrounded by an irregular ring of unfinished bone. It may have been covered with a hemispherical cap of cartilage, allowing some motion in all directions.

The deltopectoral crest is very poorly differentiated in comparison with terrestrial forms, but it is recognizable as a rugose area at the extremity of the posteroventral margin of the proximal portion of the shaft. Further distally is a small raised area marked by deep pits which might represent the limit of insertion of the pectoralis.

Opposite the deltopectoral crest, on the anterodorsal surface, are conspicuous rugosities which may have served for insertion of the subcoracoscapularis and scapulohumeralis, and more posteriorly the latissimus dorsi.

Distally, the bone is flattened, as in primitive terrestrial reptiles, but it differs significantly in the restriction of the articulating surface to the distal extremity of the bone, with no evidence for ventral articulation of the ulna and radius. Unlike eosuchians, there is not a closed ectepicondylar foramen, but a groove that passes over the dorsal surface of the bone, lateral to the ectepicondylar ridge, comparable to early growth stages of eosuchians (Currie & Carroll 1984). It cannot be said that the distal end of this bone is incompletely ossified, however, for the entepicondylar foramen is well proximal in position and the end of the bone is clearly defined, although the middle of the articulating surface is concave. Neither ventrally nor distally are there distinct areas specialized for articulation of the ulna and radius. Dorsally, the limit of the unfinished bone surface extends over the end of the ectepicondylar ridge, presumably marking the extension of the joint capsule around the end of the radius. Posteriorly, a similar extension may mark the limit of the capsule over the ulna.

The ulna and radius average respectively 45 and 54% the length of the humerus, the ulna averages 83% the length of the radius. The proportions of these bones do not change significantly over the size range of specimens examined.

As preserved, the radius is nearly always lateral in position so that the extensor surface of the lower limb is exposed dorsally. Except for the complete loss of the olecranon, the configuration of the ulna and radius follow the pattern in more primitive reptiles. This loss presumably allows the ulna to be extended straight out from the humerus. The radius extends distally well beyond the end of the ulna in primitive fashion. Proximally, the shaft is rounded and almost as thick as the ulna. Distally it narrows to about half the proximal diameter. In the smaller specimen 3758 a tuberosity for the biceps muscle is strongly developed at the medial surface of the proximal end of the radius.

Only three bones of the carpus are ossified: the relatively elongate ulnare and intermedium and a tiny round element nestling between the distal ends of these bones which may be the lateral centrale or possibly the fourth distal carpal. The proximal elements are much flattened, without any of the well-developed surfaces for support and integration seen in eosuchians such as *Thadeosaurus* or the putative sauropterygian ancestor *Claudiosaurus*. This degree of reduction of the carpus is a specialization relative to other nothosaurs, for both *Ceresiosaurus* and *Lariosaurus* retain most of the distal carpals as well as the radiale, intermedium and ulnare. The pisiform

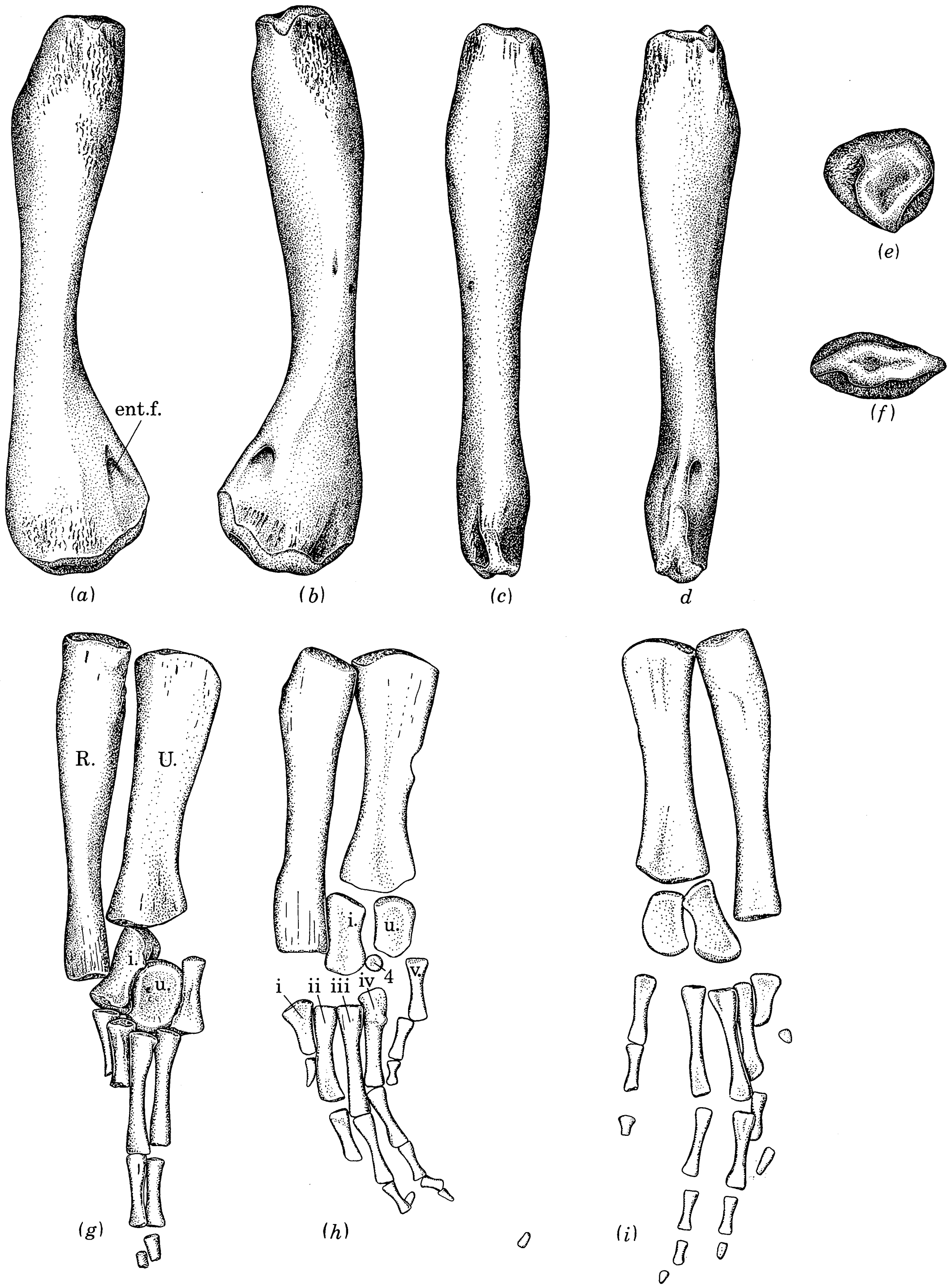

Figure 17. *Pachypleurosaurus edwardsi*, forelimb. (*a–f*) Right humerus of 3935, in dorsal, ventral, anterior, posterior, proximal and distal views. (*g*) Left lower forelimb of 3935. (*h* and *i*) Left and right lower forelimbs of 3460 (all natural size).

is apparently retained in both *Proneusticosaurus* and *Dactylosaurus*. The area of the radiale and distal carpals in *Pachypleurosaurus* is represented by a gap proximal to the metacarpals which was presumably occupied by cartilaginous elements in life.

The metacarpals and phalanges are well displayed in 3460, and the surface detail of the metacarpals is well preserved in 3806. The third, rather than the fourth metacarpal is the longest, in contrast to the condition in more primitive terrestrial reptiles. The areas of proximal and distal expansion are twisted relative to one another, a condition that, in eosuchians, is associated with overlap of the proximal ends of the bones. The bones appear so slender, especially in 3460, where they are best displayed, that little overlap is likely. The first metacarpal is much shorter than the others and the proximal end most widely expanded.

The phalangeal count is 1, 2, 3, 4 (exceptionally 5), 2. As in primitive reptiles, the length of the digits increase progressively from 1 to 4, with the fifth approximately the length of the second. The elements of the manus are very small and slender, compared with those of terrestrial eosuchians, and appear much less suitable for support or terrestrial locomotion in lacking well-developed proximal and distal articulating surfaces. The unguals are tiny flattened elements, pointed at the tip. One might argue that the digits were enclosed in a thin web of tissue, but there is no direct evidence that they did not remain distinct.

Although the structure of the carpus and manus are clearly not well adapted to life on land, neither do they show any specializations obviously associated with aquatic locomotion as discussed by Robinson (1975). Animals adapted to either paddling or subaquous flying, would be expected to show expansion of the distal elements, and a reduction of the proximal bones, just the reverse of the situation in *Pachypleurosaurus*. This genus is perhaps the most extreme of the nothosaurs in this respect, for more numerous or better ossified carpals and tarsals are common to other forms and *Ceresiosaurus* (Peyer 1932) exhibits hyperphalangy.

As in other nothosaurs, *Pachypleurosaurus* has a small ilium which is constricted dorsally, and plate-like pubis and ischium separated by a large thyroid fenestration. Three pairs of sacral ribs converge on the ilium. The area of the acetabulum is very incompletely ossified, precluding establishing the specific manner of attachment of the elements. Ventrally, the two halves of the girdle must have met at an angle of about 80° to judge by the distance between the ilia, established by the extremely well-preserved sacral region of 3459 (figure 19).

The ilium is roughly triangular in lateral view, with a truncated top. In 3806, in which the elements are disarticulated, the medial surface shows three raised areas which would have served for the attachment of the sacral ribs. Dorsally, the margin of the ilium has a medially directed ridge which would have overlapped the dorsal surface of the ends of the ribs. The relatively specific area of attachment for the sacral ribs suggests that the pelvis was rigidly connected during life rather than permitting any degree of mobility, but the small area of attachment suggests that the joint was not very strong. This notion is supported by the distribution of bones in 3459, in which both sides of the pelvis are displaced from the sacral ribs, but the three elements on both sides have remained together in more or less their natural position.

The ventral surface of the ilium is roughly oval in outline. Laterally, a great deal of cartilage must have been present in the area of the acetabulum, for the bones provide almost no direct evidence of the nature of the articulating surface. In contrast with all other nothosaurs and plesiosaurs, there is no trace of a supra-acetabular buttress. In 2466 (figure 6) the ventral margin is deeply notched laterally.

The pubis and ischium are both well displayed in medial and lateral views in 3459 (figure 19).

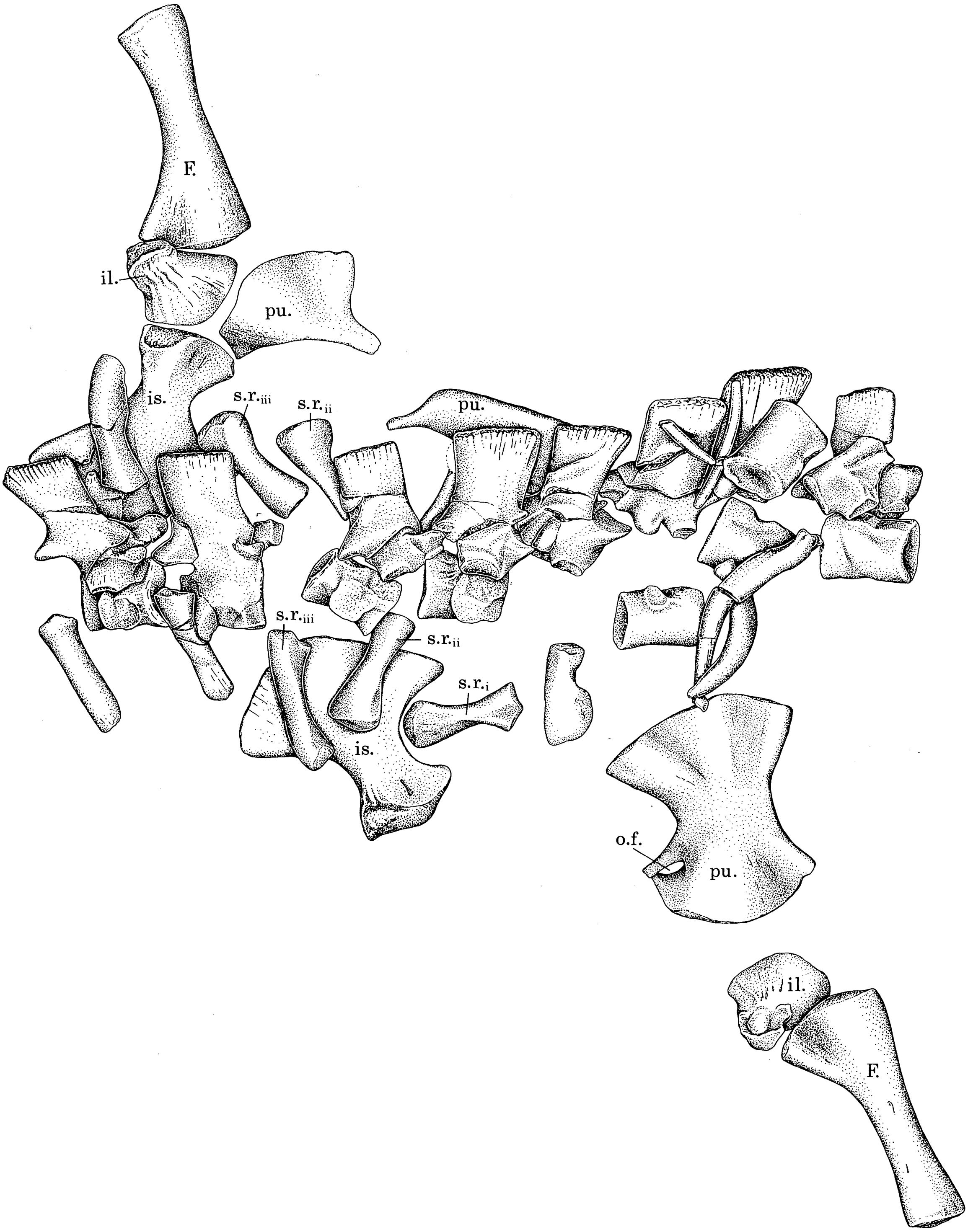

FIGURE 18. *Pachypleurosaurus edwardsi*, sacral region of 3806 (natural size).

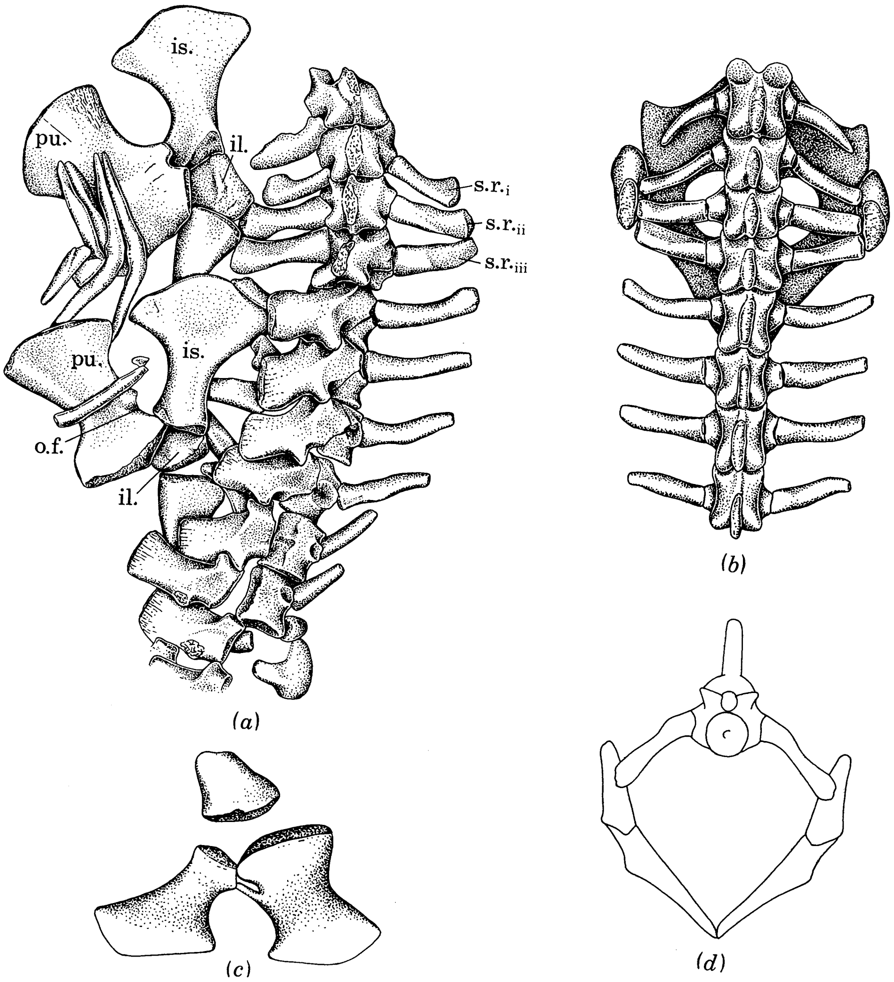

FIGURE 19. Sacral region of *Pachypleurosaurus edwardsi*. (*a*) Institute of Palaeontology, Zürich, 3459. (*b*) Restoration in dorsal view. (*c*) Restoration in lateral view. (*d*) Restoration in anterior view (all half natural size).

Both are essentially flat elements, as in primitive eosuchians, and the two sides meet at a sharp angle ventrally. The medial and lateral surfaces are almost indistinguishable, and the shape of the two bones is also broadly similar. Each has a widened and thickened area for attachment to the ilium, although that of the pubis is considerably wider; both are waisted in the middle, from which they expand to a flattened ventral plate. The thyroid fenestra is a large oval area. The pubis and ischium do not meet one another at the midline ventrally, and their proximal contact is relatively short. The obturator foramen appears as a narrow slit at the posterior margin of the pubis, just distal to the acetabulum.

The right femur of the largest specimen, 3935 has been removed from the matrix and drawn in several views (figure 20). It does not appear to have been distorted, but the extremities are strikingly compressed dorsoventrally compared with those of contemporary tetrapods. The diameter of the shaft is about 72 % as great in this direction as it is anteroposteriorly. Like the humerus, the articulating surfaces are well defined but slightly concave toward the middle. The bone is extended posteriorly from the head in the horizontal plane. A comparable structure, the trochanter major, is otherwise unique to the chelonia where it serves for insertion of the iliofemoralis (Romer 1956). There is a vaguely defined intertrochanteric fossa.

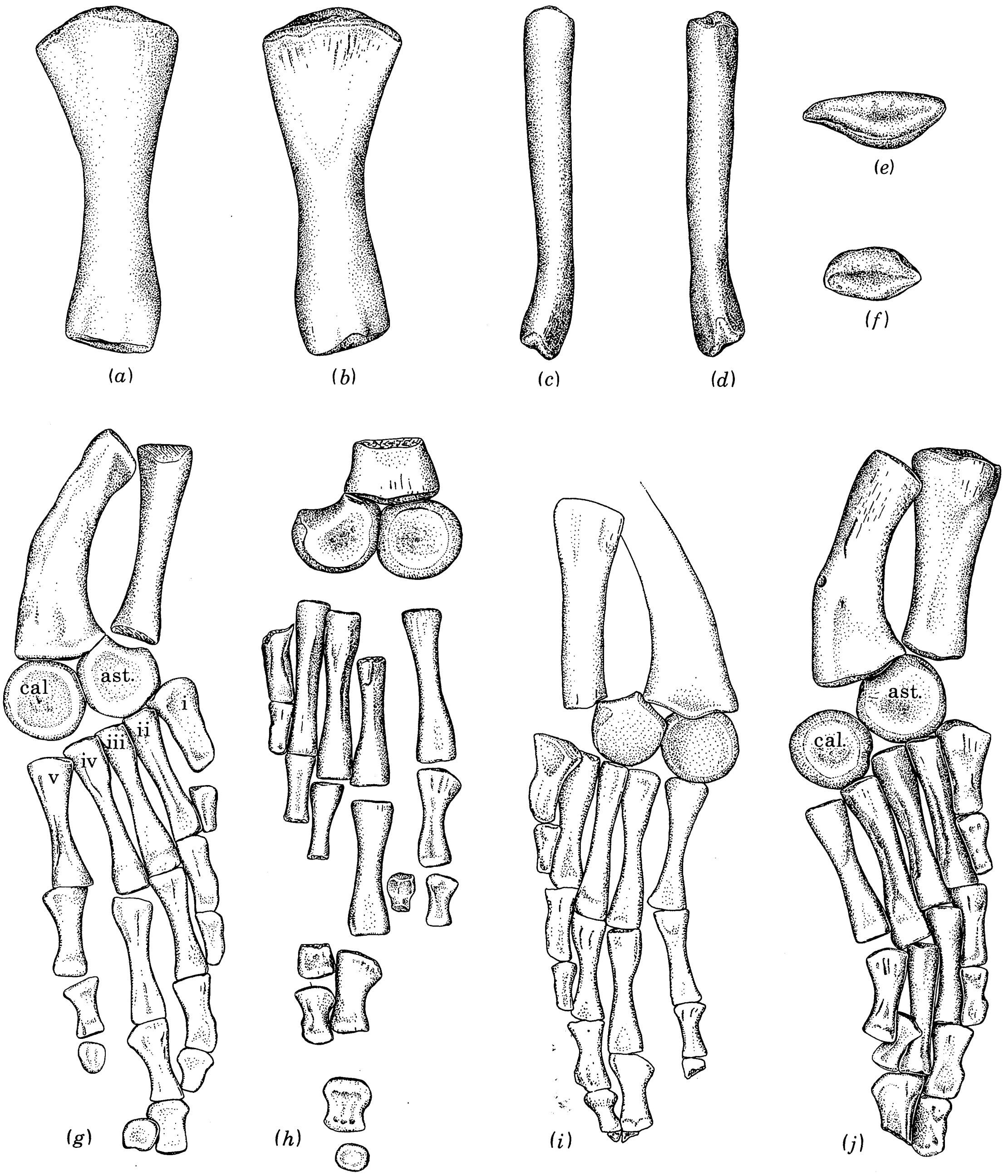

FIGURE 20. Rear limb of *Pachypleurosaurus edwardsi*. (*a–f*) Right femur of 3935 in dorsal, ventral, anterior, posterior, proximal and distal views. (*g*) Right lower limb of 3935. (*h*) Left tarsus and pes of 3935. (*i* and *j*) Left and right lower limb of 3460 (all natural size).

As is the case for the humerus, the distal articulating surface of the femur faces directly laterally, with no surface developed preferentially ventrally as would be expected if the ability to flex the lower limb were strongly developed. The distal outline is oval, with no development of distinct tibial and fibular condyles. The well-articulated specimen 3460 may retain the habitual poise of the femora, extending backward at an angle of about 45° with the lower limb and feet directed posteriorly. This is the angle favoured by the marine iguana, sea turtles and crocodiles. In these forms the rear limb is not used in propulsion but for steering (Walker 1971). Although the phalangeal count of the foot, like the hand, is reduced to 1, 2, 3 (exceptionally 4), 4 (exceptionally 5), 3, the foot as a whole is relatively broad and massive and could serve effectively as a paddle or rudder.

The tibia and fibula, best seen in 3935, are short, stocky bones resembling more those of primitive captorhinomorphs than the relatively gracile eosuchians. The distal end of the tibia is nearly as broadly expanded as the proximal. The medial edge of the shaft is continued as a narrow blade of bone. The medial edge of the shaft of the fibula is strongly concave. Distally the bone is expanded in the plane of the tarsals but is quite thin in the opposite direction. Distinct facets for articulation with the astragalus and calcaneum are evident distally.

The only bones ossified in the tarsus are the astragalus and calcaneum. The calcaneum is essentially circular, with the entire perimeter in unfinished bone. The astragalus has a crescentic indentation in the margin between the area of articulation for the tibia and fibula. There is no trace of the perforating foramen. A raised surface for articulation with the tibia is evident ventrally, but otherwise the dorsal and ventral surfaces of these bones are similarly flat.

None of the specimens show a trace of more distal tarsals. The first metatarsal is markedly shorter than the remainder and the head is expanded in an analogous manner with that of the first metacarpal. All the metatarsals are relatively broad, and the heads probably overlapped one another as in eosuchians. The fourth digit is the longest. The ungual phalanges are wide, flattened and bluntly rounded at the end. That of the fourth digit is circular.

All of the specimens show a well developed series of gastralia between the girdles ventrally. They are most clearly exposed in 3460 (figure 3). There is a minimum of 25 rows, compared with 38 in *Claudiosaurus*, and a much smaller number in plesiosaurs. The median elements are chevron-shaped. Only a single pair of more lateral elements is certain, but there may have been more, as is the case in plesiosaurs. They are much thickened from their condition in more primitive vertebrates and may have served to weight the animal down to facilitate diving.

Aquatic locomotion in sauropterygians

The primary purpose of this paper has been to establish the skeletal anatomy of the nothosaur *Pachypleurosaurus*. This information may be used as a basis for comparison with early plesiosaurs to evaluate the nature of interrelations between these two groups. Detailed osteological comparison with early plesiosaurs is not yet possible in the absence of comparable information regarding the late Triassic and earliest Jurassic members of that group. On the other hand, more general comparisons between the swimming patterns of nothosaurs and plesiosaurs are possible on the basis of patterns that are relatively uniform in both groups.

During the 140 million years of their evolution, plesiosaurs have evolved into a number of distinct lineages, characterized by differing proportions of their axial skeleton and details of skull morphology (Saint-Seine 1955). Despite significant difference in body size and proportions of the head and neck, broad similarities in the proportions of the trunk region, girdles and limbs are maintained throughout the group. Robinson (1975) has used these similarities to describe a single locomotor pattern as characteristic of the entire assemblage. Throughout the Plesiosauria, the fore and hind limbs are specialized as nearly identical paddle-shaped structures of great size. Both the pectoral and pelvic girdles are expanded ventrally in the form of extensive, horizontal plates of bone. The tail is relatively short, but the neck may be greatly elongated.

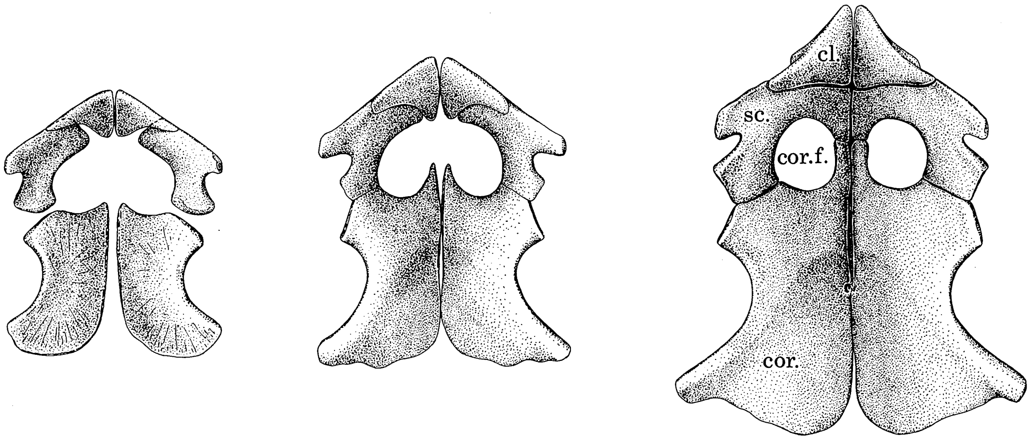

FIGURE 21. Growth stages of the pectoral girdle of *Cryptocleidus oxoniensis* from Andrews (1910).

There has long been debate as to whether the plesiosaurs rowed through the water (Watson 1924) or were subaqueous flyers (Tarlo 1958; Robinson 1975). Comparisons with the patterns of aquatic locomotion in a broad range of living vertebrates suggest that the plesiosaur mode of swimming combined the characters of rowing and flying (Godfrey 1984). Unlike modern subaqueous 'flyers' such as penguins and sea turtles, in which the major direction of limb movement is nearly vertical in its orientation, that of plesiosaurs was probably essentially horizontal. In relation to both the resistance of forces and the orientation of the major areas of muscle origin, the direction of limb movement in plesiosaurs was probably mainly antero-posterior rather than dorso-ventral. Most of the force was presumably delivered by the posterior stroke, although some dorso-ventral portion of the anterior (recovery) stroke may have provided propulsion as well. The consistency of trunk and limb proportions during their long period of evolution suggests that this particular mode of locomotion was highly successful in plesiosaurs.

A review of the nothosaurs shows an equally uniform pattern of the girdles and limbs coexisting with a considerable variety in the structure of the skull and proportions of the axial skeleton. Although the fore and hindlimbs are always modified from the pattern in terrestrial reptiles, they retain many primitive features. In most genera, the forelimb is more robust than the rear. The pubis and ischium retain a relatively primitive pattern, but the ilium is reduced dorsally, despite the presence of three to six pairs of sacral ribs. The pectoral girdle is highly specialized in the presence of a wide, median vacuity behind which the large coracoids meet in a broad symphysis. The dorsal portion of the scapula is very much reduced, and is situated well anterior to the glenoid. In marked contrast to plesiosaurs, the limbs of nothosaurs are generally small, compared with those of terrestrial genera with similar trunk proportions, and the tail is long and slender.

Although it has been argued by analogy with plesiosaurs that nothosaurs were subaqueous flyers, it is more generally thought that they paddled through the water. No detailed analysis of swimming in nothosaurs has been attempted.

The most striking feature that is apparent in the lateral restoration of *Pachypleurosaurus* is the great size of the tail (figure 4), particularly at its base, compared with the area of the limbs. However the limbs were used, they almost certainly were less effective than the tail in forward

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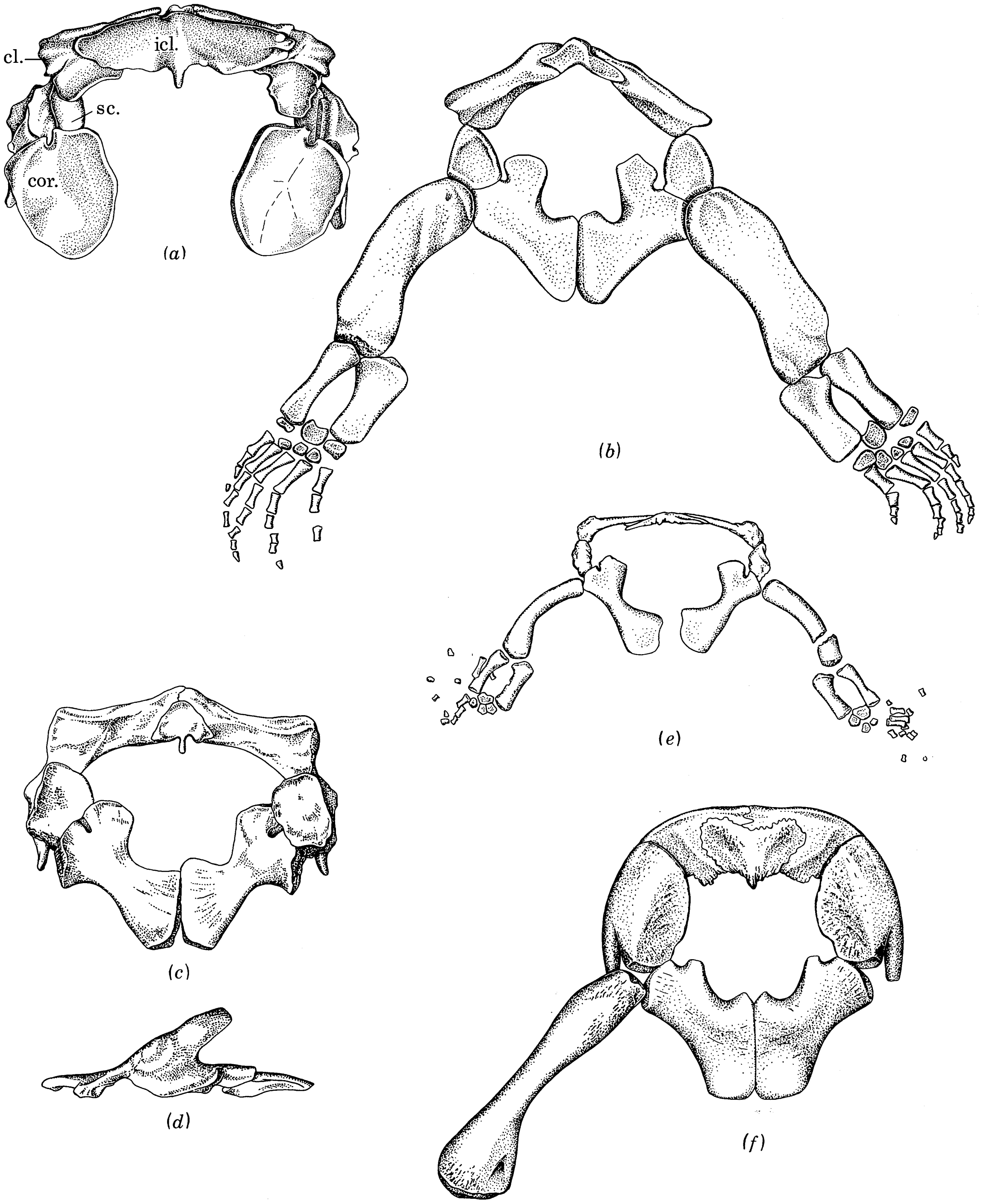

FIGURE 22. The pectoral girdle of aquatic reptiles. (*a*) The placodont *Placodus* (Romer 1956). (*b*) *Ceresiosaurus* (from Kuhn-Schnyder 1963). (*c* and *d*) *Nothosaurus* in ventral and lateral views (Romer 1956). (*e*) *Paranothosaurus* (from Peyer 1939). (*f*) *Pachypleurosaurus*.

propulsion within the water. To judge by limb and tail proportions, this was probably the case throughout the Nothosauria. If one considers the probable steps in the origin of aquatic locomotion among reptiles, this is not surprising. Studies of crocodiles (Manter 1940) and the marine iguana (Bartholomew *et al.* 1976) show that both depend mainly on the tail for aquatic propulsion. During the course of this descriptive work, experiments were performed with the green iguana which demonstrates a similar pattern. The species *Iguana iguana* commonly lives on the ground and in trees, but is capable of sustained swimming (Minton & Minton 1973). In shallow water an effort is made to reach the bottom with the forelimbs, but in deeper water they are folded back against the body and are not used at all in locomotion. Propulsion is achieved through a fish-like lateral undulation of the posterior trunk and tail. The rear limbs trail posteriorly and are occasionally thrust back in a paddling motion.

This mode of locomotion, certainly very effective in both crocodiles and the marine iguana, can be related to the basic structure and locomotor pattern of primitive tetrapods. One of the most striking features of the skeleton of Palaeozoic amphibians is the complex articulating surfaces of the forelimb and pectoral girdle. This is associated with a stereotyped pattern of movement, retained in broad features by modern salamanders and primitive lizards. It is also documented by the pattern of footprints known from the late Palaeozoic (Holmes 1977). The forelimbs are used alternatively; first one and then the other is brought forward to grip the substrate and lift the body while the muscles of the trunk provide the main propulsive thrust. This pattern of locomotion results in considerable lateral movement of the head and anterior trunk. While this appears to be a necessary feature of terrestrial locomotion in primitive vertebrates, such lateral movement would be of great disadvantage for rapid swimming. One of the major aspects of the evolution of rapidly swimming teleost fish is to reduce lateral movement of the head and trunk to a minimum (Patterson 1964). Not only is the skeletal anatomy of the early tetrapods specialized for alternative movement of the limbs, but this is apparently programmed through the neurological control of locomotor movements. If such alternating movements are inappropriate in the water, the simplest solution is to stop them altogether. The limitations imposed by both the structure and behaviour of the forelimbs in primitive tetrapods explains why they retain an essentially passive role in the swimming of crocodiles, even after millions of years of evolution in a semi-aquatic environment. In most aquatic reptiles, including marine crocodiles of the Mesozoic, mosasaurs and pleurosaurs, the forelimbs are reduced and serve for steering or perhaps as fixed hydrofoils. Plesiosaurs and sea turtles are exceptional in the elaboration of the forelimbs.

Reduction of the shoulder girdle, particularly the blade of the scapula, in most aquatic reptiles may be associated with the buoyancy of the water which would have made it unnecessary for the use of the shoulder girdle in supporting the head and trunk. In addition, the medial portion of the coracoids and clavicles are typically reduced since they are no longer necessary to resist the force of the muscles needed to lift the body on the forelimbs (Jenkins 1971).

If nothosaurs are correctly assumed to have evolved from primitive lepidosaurian reptiles such as the early eosuchians, they must have lost the sternum which is such an important element in that group. In *Claudiosaurus*, the sternum was no longer calcified, but it persisted in cartilage. Jenkins & Goslow (1983) have recently demonstrated how the sternum in lizards acts to facilitate rotation of the forelimbs in the primitive tetrapod fashion of alternative movement. The pattern would certainly have no advantage in aquatic forms, and was presumably lost at an early stage in nothosaur evolution.

By analogy with modern crocodiles, the marine iguana and the skeletal pattern of most other groups of aquatic reptiles, it may be assumed that the ancestors of nothosaurs made little, if any use of the forelimbs in aquatic locomotion. If the tail and rear portion of the trunk provided the primary force in aquatic locomotion, selection would act to reduce the size of the forelimbs to minimize drag. The pectoral girdle would be reduced as less force was required for support of the body, and as less area was required for attachment of limb muscles.

A pattern like that of the placodont *Placodus* (figure 22) may have been characteristic of an early stage in sauropterygian evolution. The interclavicle is much reduced, the clavicles form a narrow transverse rod and there is little contact between the dermal and endochondral elements.

It is more difficult to account for the relatively large size and apparently rigid outline of the dermal elements at the anterior margin of the nothosaur girdle, characteristic of most genera. This may be attributed to their use in supporting and protecting the front part of the body when the nothosaurs came out of the water to breed and bask. Particularly in *Pachypleurosaurus*, the rear limbs seem ill-suited for movement on land, and the body would have had to be dragged along by the forelimbs. In this respect, the modern otariids may provide a good analogy.

Within the early evolution of nothosaurs some factor, perhaps the use of the forelimbs for occasional terrestrial locomotion as common to modern pinnipeds, led to a re-elaboration of the limbs for aquatic locomotion, presumably based on symmetrical movements.

Although the length of the forelimbs in nothosaurs is shorter relative to the trunk than it is in plausible ancestors such as the eosuchians, it is typically larger than the rear limb, and the pectoral girdle is highly specialized in a manner divergent from that of all other aquatic reptiles with the exception of the plesiosaurs. It is difficult to escape the conclusion that nothosaurs represent an intermediate stage in the evolution of a plesiosaur style of aquatic locomotion.

The consistently high degree of elaboration of the posteriorly directed coracoids suggests that the major force of locomotion was mainly posterior. The anterior, dermal portion of the shoulder girdle is variably elaborated in nothosaurs. The pattern in *Paranothosaurus* (figure 22*e*) represents one extreme, while *Pachypleurosaurus* shows the other.

The narrow dermal elements and the low degree of development of the ventral portion of the scapula might be expected in forms that retained the primitive condition in which the forelimb was little used in locomotion. Re-elaboration of the scapula after such reduction could explain the reversal in relation between the dermal and endochondral elements. *Pachypleurosaurus* provides the best analogue of the plesiosaur pectoral girdle among nothosaurs. There is still an extensive medial opening and the dermal elements are much larger than those of any of the post-Triassic plesiosaurs. This difference is somewhat less remarkable if we look at the changes during growth in the plesiosaur *Cryptocleidus* (figure 21). In the earliest growth stage illustrated by Andrews, the scapulae are limited to marginal elements which do not meet at the midline, and behind which there are large vacuities. In later stages, the scapulae grow medially and posteriorly to meet at the midline and to make contact with the coracoids, enclosing the coracoid foramen. One can almost see the plesiosaur condition evolving from that of the nothosaurs during ontogeny. This does not of course prove that such a change did occur phylogenetically, but it does increase the probability that a pattern like that of the known nothosaurs was antecedent to that of the plesiosaurs.

RELATIONS

Nothosaurs are known mainly from the Middle Triassic, a period of time that may be shorter than the longevity of many of the included genera. All nothosaurs show a similar complex of characters of the skull and girdles which are advanced over the condition in primitive eosuchian reptiles, indicating a single common ancestry. Other features, including the configuration of the temporal region and details of the pectoral girdle and limbs may be used to recognize subgroups within the Nothosauria (Sanz 1984).

The closest affinities of *Pachypleurosaurus* certainly lie with the genera *Neusticosaurus*, *Anarosaurus* and *Dactylosaurus*. Many similarities of the skull in this assemblage are mainly of a primitive nature, judged by comparison with other diapsid reptiles, although the small size of the upper temporal opening is a derived character, not described in other adequately studied nothosaurs. The reduction in the number of carpals and tarsals, compared with most other nothosaurs, is another specialized feature that may be used to support the monophyletic nature of this assemblage.

The generally primitive nature of the skull and the small body size suggest that pachypleurosaurids represent an early stage in the evolution of aquatic adaptation among the nothosaurs, broadly intermediate between the pattern of aquatic eosuchians and *Claudiosaurus* and the larger nothosaurs such as *Nothosaurus*, *Ceresiosaurus*, *Simosaurus* and *Paranothosaurus*. In other respects, however, the smaller sized genera appear to have specialized in a different direction. *Pachypleurosaurus* in particular is divergent in the reduction of the number of phalanges, the considerably smaller size of the rear limb and the degree of elaboration of the tail as a swimming organ, as well as the reduced number of carpals and tarsals. On the other hand, the shoulder girdle of *Pachypleurosaurus* appears the most plesiosaur-like of any nothosaur in the elaboration of the anterior portion and especially the ventral extension of the scapula. This feature suggests that the forelimb had a more active role in swimming than that of other nothosaurs, with the development of a strong recovery stroke.

The genera *Nothosaurus*, *Ceresiosaurus*, *Lariosaurus*, *Simosaurus* and *Paranothosaurus* appear more similar to plesiosaurs in their greater body size and the configuration of the skull, especially the greater elaboration of the postorbital region with the upper temporal opening far larger than the orbit. The shoulder girdle and limb structure retain the same basic pattern as the pachypleurosaurids, however. *Ceresiosaurus* is exceptional in the presence of extra phalanges, but the limb proportions remain conservative.

The structure of the palate in all nothosaurs seems to preclude their being directly ancestral to plesiosaurs. The only Triassic sauropterygian that might have that role is *Pistosaurus*. The skull resembles that of plesiosaurs in the retention of interpterygoid and suborbital vacuities, but the postcranial skeleton attributed to this taxon is typically nothosaurian (von Huene 1948).

No articulated skeletons of nothosaurs or plesiosaurs have been described from the late Triassic. Considerable disarticulated material from the Muschelkalk and the Rhaetic has been recognized as possibly belonging to plesiosaurs but it is difficult to establish its identity without evidence of limb proportions and detailed structure of the girdles.

Among the early plesiosaurs of the Liassic, elements of the axial skeleton, pectoral girdle and limbs show an intermediate pattern between those of nothosaurs and more advanced plesiosaurs. The trunk vertebrae of most nothosaurs have wide neural arches, extending well beyond the margin of the centra and relatively short transverse processes. In advanced plesiosaurs the arches are narrow, and the transverse processes greatly elongated. *Pistosaurus* shows an intermediate condition in which the zygapophyses extend to about the same distance laterally as the ends of the centra. There is a general decrease in the relative extent of the arches and an increase in the length of the transverse processes from *Claudiosaurus* through typical nothosaurs, *Pistosaurus* and primitive plesiosaurs (figure 23).

The structure of the shoulder girdle is of particular importance in linking nothosaurs and plesiosaurs. In dorsal or ventral views the girdle appears very distinct in the two groups, with the scapula and coracoid forming a nearly continuous plate in most plesiosaurs, while both bones are much less expanded ventrally in nothosaurs, leaving a large median vacuity. In lateral view,

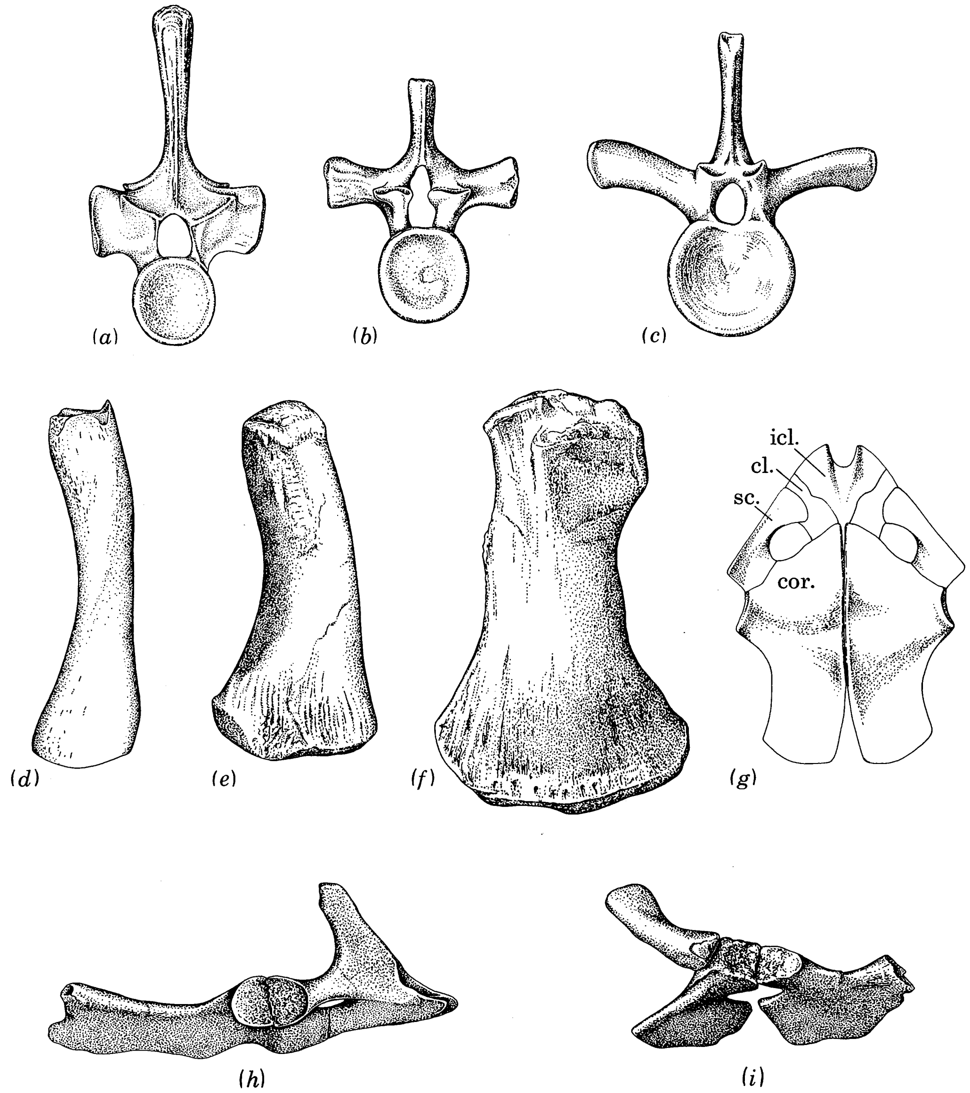

FIGURE 23. Comparable elements of nothosaurs and plesiosaurs. (*a*) Anterior view of trunk vertebra of *Nothosaurus* (from von Meyer 1855, plate 24). (*b*) *Pistosaurus* (from von Meyer 1855, plate 26). (*c*) *Cryptocleidus* (from Andrews 1910, figure 82). (*d*) Humerus of *Pistosaurus* (British Museum, R. 2011). (*c*) Humerus of *Plesiosaurus hawkinsii* (from Hawkins 1840, plate 24). (*f*) Humerus of *Muraenosaurus platyclis* (from Andrews 1910, figure 69). (*g*) Dorsal view of the shoulder girdle of *Plesiosaurus* ? *rostratus* showing the limited extent of the scapulae in primitive plesiosaurs (from Andrews 1910, figure 61). (*h* and *i*) Lateral views of the pectoral and pelvic girdles of *Cryptocleidus oxoniensis* (from Andrews 1910, plate X).

in contrast (figures 16*e* and 23), it can be seen that the basic proportions are similar. In both groups the girdle is expanded mainly in the horizontal plane. The scapular blade is narrow and well anterior to the glenoid. The glenoid is near the middle of the length of the girdle and faces mainly laterally. The horizontal, rather than vertical elaboration of the shoulder girdle in both groups suggests that the distribution of the major swimming muscles was mainly anterior and posterior to the glenoid, with no evidence of specialized areas of origin for muscles above and below the glenoid. In both groups this suggests a type of paddling motion like that of modern otariids, in contrast to the pattern of subaqueous flying frequently suggested by analogy with penguins and sea turtles, in which the configuration of the girdles is much different. The major change in plesiosaurs is the elaboration of the coracoids to fill in much of the central opening. In some primitive plesiosaurs (figure 23) the scapula still has relatively little ventral exposure and the sides do not meet at the midline but are separated by a broad extent of the clavicle and interclavicle as in nothosaurs.

In advanced plesiosaurs the most striking feature of the pelvis is the posterior position of the ilium which is attached only to the ischium at the posterior limit of the acetabulum. There is no approach to this condition in any nothosaurs or *Pistosaurus* (von Huene 1948) (figure 24). As in the shoulder girdle, the ventral elements of the pelvic girdle are greatly expanded in the horizontal plane. The similarity of configuration of the pelvic and pectoral girdles in plesiosaurs implies a similar function in aquatic locomotion. In nothosaurs, by contrast, the pectoral and pelvic girdle remain very distinct, as do the limbs, suggesting important differences in their function. Despite the difference in the anatomy of the ilium, the configuration of the pubis and ischium are not fundamentally different in nothosaurs and plesiosaurs. The most notable change is in the angle at which they meet at the symphysis, which is much broader in plesiosaurs. This suggests much less mechanical efficiency for ventral muscles that would depress the limbs. This implies that the motion of the pelvic limb, like the pectoral, was mainly antero-posterior not dorso-ventral as would be implied by the notion of subaqueous flying.

The humeri and femora of plesiosaurs have a very similar paddle-shaped configuration. In

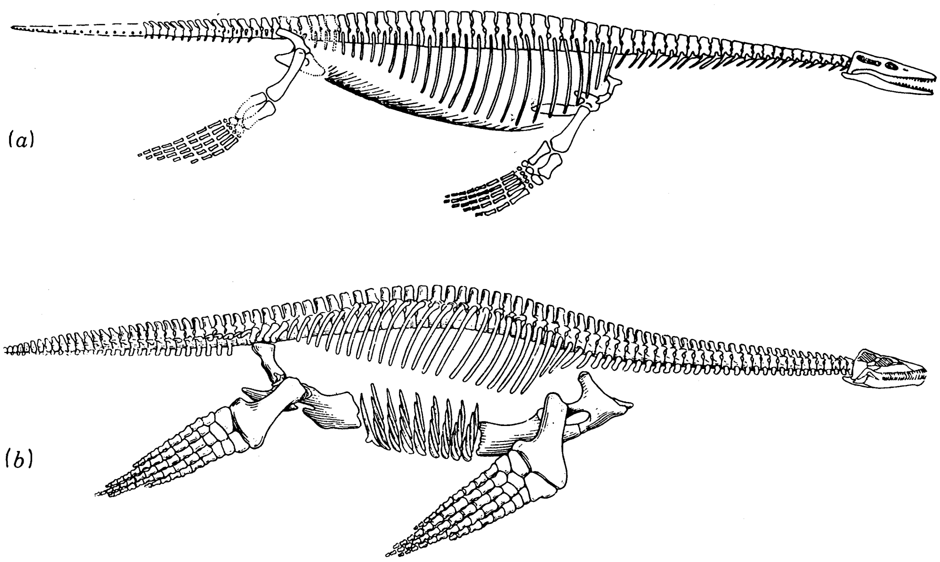

FIGURE 24. (*a*) *Pistosaurus*, Middle Triassic (from von Huene 1948). (*b*) *Cryptocleidus oxoniensis*, a Middle Jurassic plesiosaur (from Saint-Seine 1955).

later genera they are nearly symmetrical both dorsal and ventral to the long axis, and also anteriorly and posteriorly. In nothosaurs they resemble their terrestrial counterparts to a much greater degree. The humerus retains an entepicondylar foramen and is curved posteriorly, although both proximal and distal articulating surfaces are much modified.

The humerus of *Pistosaurus* approaches the pattern of plesiosaurs in the loss of the entepicondylar foramen and the reduction of posterior curvature. Early Liassic plesiosaurs show a configuration that is intermediate between that of *Pistosaurus* and the later plesiosaurs (figure 23). A similar sequence of changes can be seen in the distal limb elements. In *Plesiosaurus hawkinsi* (Hawkins 1840), for example, the ulna and radius and tibia and fibula still retain the character of their terrestrial antecedents while those of later plesiosaurs are almost indistinguishable from the carpals and tarsals. The carpals and tarsals in early plesiosaurs also retain some of the characteristics seen in nothosaurs, with the radial and tibial side still incompletely ossified.

Although there appears to be a gradual change in the character of the vertebrae and isolated bones of the girdles and limbs between nothosaurs and advanced plesiosaurs, the major body proportions of the two groups are clearly distinct (table 4 and figures 2, 24 and 25). In these features *Pistosaurus* is typically nothosaurian and the earliest described Liassic genera are similar to later plesiosaurs. By using the distance between the glenoid and the acetabulum as a standard, the total length of the limbs is substantially longer in plesiosaurs, as is the relative length of the pectoral and pelvic girdles.

TABLE 4. PROPORTIONS OF NOTHOSAURS AND PLESIOSAURS

	G–A	P+P	$\frac{\text{P+P}}{\text{G–A}}$	H	$\frac{\text{H}}{\text{G–A}}$	DF	$\frac{\text{DF}}{\text{H}}$	$\frac{\text{TF}}{\text{G–A}}$	F	$\frac{\text{F}}{\text{G–A}}$	DH	$\frac{\text{DH}}{\text{F}}$	$\frac{\text{TH}}{\text{A–G}}$
nothosaurs													
Paranothosaurus	101	65	64%	26	26%	—	—	—	26	26%	36	139%	61%
Pistosaurus	96	43	45%	18	19%	38*	210%	58%	20	21%	42*	210%	62%
Neusticosaurus	7	3.8	54%	1.7	24%	2	118%	53%	1.6	23%	2.4	150%	57%
Pachypleurosaurus	32	17	53%	9	28%	10	111%	59%	5	16%	11	220%	50%
Ceresiosaurus	53	38	72%	18	34%	20	111%	72%	13	24%	23	177%	68%
Dactylosaurus	7.1	4.6	64%	2.1	30%	2.4	114%	63%	—	—	2.9	—	—
Nothosaurus	25	16	64%	6.2	25%	9.4	152%	62%	7.2	29%	10.4	144%	70%
plesiosaurs													
Plesiosaurus hawkinsii	36	40	111%	14	39%	27	192%	120%	14	39%	29	207%	122%
Muraenosaurus	154	162	105%	37	24%	70	187%	69%	30	19%	62	204%	60%
Peloneustes	92	120	130%	43	47%	60	138%	112%	53	58%	67	128%	130%
Cryptocleidus	96	96	100%	34	35%	62	182%	100%	32	33%	56	227%	92%
Thaumatosaurus	107	115	107%	59	55%	89	162%	134%	48	45%	85	177%	121%
Liopleuron	285	331	116%	87	31%	149	171%	83%	96	34%	161	168%	90%

G–A, Distance from glenoid to acetabulum; P+P, length of pectoral plus pelvic girdle; H, length of humerus; DF, length of forelimbs distal to humerus; TF, total length of forelimbs; F, length of femur; DH, length of hind limb distal to femur; TH, total length of hind limb. Measurements in centimetres.

The expansion of the girdles implies a marked increase in swimming force in plesiosaurs. In addition, the similarity of the pectoral and pelvic girdles and limbs implies a similarity of function not evident in nothosaurs. It appears that the pelvic limb has taken on an active swimming role, not apparent in nothosaurs. The pectoral girdle, in contrast, has not changed

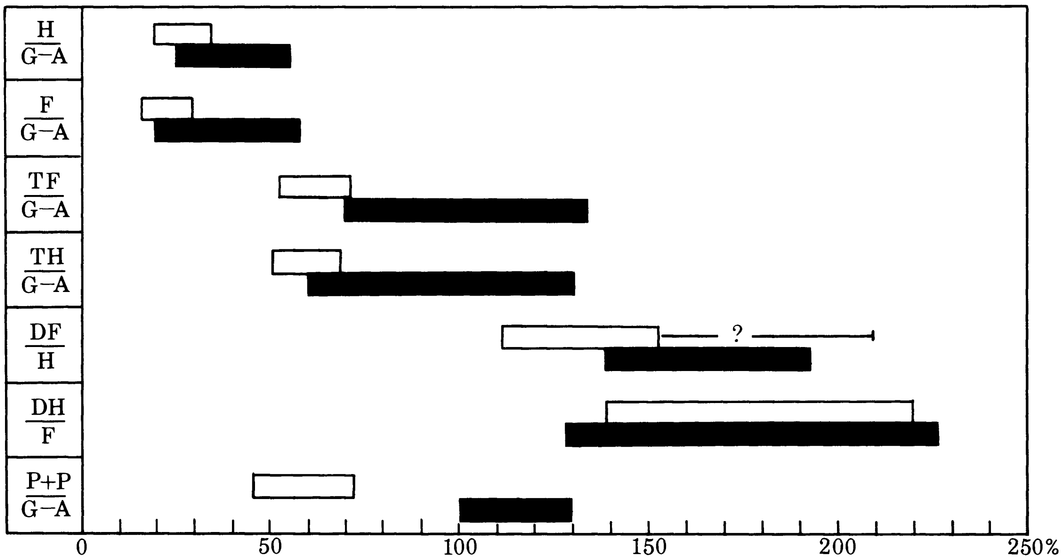

FIGURE 25. Graphic representation of proportions of nothosaurs and plesiosaurs. Open bars, range of proportions observed in nothosaurs; solid bars, range of proportions observed in plesiosaurs; ?, possible range extension based on questionable restoration of *Pistosaurus*. Data and abbreviations from table 4.

as significantly, suggesting an intensification rather than a change in function from the nothosaur pattern.

Another significant proportional change is the marked reduction in the distance between the girdles in plesiosaurs. Together with the presence of very massive gastralia this would have significantly reduced the amount of lateral flexure possible within the trunk region. Sinuous movement of the trunk was almost certainly an important feature of locomotion in ancestral sauropterygians and probably continued to be so throughout the Nothosauria. If we are correct in assuming that limb movements in plesiosaurs were mainly in a horizontal plane, it is very difficult to imagine an effective use of the very long forelimbs together with sinuous movement of the trunk. The arc of both the fore- and hindlimb would have been severely restricted if this were the case. Even if there had been a large vertical component to limb movement, as would be associated with subaqueous 'flying', it would be much more efficient if coupled with a rigid trunk as in the case of both penguins and sea turtles. A significant reduction in the degree of lateral mobility of the trunk region would appear to be a requisite for the development of the plesiosaur pattern of locomotion.

In the absence of any fossils that show body proportions intermediate between the patterns of nothosaurs and plesiosaurs, it is difficult to evaluate the manner of transition between these two groups, if they actually represent an ancestor–descendant sequence.

The nature of the disarticulated sauropterygian remains from the late Triassic is suggestive of a transition between the two groups, but only more complete knowledge of fossils from the late Triassic and early Jurassic will allow us to establish the specific nature of the relations between nothosaurs and plesiosaurs.

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KEY TO ABBREVIATIONS USED IN FIGURES

a.	angular	ect.	ectopterygoid
a.a.	atlas arch	ent.f.	entepicondylar foramen
a.c.	atlas centrum	e.o.	exoccipital
a.i.c.	atlas intercentrum	ept.	epipterygoid
a.r.	atlas rib	F.	femur
art.	articular	Fi.	fibula
ast.	astragalus	f.	frontal
ax.a.	axis arch	i.	intermedium
ax.c.	axis centrum	icl.	interclavicle
ax.r.	axis rib	il.	ilium
bo.	basioccipital	is.	ischium
bs.	basisphenoid	j.	jugal
cal.	calcaneum	l.	lacrimal
cb.1	first ceratobranchial	m.	maxilla
cl.	clavicle	n.	nasal
cor.	coracoid	o.f.	obturator foramen
cor.f.	coracoid foramen	opis.	opisthotic
d.	dentary	p.	parietal

pal.	palatine
p.f.	postfrontal
p.m.	premaxilla
p.o.	postorbital
p.r.f.	prefrontal
pt.	pterygoid
pu.	pubis
q.	quadrate
q.j.	quadratojugal
R.	radius
sa.	surangular
s.a.b.	supra acetabular buttress
sc.	scapula
s.o.	supraoccipital
sp.	splenial
sph.	sphenethmoid
sq.	squamosal
$s.r._{i-iii}$	sacral ribs i to iii
U.	ulna
u.	ulnare
v.	vomer
4	fourth distal carpal
i–v	metacarpals and metatarsals

FIGURE 1. Pachypleurosaurids (a) Type of *Pachypleurosaurus edwardsi* (Cornalia) Museo Civico di Storia Naturale, Milano (natural size). Primarily dorsal view; because of the great length of the neural spines the proximal caudal vertebrae are displayed in lateral view. (b) Dorsal view of *Neusticosaurus* sp., specimen 3804 in the collection of the Institute of Palaeontology, Zürich. Neural spines are short throughout the column (natural size). (c) Ventral view of *Neusticosaurus* sp., specimen 1057, Museum of Comparative Zoology, Harvard (natural size).

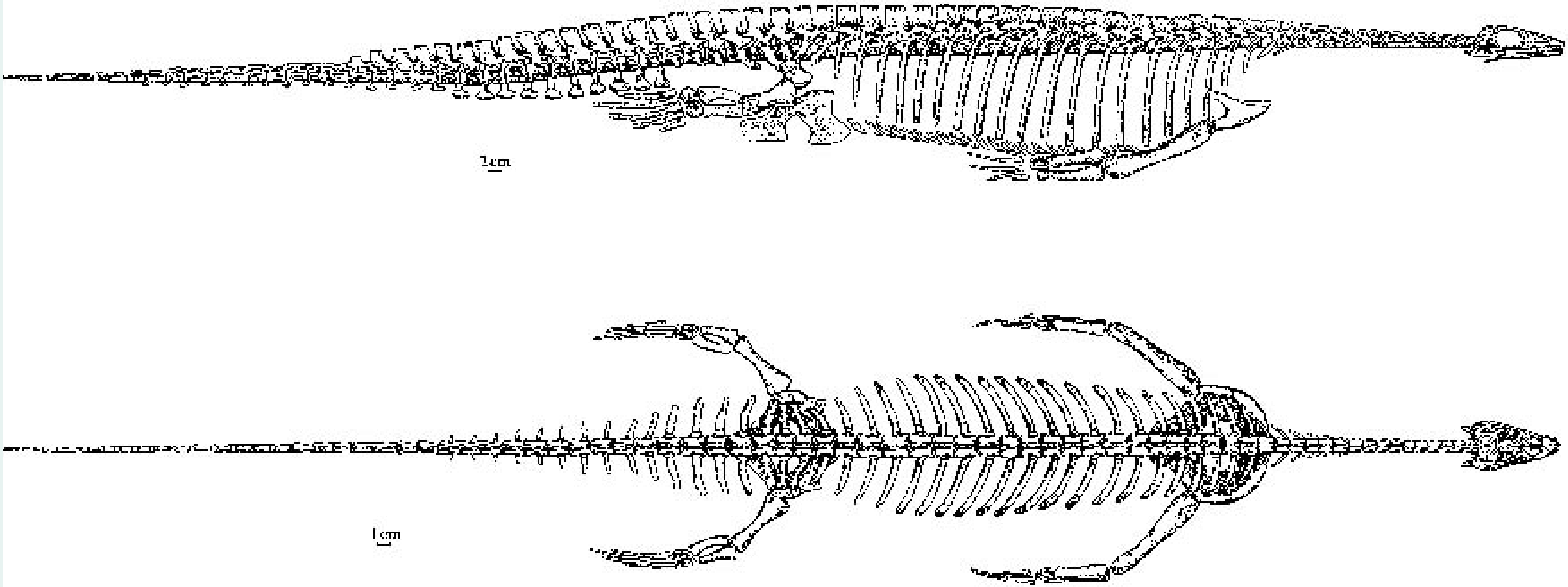

FIGURE 4. *Pachypleurosaurus edwardsi*. Restorations of skeleton in lateral and dorsal views, based on adult proportions.

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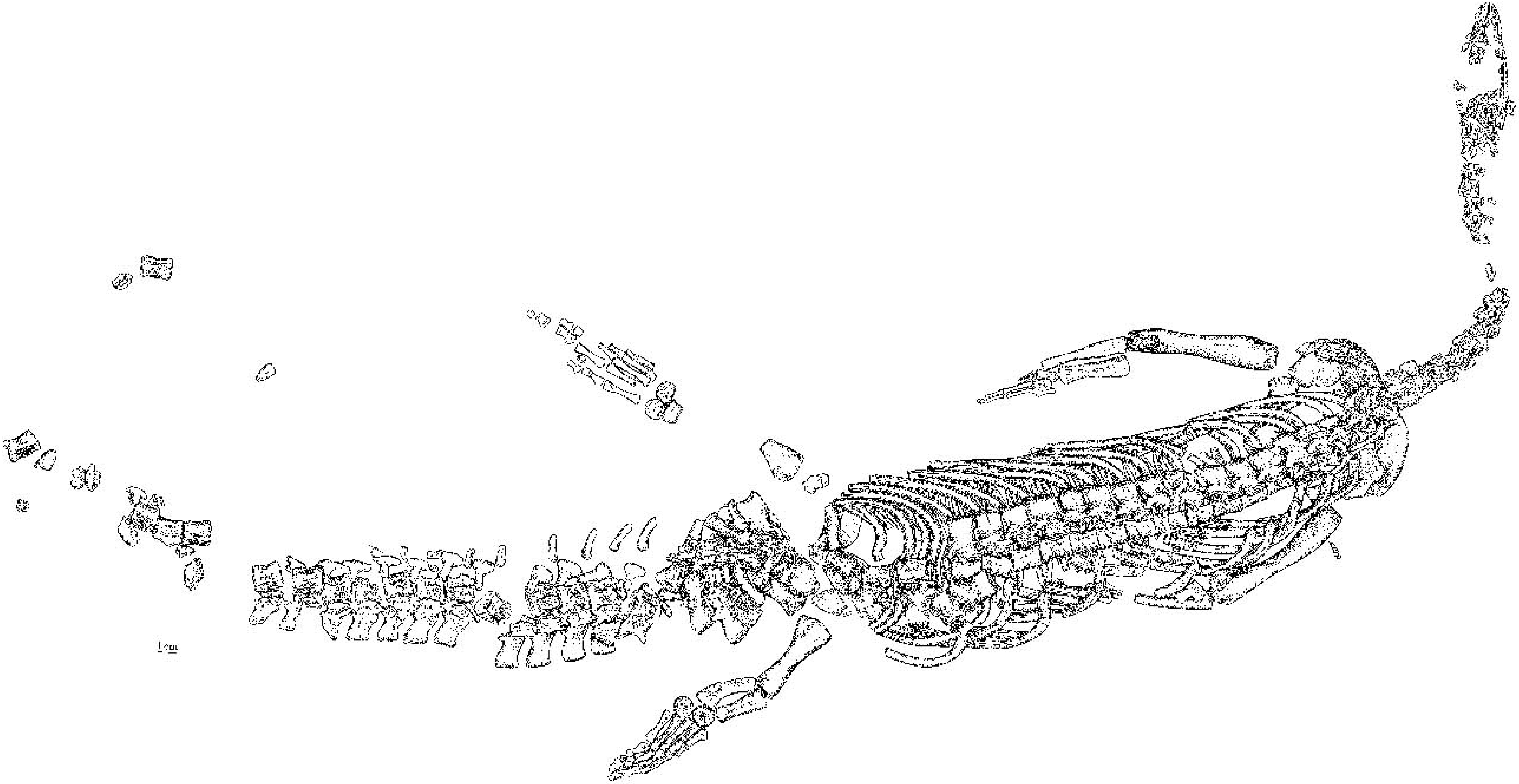

FIGURE 2. *Pachypleurosaurus edwardsi*. Largest known individual: dorsal view; Institute of Palaeontology, Zürich, 3935.

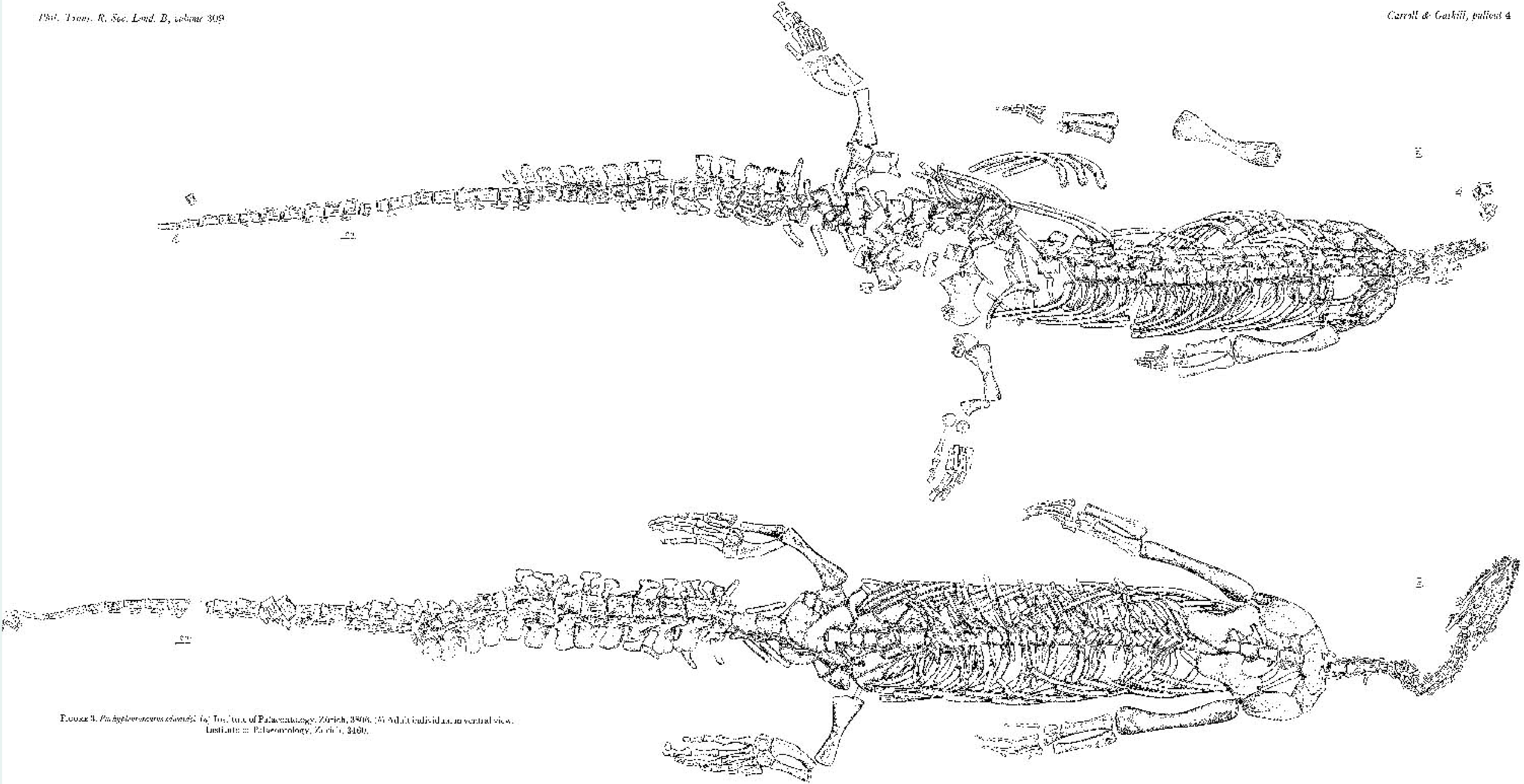

Figure 8. *Pachypleurosaurus edwardsi.* (a) Institute of Palaeontology, Zürich, 3506. (b) Adult individual in ventral view. Institute of Palaeontology, Zürich, 3460.

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