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Hupehsuchus, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships

ROBERT L. CARROLL[1] AND DONG ZHI-MING[2]

[1] *Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6*
[2] *Institute for Vertebrate Paleontology and Paleoanthropology Academia Sinica, P.O. Box 643, Beijing, People's Republic of China*

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SUMMARY

Hupehsuchus, an aquatic reptile from the Triassic of China, represents a previously unrecognized diapsid order, the Hupehsuchia. *Hupehsuchus* exhibits a unique combination of skeletal features including very long, completely toothless jaws, bipartite neural spines, a complex pattern of dermal armour above the vertebral column, and laterally compressed, spindle-shaped body form. The pattern of vertebral articulation focuses the greatest amplitude of lateral undulation in the posterior trunk and caudal region. Many derived features of *Hupehsuchus* are also observed in other groups of Mesozoic diapsid reptiles, but no specific sister-group relationship can be established. The difficulty in determining the relationship of the Hupehsuchia may be attributed to the limited knowledge of the fossil record of diapsid reptiles in the late Permian and early Triassic, as well as the great amount of convergence exhibited by secondarily aquatic reptiles. The principle of parsimony cannot be used directly to identify homologous characters if most of the derived characters are convergent.

INTRODUCTION

Despite ever increasing knowledge of the history of life, fossils are still being discovered and described that provide evidence of previously unknown groups. These discoveries not only demonstrate the greater diversity of organisms in earlier periods of the Earth's history, but frequently force us to reconsider previously accepted ideas of the patterns of evolution and the methods of classification. The recent restudy of the Burgess Shale fauna by Whittington, Conway-Morris and Briggs (Briggs & Whittington 1985; Conway Morris 1985) and its review by Gould (1989) provide a spectacular example of a pattern of evolution in which striking anatomical diversity was reached during the early stages of a group's radiation. This pattern

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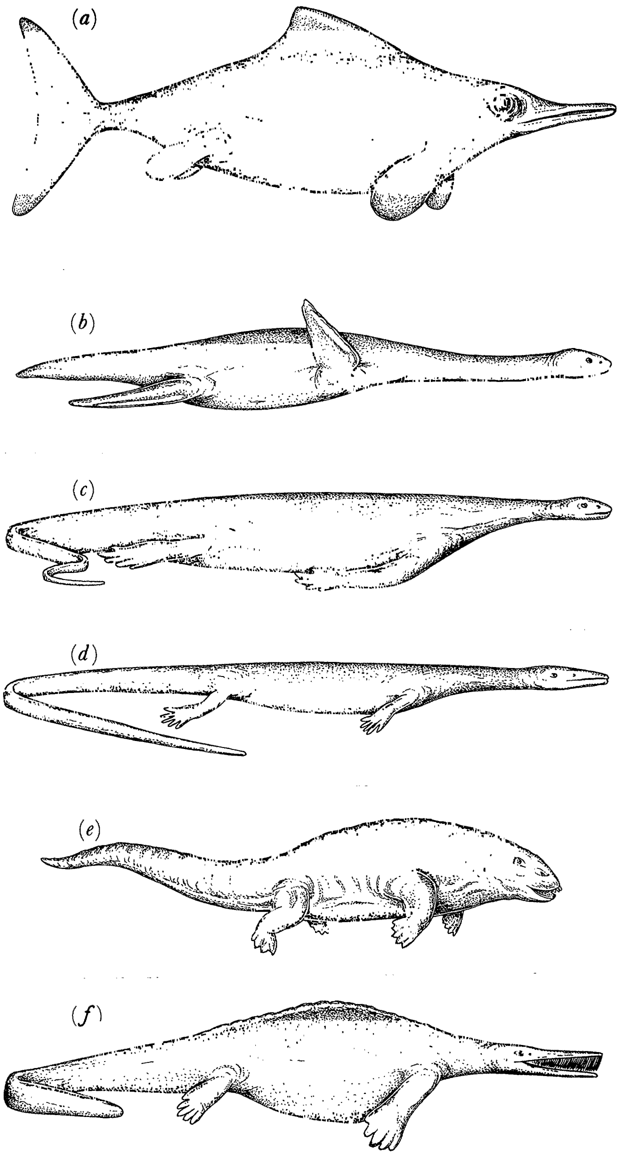

Figure 1. Reconstructions of Mesozoic aquatic reptiles. (*a*) The Upper Jurassic ichthyosaur *Opthalmosaurus*. The body form parallels that of the fastest swimming living fish. Approximately $3\frac{1}{2}$ m long. From McGowan (1983). (*b*) The Upper Jurassic plesiosaur *Cryptoclidus*, approximately 3 m long. Plesiosaurs are exceptional among diapsid reptiles in elaborating both the front and hind limbs as large paddles to 'row' the body through the water in the manner of living sea lions. The trunk is dorsoventrally compressed and the tail serves as a rudder. From Brown (1981). (*c*) The Triassic nothosaur *Pachypleurosaurus*, approximately 1 m long. The tail was long and laterally compressed. The forelimbs may have been used for propulsion, but the rear limbs served as rudders. Based on Carroll & Gaskill (1985). (*d*) The Middle Triassic thalattosaur *Askeptosaurus*. The body is elongated to facilitate anguilliform swimming. The size and degree of ossification of the limbs was reduced, but they are little modified for aquatic propulsion. Approximately 2 m long. Based on Kuhn-Schnyder (1952) (*e*) The placodont *Placodus* from the middle Triassic. Approximately 1 m long. Limbs were little modified for aquatic propulsion. (*f*) *Hupehsuchus* from the Middle Triassic of China. Up to 2 m long.

makes it very difficult to fit extinct organisms into systems of classification based on their living relatives. Another example is provided in this paper.

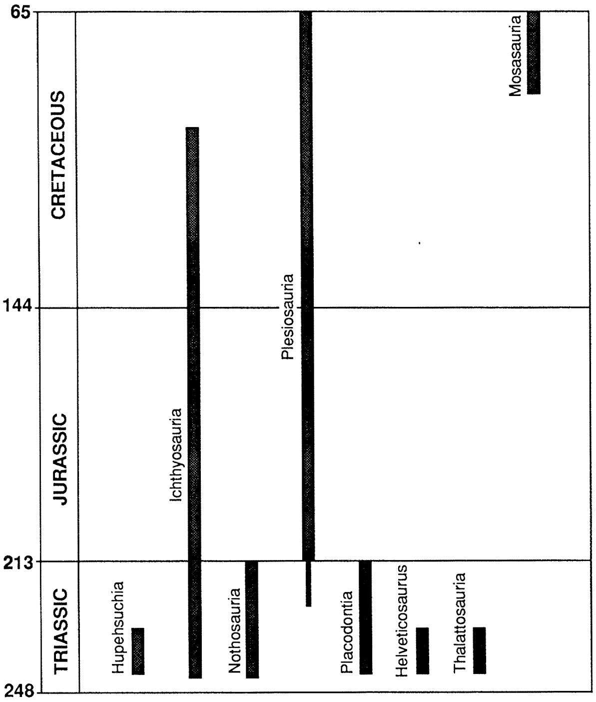

Figure 2. Mesozoic time scale (based on Harland *et al.* 1982) showing ranges of aquatic diapsid reptiles.

The Mesozoic Era is thought of as the age of dinosaurs, but during this time there was also an extensive radiation of aquatic reptiles in the oceans of the world. These include ichthyosaurs, plesiosaurs, nothosaurs, placodonts and thalattosaurs (figures 1 and 2). Most, if not all, of these aquatic groups are thought to share a common ancestry with the lineages that gave rise on the one hand to crocodiles and dinosaurs, and on the other to *Sphenodon*, lizards and snakes. However, it has not been possible to establish specific, sister-group relationships between any of these aquatic reptiles and particular terrestrial antecedents. The ichthyosaurs in particular are so highly adapted to an aquatic way of life when they first appear in the fossil record in the early Triassic that they cannot be compared in detail with any group of early terrestrial reptiles (see Massare & Callaway 1990). To what degree is this difficulty in establishing relationships a result of our incomplete knowledge of the fossil record, a problem in the current methodology of establishing relationships, or a result of inherent aspects of the process of evolutionary radiation?

These problems are emphasized by the discovery of fossils from the Triassic of China that represent a previously unrecognized group of marine reptiles. An initial description naming a new genus, *Hupehsuchus*, was published by Young & Dong (1972). They described a combination of derived characters that could be interpreted as indicating relationships with several, otherwise very distinct, groups of Triassic reptiles. Recently, the availability of new equipment made it possible to prepare the type and other specimens from this locality much more completely than was the case at the time of their initial description. Some aspects of the skeleton are still poorly known, but enough is clearly determined to demonstrate the presence of a new order of marine reptiles.

Class Reptilia
Subclass Diapsida
Infraclass uncertain
Hupehsuchia **Order nov.**

Order diagnosis. Aquatic diapsid reptiles differing from other orders in the following combination of derived characters: antorbital portion of skull greatly elongate with flattened edentulous snout and long narrow lower jaws, long retroarticular process; dorsal temporal fenestra but no clearly defined lateral opening; at least 34 presacral vertebrae, dermal plates above cervical and trunk neural spines; transverse processes much abbreviated, but supporting tuberculum of ribs throughout trunk region; ribs pachyostotic; limbs in the form of flippers but retaining many features of their terrestrial ancestors; gastralia in the form of wide, overlapping medial plates and one row of smaller lateral elements.

Two recognized genera: *Nanchangosaurus* and *Hupehsuchus* from the Middle Triassic of Hubei Province, China. Name coined as a suborder of the Thecodontia by Young & Dong (1972).

Family Nanchangosauridae Wang, 1959

Family diagnosis. Same as for order.

Hupehsuchus Young and Dong, 1972

Type species. Hupehsuchus nanchangensis

Diagnosis. Member of the family Nanchangosauridae, differing from *Nanchangosaurus* in having three layers of dermal plates above the neural spines in the trunk region, and in the division of the neural spines into proximal and distal elements. Body laterally compressed, 37 rather than 34 presacral vertebrae.

Hupehsuchus nanchangensis Young and Dong, 1972

Diagnosis. Same as for genus.

Holotype. IVPP V3232; a nearly complete, articulated skeleton in the collection of the Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China (figures 3, 4 and 5).

Referred material. (All in the collection of the IVPP.) V4068; much of the skeleton was originally present, but bone is preserved only in the skull region. The trunk and tail are represented by a natural mould that has been cast in latex (figures 6 and 7). V4069a; section of tail of a specimen at least twice as long as the type (figure 8). V4069b; section of trunk and rear limb (not figured).

Locality. Xunjian Commune, Nanzhang County, Hubei Province, People's Republic of China.

Horizon. All these specimens came from the lower part of the Jialingjiang Formation (Anisian) or the upper part of the Daye Limestone, both of which are Middle Triassic in age (Young & Dong 1972).

A single mid-trunk vertebra that may belong to this

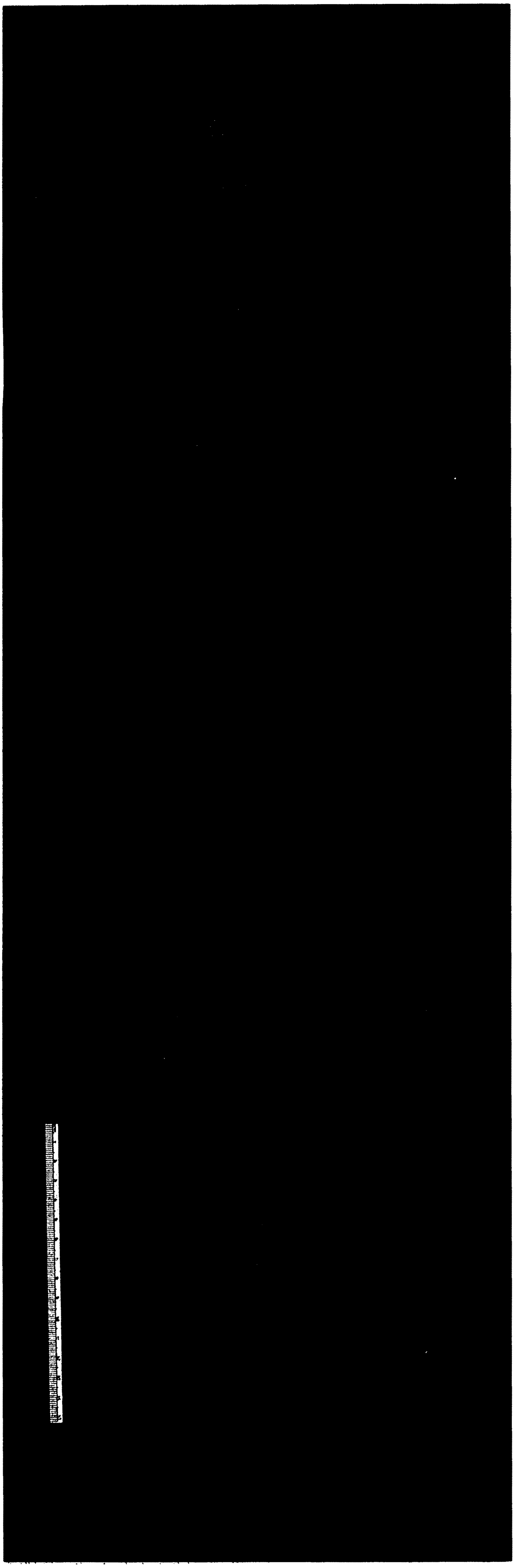

Figure 3. The holotype of *Hupehsuchus nanchangensis*, V3232, in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. Photograph of cast. Specimen 73 cm in length.

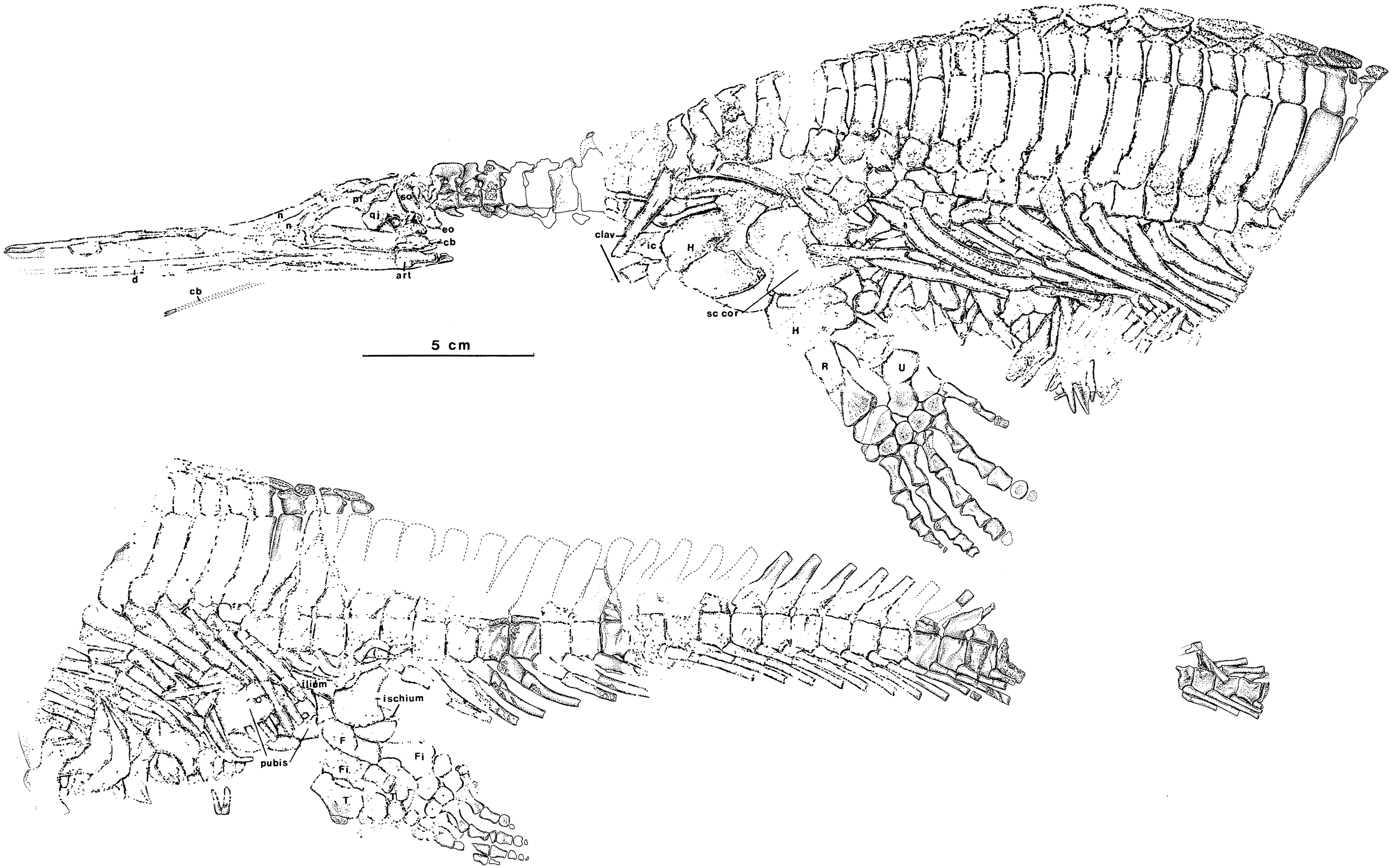

Figure 4. The type of *Hupehsuchus nanchangensis*. Front and back portions divided along a natural crack. Broken lines outline areas preserved as natural casts of the bone. The surface of the unshaded cervical vertebrae is badly disrupted by gypsum infiltration. Abbreviations are listed before the references.

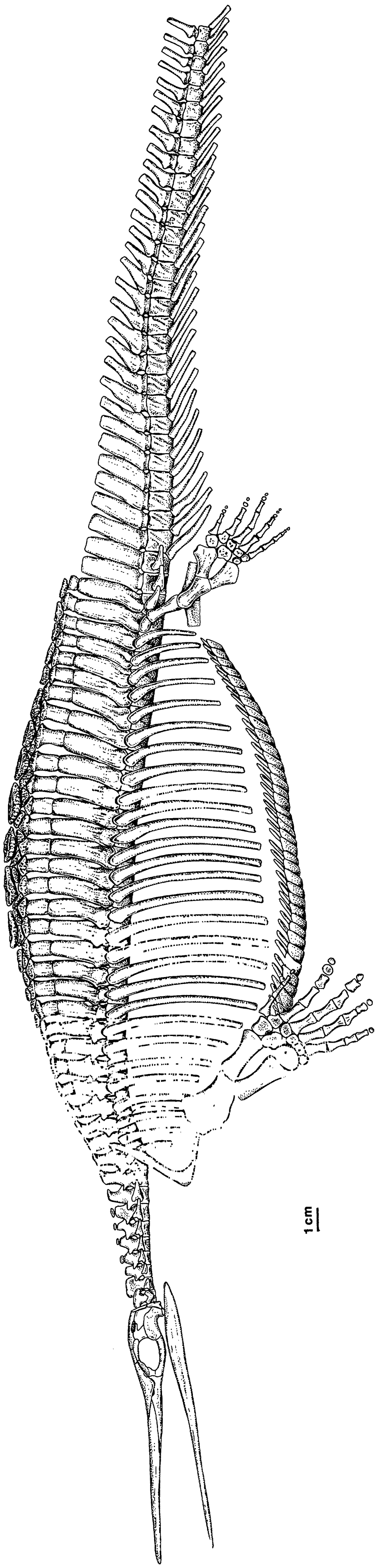

Figure 5. *Hupehsuchus*, skeletal reconstruction based primarily on the holotype.

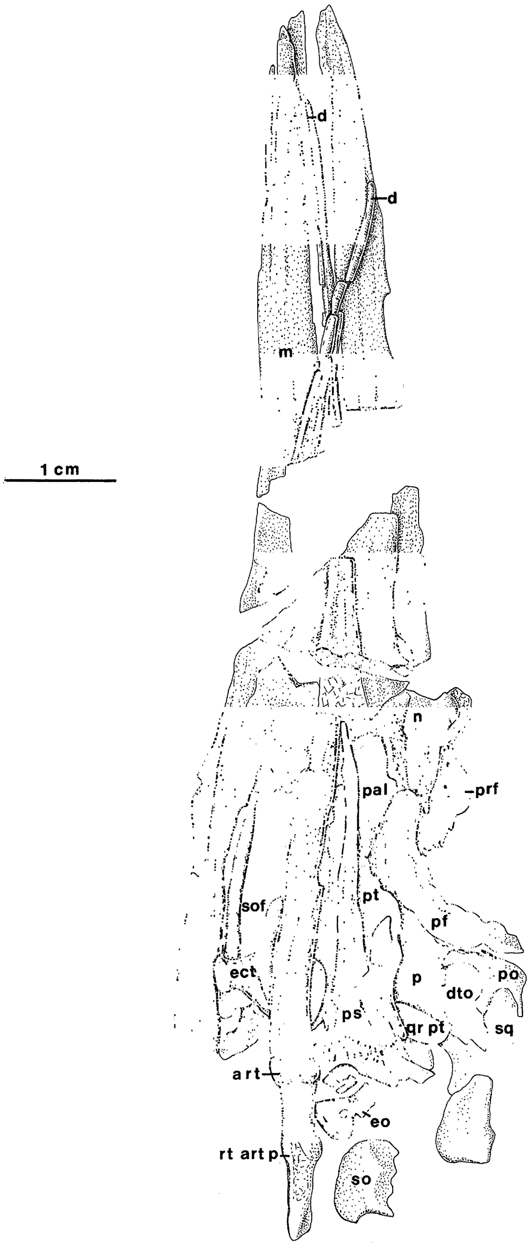

Figure 6. *Hupehsuchus*, palatal view of V4068.

genus was collected by the Mid-South China Geological Institute in 1970 from Maoping (97 km south of Nanzhang County) in Yuan'an Province. This specimen came from the mid-Triassic Bedong Formation.

ANATOMY OF *HUPEHSUCHUS*

The body outline is spindle shaped, with a moderately long neck and an extremely slender skull. The nearly complete skeleton of the type is 74 cm long, minus the end of the tail. It is impossible to give an accurate estimate of the amount of the tail that was lost, but this individual might have reached nearly a metre in total length. The limbs are in the form of short paddles. *Hupehsuchus* differs from all other rapidly swimming early reptiles in being completely toothless, and having a complex pattern of dermal plates above the vertebral column.

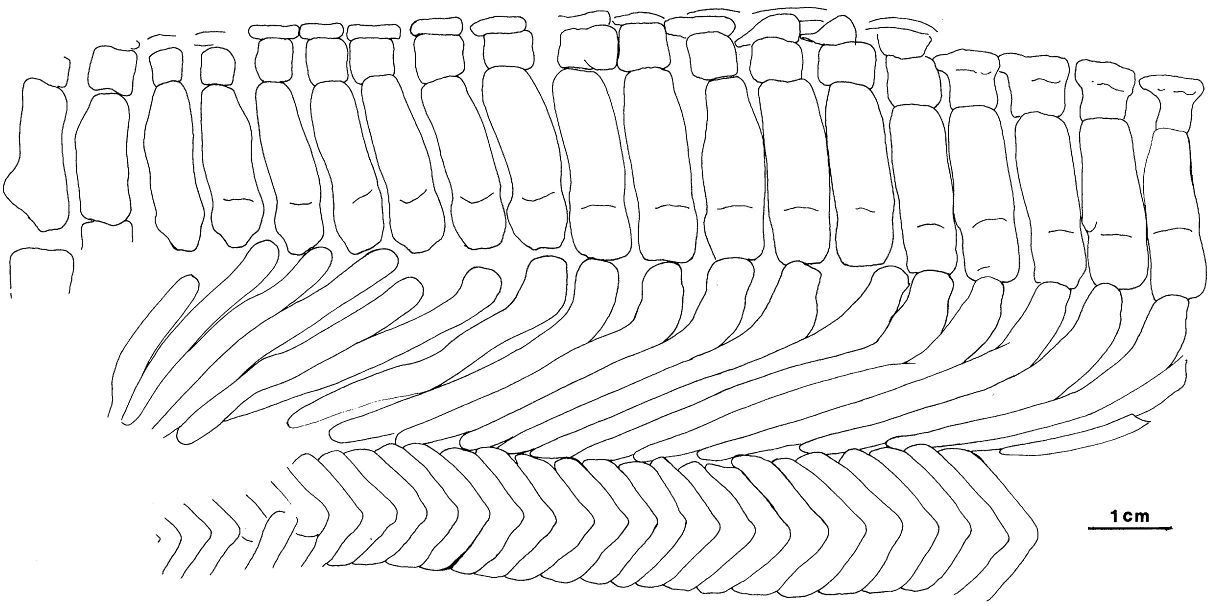

Figure 7. *Hupehsuchus*, trunk region of V4068 sketched from latex cast. Very little detail is visible in the original specimen.

Skull

Description of the skull is based on two specimens, the holotype, V3232, in which it is visible primarily in lateral view, and V4068, which is exposed in palatal view (figures 4 and 6). The type skull is nearly complete, but the posterior portion is crushed and has suffered from surface erosion and intrusion by gypsum. Much of the rostrum is preserved as an impression where the original bone has been lost. In V4068, key areas of the palate are missing, but some of the skull table can be seen in ventral view. The general outline and major features of the skull can be established in both specimens, but many important aspects cannot be seen in either.

The skull in the type is 12.6 cm long at the midline, that of V4086, 10 cm. In both specimens, the skull is complete to the tip of the rostrum, but the occipital area is slightly disarticulated, making exact determination of the length difficult. Based on the composite reconstruction (adjusted to the size of the type) the width is 3.5 cm, and the height at the back of the skull is 1.7 cm (figure 9). The midpoint of the orbit is far posterior in position. The antorbital length is 75 % of the total length of the skull. There is no evidence of sclerotic plates. The cheek region and the orbit are of approximately equal length. The skull table is not visible in dorsal view in either specimen. As noted by Dong (1979) the skull superficially resembles that of a bird. This is particularly true in lateral view. It has a long and completely edentulous rostrum. This is clearly seen in V4068 in which nearly the entire length of the rostrum is exposed in ventral view. The lower jaws are slender, tapering rods, much narrower than the elements of the upper jaw. The jaws are distinctly non-avian, having very long retroarticular processes, extending behind the skull for some 14 % of its length. In contrast with the very thin bone in the rostral area, that of the back of the skull appears quite massive. An upper temporal opening is clearly evident in ventral view in V4068. The cheek region seems solidly ossified without an orthodox lateral temporal opening, but may be emarginated ventrally to a limited extent.

An opening in front of the orbit in the type was identified by Young and Dong as a possible antorbital fenestra, as in archosaurs. It occupies a space between the nasal dorsally and the prefrontal bone posteroventrally. This is not comparable to the position of the antorbital opening in archosaurs, which is surrounded primarily by the maxilla and the lacrimal (Charig *et al.* 1976). Neither does its position resemble that of a narial opening. The margins are broken and it may be an artefact caused by damage to the surrounding bones. The prefrontal is clearly an extensive bone in V4068, although its lateral extent in that specimen cannot be established. If the midline has been correctly identified in the type, the right nasal covers much of the area occupied by the fenestra on the left side. A smaller opening, more anterior and ventral, between the nasal and the maxilla, might be the external naris, but the area is not sufficiently well preserved to be certain. This is the approximate position of the naris in ichthyosaurs.

There are many problems regarding the specific identity and extent of the individual bones, both because of poor preservation and because of the unusual configuration of the skull as a whole. Neither the skull nor the postcranial skeleton offers strong evidence of the specific affinities of this genus, precluding close comparison with any other taxon. It shares some important synapomorphies with primitive terrestrial diapsids. Derivation from that group implies a major habitat shift and significant changes in the general anatomy. The configuration of the rostral region and the lower jaws in particular were presumably more dependent on changes in adaptive design than on the specific ancestral pattern. Comparison has been made with a spectrum of forms:

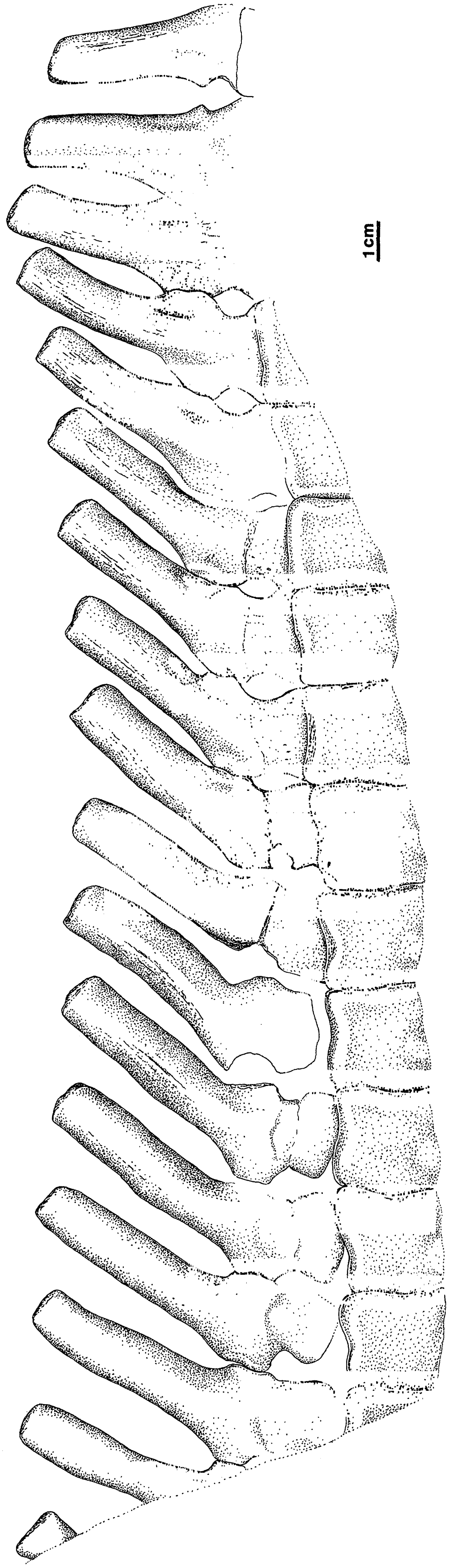

Figure 8. *Hupehsuchus*, V4069a, section of tail of an individual approximately twice as long as the holotype.

ichthyosaurs, plesiosaurs, whales and the Cretaceous bird *Hesperornis*. Even then, several major problems remain.

Much of the rostrum is exposed in both specimens. In V4068 it is visible in strictly ventral view. There appears to be only a single bone on each side, without trace of sutures or overlap from the tip of the snout to about the front of the orbits, although a wide gap resulting from a break in the matrix separates the anterior and posterior portions of the rostrum. If there is only a single bone exposed in ventral view, it is probably the maxilla, by analogy with the pattern in modern baleen whales. In the type, the rostrum is poorly preserved, but reveals in one area or another four overlapping layers of bone. This is clearly evident both near the base of the rostrum and near its extremity. This suggests that for much of its length the rostrum is formed by overlapping portions of the maxilla and premaxilla on both sides. If the maxilla is correctly identified as making up most of the ventral surface, then the premaxilla must occupy much of the dorsal surface, except at the base of the rostrum where the maxilla was presumably exposed laterally. The rostrum was presumably flat or slightly concave ventrally, and arched dorsally. The ventral surface of the rostrum is basically smooth, without a trace of alveoli for teeth. There may have been a material resembling baleen, but such tissue is not normally capable of fossilization. In V4068, the left and right sides are slightly separated. The two sides of the rostrum do not appear to be strongly attached to one another, although a shallow groove, that may have received a ridge from the opposite side, can be seen in one side at the very end in the type specimen.

The nasal openings certainly are not near the end of the rostrum. Presumably, both the internal and external nares were located near the base, but neither specimen is sufficiently well preserved to specify their position.

The only bones of the skull roof that are adequately shown in dorsal view in the type are the nasals. They are large, roughly triangular bones, running down from the skull table to the base of the snout. They embrace between them the posterior end of the maxillae that run along the midline. Very little of the dorsal surface of the frontals and parietals is preserved in the type. The anterior extremity of the parietal can be seen in ventral view in V4068, indicating that the frontal is very short. It is interesting to note in this Mesozoic marine reptile the same sort of telescoping of the skull that occurs in Cainozoic whales. This is clear in the type, based simply on the great posterior extent of the nasals.

The dorsal circumorbital bones and the lateral portion of the skull table are visible in ventral view in V4068. This pattern has been incorporated in the dorsal view of the reconstruction, but the specific configuration of the sutures probably differed from that seen ventrally. It is clear that the prefrontal widely overlaps the anterior end of the postfrontal, and that the medial extent of the anterior margin of the postorbital is greater on the ventral surface. The prefrontal extends widely over the area of the orbit in

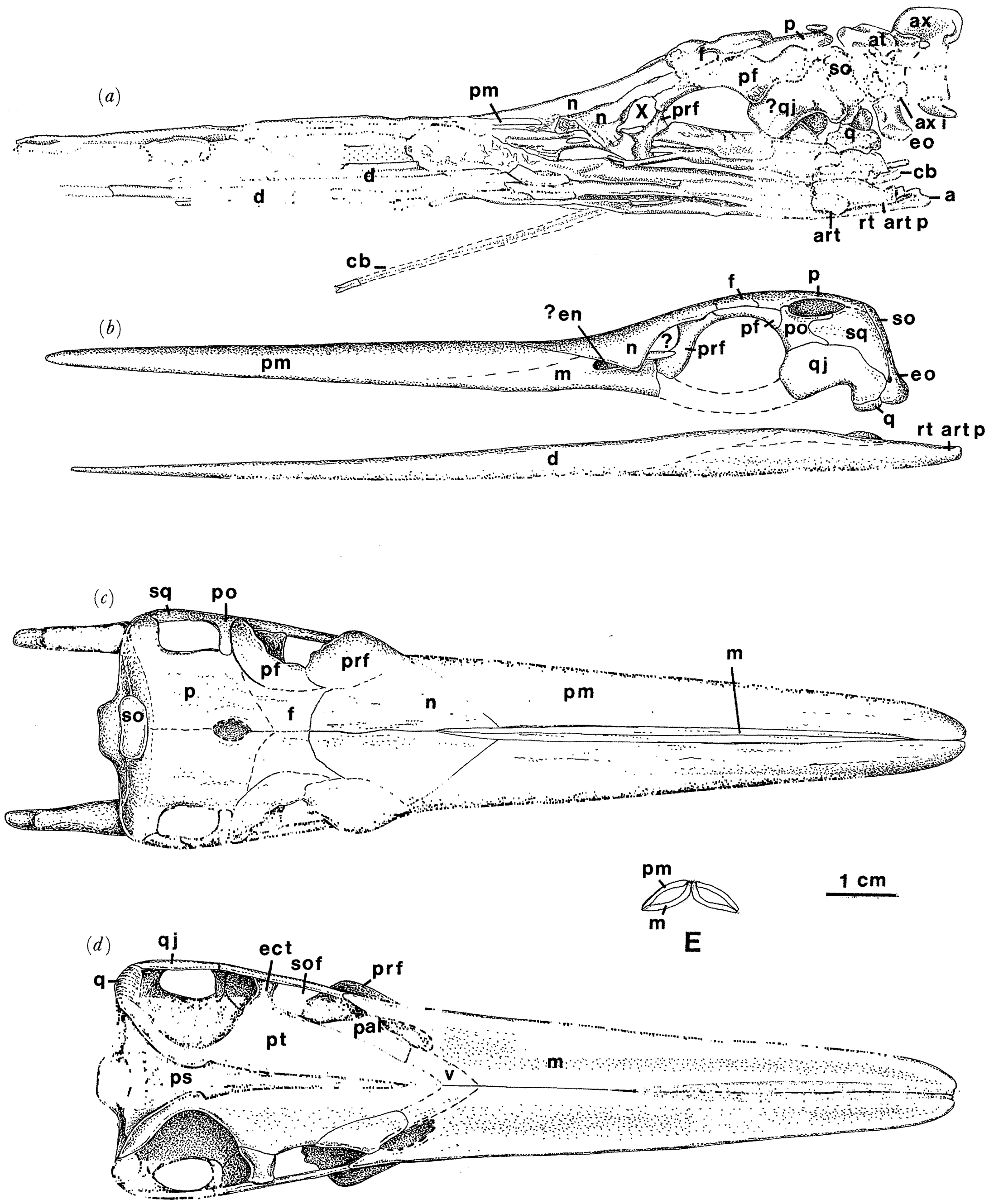

Figure 9. Skull of *Hupehsuchus*. (*a*) Drawing of skull of holotype, seen primarily in lateral view. X shows position of opening referred to as an antorbital fenestra by Young and Dong. Guide to other abbreviations at end of text. (*b–d*) Restoration of skull in lateral, dorsal and palatal views, based on the type and V4068. (*e*) Schematic cross section of snout. All approximately life size.

a way paralleled by some marine crocodiles and mosasaurs. This overhang presumably served to protect the eyes from the rapid flow of the water. The postfrontal also has a wide and wavy margin above the orbit. A process of the postorbital extends behind the postfrontal to form all of the anterior border of the upper temporal opening. The medial portion of the parietal is covered by the palate so that the position (or even the presence) of a pineal opening cannot be established. The posterior margin of the parietal is also largely obscured so that the nature of its connection with the back of the cheek and the occiput cannot be established. The posterolateral portion of the upper temporal bar is formed by a relatively thick but short squamosal. This bone appears to be confined primarily to the dorsal surface of the skull. Below it, most of the cheek is occupied by what appears to be a separate ossification that may be compared to the large quadratojugal of some ichthyosaurs and placodonts. This bone appears to be emarginated ventrally as in some members of both groups. This emargination cannot be compared with the lower temporal fenestra of orthodox diapsids, which is above the quadratojugal. Neither specimen shows the surface of the quadrate.

The area below the orbit is difficult to interpret. In the type, the right lower jaw is crushed into the palatal area. It is not possible to determine whether some of the broken bone represented the palate or a jugal.

Both specimens show a large platelike bone behind the skull. Although it is disarticulated, it can be identified with some confidence as the supraoccipital. The supraoccipital has a similar shape in early ichthyosaurs. A massive, disarticulated exoccipital, bearing a large foramen for the XIIth cranial nerve, lies just behind the skull in both specimens. In neither specimen can the basioccipital or stapes be identified.

The posterior portion of the palate appears much as in more orthodox primitive diapsids. The cultriform process of the parasphenoid extends forward between the palatal rami of the pterygoids. The posterior plate extends out above the quadrate rami of the pterygoids. The plate is marked by a posterior ornamentation of short, roughened ridges. Clearly defined basicranial processes cannot be seen, but the pterygoids appear to underlie the sides of the parasphenoid at the base of the cultriform process. The pterygoids do not meet one another beneath the back of the braincase such as occurs in notosaurs or the Middle Triassic ichthyosaur *Mixosaurus*. The transverse flange of the pterygoid that is conspicuous in other early diapsids is not evident in this specimen. The pterygoid appears to form a smooth margin of the subtemporal fossa.

In V4068, a bar of bone extends laterally from the right pterygoid. This bone appears to be the ectopterygoid, linking the palate to the back of the cheek. Anteriorly is an extensive opening that appears comparable to the suborbital fenestra of primitive diapsids. On the left side a triangular palatine bone can be seen anterior to this space. Further anteriorly there is a gap in the preserved area of the palate, beyond which the rostrum begins. The anterior end of the pterygoids, the vomers and the margins of the internal nares can only be restored by analogy with other early diapsids.

Lower jaws and hyoid

The lower jaws are long, narrow structures, tapering gradually to the front. They do not show evidence of being firmly attached to one another anteriorly. Posteriorly they are crushed and fragmented. In V4068, the left jaw has been displaced so that it appears in dorsal view on the right side. The right jaw is displaced beyond the skull margin and badly crushed. In the type, the two jaws are side by side. The articular and retroarticular process of the left lower jaw are rotated laterally. Other early aquatic reptiles such as the nothosaurs retain a fairly normal arrangement of bones around the Meckelian fossa. In V4068, the bones seem to form a simple, nearly cylindrical structure anterior to the articular. In the type, the jaw is poorly preserved in this area. Further anteriorly there appears to be a groove where the teeth were primitively present. The angular appears to extend posteriorly behind the articular, forming an additional surface for attachment of the depressor mandibulea or a continuation of that on the articular. Below the lower jaw is a very long and narrow hyoid element.

Vertebrae and dermal plates

The vertebral column is preserved in almost perfect articulation in the type specimen, back to the 23rd caudal. Beyond this, a space the length of approximately five caudal vertebrae has been eroded. It is followed by parts of five additional vertebrae, making a total of 33 caudals. The last caudals are quite robust, indicating that a significant portion of the tail is missing.

Nine vertebrae are identified as cervicals since they lie anterior to the shoulder girdle and bear ribs that are much shorter than those in the trunk region. Twenty-eight trunk vertebrae bear long ribs. The twenty-ninth postcervical vertebra, bearing short, posteriorly directed ribs, is considered the sacral. All vertebrae retain a suture between the centrum and the neural arch and in the anterior trunk region the elements have become disarticulated. Where they are exposed, the ends of the centra are nearly flat, rather than conspicuously amphicoelous as in primitive diapsids. They clearly differ from the conspicuously biconcave vertebrae of most ichthyosaurs.

The atlas–axis complex differs little from that of primitive diapsids. The atlas has large, paired arches. Ventral exposure of its pleurocentrum is precluded by the contact beneath it of the atlas and axis intercentra. As in primitive reptiles, the atlas arch is much larger than those of more posterior cervicals. The cervical centra are all shorter than those in the trunk region. The lateral surfaces of the cervical vertebrae are damaged, making it impossible to establish the exact nature of rib articulation. The more posterior cervical vertebrae have been infiltrated with gypsum, so that only their outlines are preserved. Lying against the side of the neural spine of the fourth cervical is an oval piece of dermal bone, resembling the large elements preserved in the trunk region. The neural spines become progressively elongate behind the sixth cervical.

One of the strangest features of this species is the bipartite nature of the neural spines throughout the trunk region (figure 10). The posterior cervicals and the first trunk vertebra are too poorly preserved to reveal this feature, but from the 11th vertebra to at least the first caudal, the neural spines are divided into proximal and distal units by a horizontal suture. Several vertebrae show slight displacement along this suture line, indicating that the two parts were not coossified. The distal portion of the neural spine is in continuity with sculptured elements that presumably extended into the dermis of the overlying skin. The slightly roughened appearance of the distal portion of the spine suggests that it may have originated as dermal bone that extended into deeper tissue to meet the endoskeletal portion of the neural spine. The bipartite nature of the neural spines may be unique among vertebrates.

The neural spines are nearly confluent for most of their length from the central portion of the trunk region through the anterior portion of the tail. By the

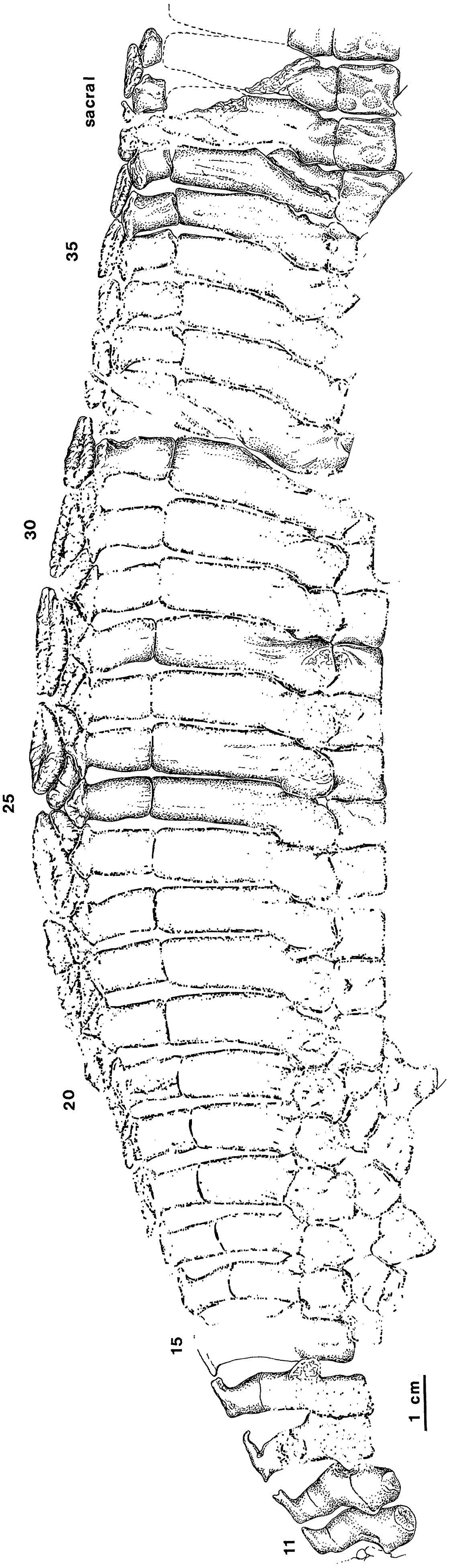

Figure 10. *Hupehsuchus*. Trunk vertebrae and dermal plates of the holotype. Figures indicate the number of presacral vertebra.

tenth caudal, the spines become more narrow distally and angle toward the rear. By the last preserved vertebrae, caudals 29–32, the neural arches are narrow, cylindrical rods, angled sharply posteriorly.

Dermal plates are associated with the neural spines as far anteriorly as the fourth cervical, and as far back as the first caudal (figures 4 and 10). The distal portion of the neural spines of vertebrae 8–14 is expanded posteriorly; further back, it extends anteriorly as well. The anterior trunk spines are not well preserved, but from the 16th vertebrae to the base of the tail the expanded portion of the spine is sculptured dorsally. From vertebra 17 to the first caudal, there are separate pieces of dermal bone, linking the tops of adjacent spines. Larger, more distal elements lie above the centre of even numbered spines from vertebrae 20–30. They alternate with the ends of the spines of the most posterior trunk and the most anterior caudal vertebrae. All the dermal plates appears to be medial in position.

Comparison was made with the armour in thecodonts by Young and Dong, but no known thecodont has a similar pattern (Charig *et al.* 1976).

The neural spines of caudal vertebrae 1–13 are preserved only as impressions. Only the first shows the distal portion of the neural spine and a dermal plate; these elements might originally have been present more posteriorly, but were lost after death. The proximal portion of the neural spines is preserved from the 14th through the 32nd caudal, but there is no trace of a distal element or any dermal plates. In another specimen from this locality (figure 12), which might belong to a distinct species, dermal plates are associated with the first seven caudal vertebrae.

The zygapophyses of the cervical vertebrae resemble those of early terrestrial reptiles. They are nearly flat and extend anteriorly and posteriorly from the margins of the neural arch. This pattern continues into the anterior trunk region, with a gradual shortening and loss of clear distinction from the arch. By the 20th vertebra, the base of the postzygapophysis is confluent with the neural spine. The articulating surface is essentially flat in this area of the column, but becomes more steeply angled in the posterior vertebrae. By vertebra 28, the postzygapophyses are covered in lateral view by the lateral surfaces of the succeeding arch, which appears to wrap around the base of the more anterior spine. This configuration would increase the degree of lateral undulation toward the rear of the trunk, while greatly restricting rotation around the long axis. The most posterior trunk, sacral and caudal vertebrae do not have distinct zygapophyses. In the tail, the bases of the neural spines overlap one another in an irregular fashion. In caudal vertebra 17 of the type, the anterior and posterior margins appear to overlap both the posterior margin of the next more anterior spine, and the anterior margin of the next posterior spine. In the larger specimen, V4069A, a vertically oriented hinge joint appears to unite the spines in part of the tail.

Details of the areas for rib articulation are poorly exposed throughout the column. In the trunk region, the transverse processes are nowhere clearly defined.

The neural arch widens above the area for articulation with the centrum. Several vertebrae show an oval area at their distal extremity for articulation with the tuberculum of the rib. The head of the rib is too large to be confined to this area, and a further area of rib articulation must have occupied the mediodorsal portion of the centrum, but this is nowhere clearly shown. Toward the end of the trunk region, from about the level of the 33rd vertebra, the area of articulation at the margin of the arch becomes reduced in size. The last trunk and sacral ribs must have been almost if not entirely accommodated by the centrum. One or two oval areas with slightly raised edges served for articulation of the three caudal ribs.

The pattern of rib articulation in the trunk region is unlike that of any other early aquatic reptile. In ichthyosaurs, the ribs articulate only with the centra. In nothosaurs, plesiosaurs, thalattosaurs and placodonts, articulation is restricted to the ends of clearly distinct transverse processes.

No intercentra are preserved posterior to the atlas–axis complex. Haemal arches begin anterior to the fourth caudal centrum. The most anterior is equal in length to three centra. The length of the centra diminishes posteriorly, with the haemal arches shortening to a comparable degree. Even the last complete haemal, associated with the 31st caudal, is the length of $2\frac{1}{2}$ centra.

Ribs

The area of the atlas is not sufficiently well preserved to establish whether or not there were atlas ribs. Ribs are otherwise present throughout the neck, trunk and tail, back to the third caudal. The cervical ribs are very short, but appear to have two heads, separated by a gap for the vertebral artery. They broadly resemble the cervical ribs of nothosaurs (Carroll & Gaskill 1985). The heads probably straddled the suture between the arch and centrum.

The ribs of vertebrae 6–9 are very poorly preserved, but were apparently all very short and slender. The ribs associated with vertebrae 10–37 are much longer and very thick proximally, suggesting the pachyostotic nature of the ribs of nothosaurs and sirenians. The heads of the ribs are deep and have two confluent facets, one for articulation with the lateral extension of the arch, and the second with the side of the centrum. This pattern is clearly distinct from that in any other group of Mesozoic aquatic reptiles.

Most of the trunk ribs are well exposed in the type and in V4068, but their natural orientation is difficult to establish. In V4068, the ribs are orientated at an angle of approximately 45° relative to the horizontal (figure 7). At this orientation they form a nearly continuous lateral wall to the body cavity. The distal ends of the ribs in the type are also displaced to the rear, but in addition, many have rotated along the long axis so that the heads are visible in primarily anterior or posterior view such that they appear much wider than they would in their natural orientation.

The first ten trunk ribs are all incomplete distally, but their length appears to have increased progressively. The rib associated with the 20th vertebra is approximately the length of ten trunk centra. The next several ribs are of similar length. The ribs become gradually shorter in the more posterior portion of the trunk, but even the last trunk rib is the length of almost four centra, in contrast with the much greater diminution in rib length anterior to the sacrum common to most primitive reptiles. All of the trunk ribs end bluntly, as if they might have been continued in cartilage. Camp (1980) described ossified cone-shaped accessory extensions from the ends of the trunk ribs in the Triassic ichthyosaur *Shonisaurus*.

Much shorter ribs are associated with the next four vertebrae. The first of these may be termed a sacral, although it does not appear to have been expanded distally as in terrestrial reptiles. These ribs appear to have two, non-confluent heads, both of which articulate with the centrum rather than with the neural arch. All angle to the rear. In most terrestrial diapsids, the caudal ribs are fused to the transverse processes.

Appendicular skeleton

In V3232 most of the bones of the shoulder girdle are displaced from their natural position and few anatomical details are evident. A long flat element extending anteroventrally from the base of the 11th neural arch to below the eighth cervical is the stem of the left clavicle (figure 4). A broken portion of a narrow clavicular blade is preserved adjacent to the base of the stem. It is oriented horizontally, and extends obliquely posteriorly. It is not possible to determine whether it is from the left or right side. Overlying the posterior portion of the clavicular blade is the anterior portion of the interclavicle. It is too incompletely exposed to establish its original shape.

In addition to the humeri, two other bones of large size, with generally flat surface exposure, are visible behind the dermal shoulder girdle. Much of their surface is covered by overlying bones so that their margins cannot be fully established. In all other Triassic marine reptiles, the scapula and coracoid form discrete areas of ossification. This is probably the case for *Hupehsuchus* as well, but the natural orientation of these two bones and whether one or both come from the right or left side cannot be established. Tentatively, the more anterior bone is identified as the scapula, and the somewhat thicker posterior bone is considered a coracoid. Both bones appear to be exposed in internal view, since neither shows the area of the glenoid. Neither bone exhibits the distinctive elongate configuration of the coracoid of nothosaurs. The approximate outline of the endochondral shoulder girdle is indicated by a broken line in the restoration.

Both humeri are present. The distal end of the right humerus is visible in medial view, in articulation with the ulna and radius. The left is visible in lateral view just posterior to the dermal shoulder girdle. It is broken in the middle of the shaft and the posterior margin is badly eroded. The head is extremely broad, anteroposteriorly, but relatively flat. There appears to have been a very long articulating surface. Anteriorly the unfinished surface of the bone is deeply rugose,

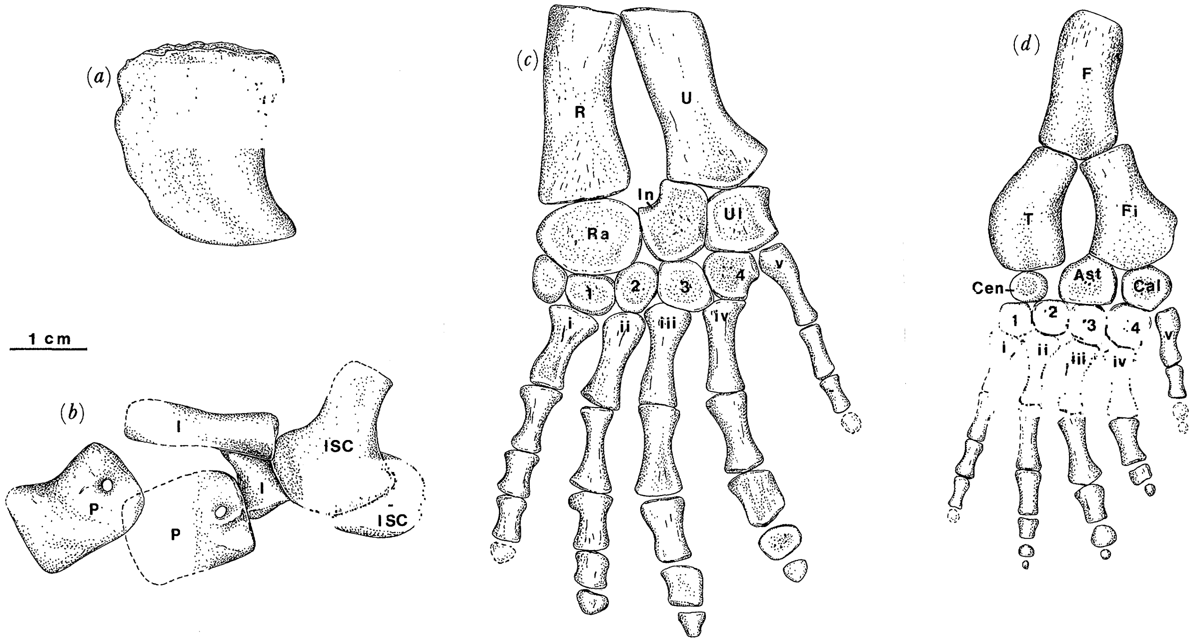

Figure 11. *Hupehsuchus*. (*a*) Reconstruction of left humerus of the type. (*b*) Elements of pelvic girdle; broken lines indicate the areas covered by other bones. (*c*) Reconstruction of right lower forelimb. (*d*) Reconstruction of right lower hindlimb.

suggesting strong attachment to a thick cartilaginous surface. The shaft is little constricted relative to the wide, flattened ends. The distal extremity, visible in dorsal and ventral views on the two sides, appears thin and flat, without specific articulating surfaces for the ulna and radius. There appears to have been a simple hinge joint between the humerus and the epipodials. Presumably the entire forelimb formed a flattened paddle.

In contrast with the humerus, the basic pattern of the distal elements of the forelimb resembles that of primitive terrestrial diapsids (figure 11). Elements of the left forelimb are scattered above the area of the right humerus. The right limb, in contrast, is in almost perfect articulation. The ulna and radius are flattened. The flat proximal ends are at right angles to the shaft. The ulna shows no olecranon. The distal ends are gently rounded where they make contact with the carpals.

There are three large, flat proximal carpals, identifiable as the radiale (very large), the intermedium and the ulnare. These bones are well ossified. Their corners are rounded, but there are relatively straight margins where they are in contact with one another, leaving little space for cartilage. No centralia are present. There are five carpals in a distal row, but they are not directly homologous with the five distal carpals that support the five digits in primitive amniotes. The most medial element is not associated with any digit. The next four are associated with digits 1–4. The fifth digit articulates with a small proximolateral facet on the fourth distal carpal and the posterolateral corner of the ulnare. There is no evidence that these bones are disarticulated from their natural position. As in most early reptiles, the bone identified as the fourth distal carpal is the largest in the series. It is conceivable that the most medial element in the row of distal carpals supported an accessory digit, but this seems unlikely in light of the excellent preservation in this area. The metacarpals and proximal phalanges are elongate, as in most early diapsids, but the succeeding phalanges are flattened and some have nearly circular outlines. Terminal phalanges appear to be missing in digits 1 and 5. If only a single element is missing in each digit, the phalangeal count would have been 4, 4, 4, 4, 3. The rounded and flattened nature of the distal phalanges suggests that they were embedded in a flattened paddle.

Elements of the pelvic girdle are jumbled with the posterior trunk and anterior caudal ribs. All are much smaller than in terrestrial diapsids. Both pubes are readily identified by the obturator foramen. They are rectangular bones, slightly thicker on one side. It is not certain whether this was the medial or lateral surface. One of the pair is exposed in dorsal view and the other ventrally, but it is uncertain which is which. The ischia lie one atop the other and are rotated away from their normal orientation. A stout bar of bone extends anterodorsally from between the pubes and ischia. It is presumably the left ilium. If it is exposed in more or less its natural position, the acetabulum is not evident, and the bone is oriented as in primitive ichthyosaurs rather than posterodorsally, as in terrestrial reptiles. There is no evidence as to whether it actually articulated with the presumed sacral rib, or was supported by connective tissue or musculature.

The left femur is apparently missing. The right is a short bone with widely expanded proximal and distal articulating areas. If it has retained its original orientation, the ventral surface is smoothly rounded, in contrast with the pattern in primitive terrestrial reptiles.

In common with the forelimbs, the left rear limb is scattered above the right, which remains well articulated in its natural position. The right tibia is obscured by elements of the left tarsus, but the left tibia is well exposed in lateral view. Both tibia and fibula are short, very widely expanded distally, and form a fairly simple hinge joint with the femur. The tarsus comprises three bones in the proximal row – the astragalus and calcaneum in close articulation with the fibula, and a rounded centrale distal to the tibia – and four distal tarsals associated with the first four metapodials. The fifth metatarsal articulates with the lateral margin of the fourth distal tarsal and the distal end of the calcaneum. The metatarsals and the proximal phalanges are cylindrical, as in terrestrial reptiles, but the more distal elements are flattened with rounded outlines, as in the manus. The distal elements of digits 1 and 4 are missing, but the phalangeal count was apparently 4, 5, 4, 3, 3. The entire ankle and foot are much smaller than their anterior counterparts. The rear limb was presumably used primarily for steering, rather than for propulsion.

Gastralia

A striking feature of the skeleton is massive ventral armour between the pectoral and pelvic girdles. It is visible in ventral view in almost natural articulation in V4068 (figure 7), but this specimen does not show details of the individual elements. This is revealed in the type in which they are disarticulated to show both their internal and external surfaces. The medial row of gastralia is much widened and thickened to form an overlapping row of massive, V-shaped elements. There appears to be a single lateral row of more nearly cylindrical bones. There are approximately two rows of gastralia per segment.

A SECOND GENUS

In addition to the material already described, a fifth specimen has been collected from this locality, V4070 (figures 12 and 13). The back of the skull, neck and shoulder girdle are represented by very badly weathered bone. In places, impressions are visible in the underlying matrix, but reveal few details. It would be very difficult to gain further information of this area. Much of the postcranial skeleton is preserved as a weathered impression in the matrix, making detailed comparison of most elements impossible. The outline of the skeleton, the size of the major limb elements, the distance between the limbs, and the anterior–posterior length of the neural spines are very similar to those of the type of *Hupehsuchus*. The tail is approximately 93 % as long, measured on the basis of equivalent numbers of vertebrae. In contrast, the portions of the skeleton that are best preserved – the fore- and hindlimbs – appear significantly different in many features. In addition, the neural and haemal arches of the caudal region are significantly shorter than those in the type, although the major dimensions of the body are very similar. The neural spines in the trunk region are only about half the length of those in the type, but poor preservation makes it impossible to determine whether the upper half of the spines was preserved. The neural spines of caudal vertebrae 6–13 of V4070 range from 65 to 76 % the length of those in the type of *Hupehsuchus*. Near the end of the preserved column, the neural spines are 30 % longer than those in *Hupehsuchus*. The haemal spines at the base of the tail in V4070 are 67 %

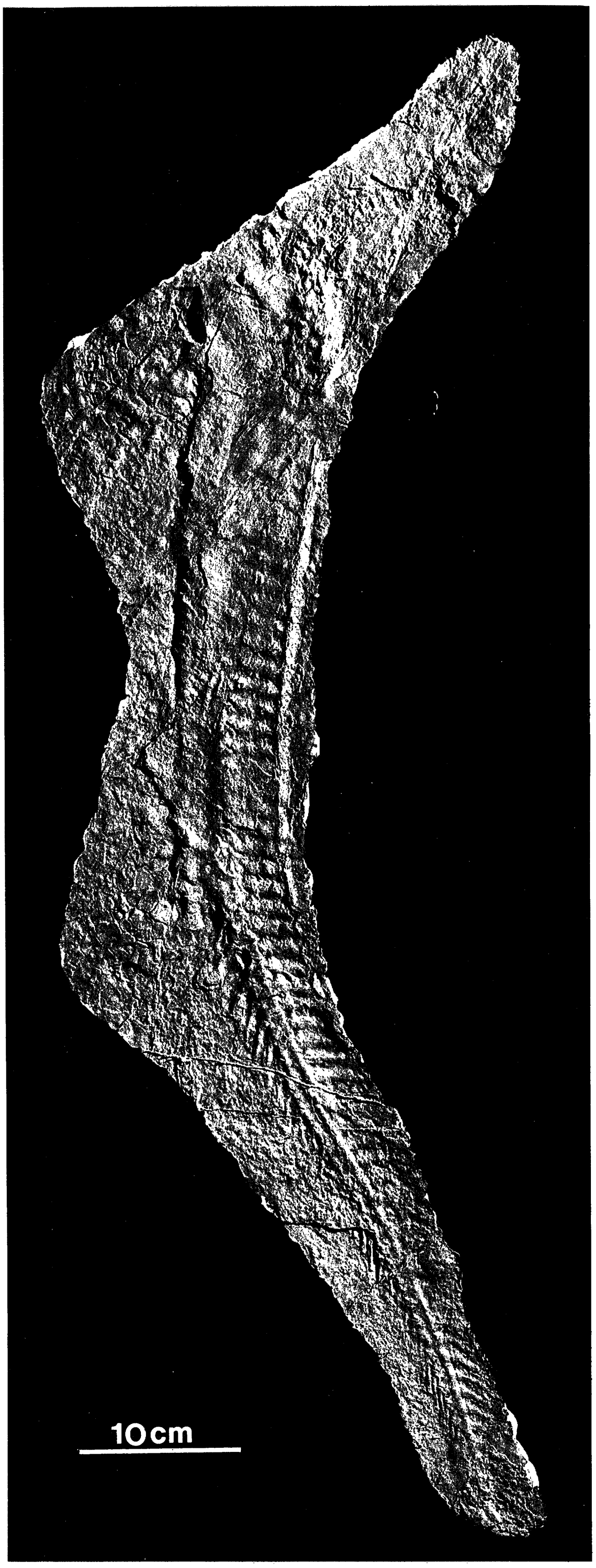

Figure 12. V4070. Unnamed species. Photograph of latex cast of entire specimen. Little detail can be seen except for the fore- and hindlimbs. Approximately one third life size.

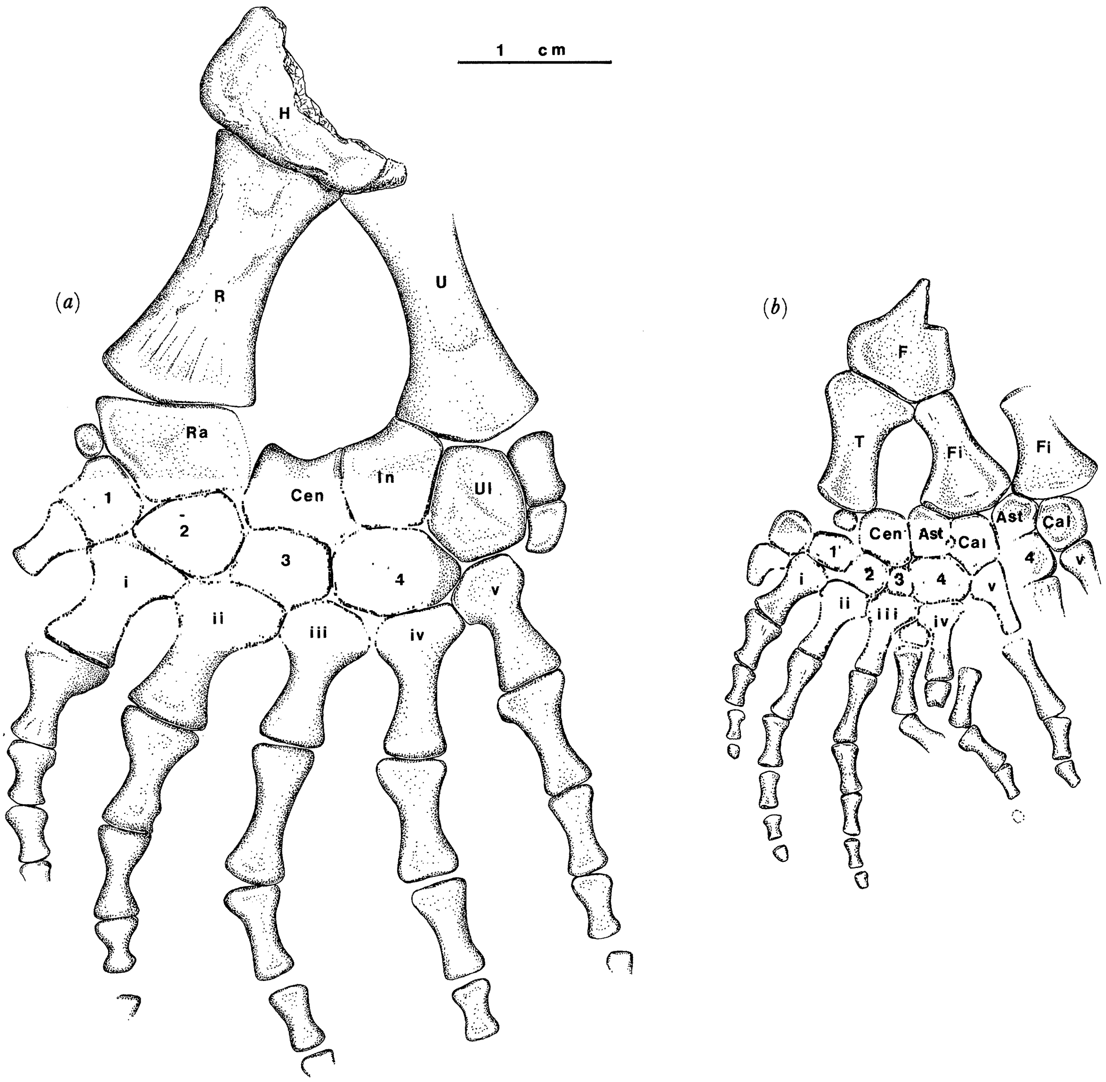

Figure 13. V4070. Unnamed species. (*a*) Lower forelimb. (*b*) Left and underlying right lower hindlimb. Note perforating foramen between astragalus and calcaneum.

as long as those of the type of *Hupehsuchus*, less than 50% at vertebra 14, but increase to 70% at number 22. This is also their relative size at vertebrae 31 and 32. Dermal plates are preserved atop or between the end of the neural spines of caudal vertebrae 5–8. Spines 12 and 13 almost certainly lack dermal elements. No plates are present behind the first caudal spine in the type, but many of the anterior caudal neural spines are represented only by impressions, and the plates may have been lost with the bony elements of the vertebrae. The proportional differences are not overwhelming and might be attributed to differences in relative maturity, even in animals of nearly similar size (Brinkman 1988). Given the marked differences in the structure of the limbs, it seems likely that these animals do belong to different species or genera.

The ulna and radius of V4070 and the holotype of *Hupehsuchus* are comparable in size and the minor differences in morphology might be attributed to differences in the particular orientation and nature of preservation. The carpus, in contrast, differs in several important features. That of V4070 is relatively much wider. There are four, rather than three, carpals in the proximal row. One between the radiale and the intermedium is presumably the homologue of a centrale in other early reptiles. Of even greater significance, a short digit, comprising two elements, occupies a position lateral to the ulnare, in a position comparable to that of the pisiform in primitive terrestrial diapsids. A small, nearly hemispherical bone is present medial to the radiale. There are only four distal carpals, in contrast with five in the type of *Hupehsuchus*, but all are larger. The most medial supports a single small metacarpal or phalanx of an accessory digit. The remaining metacarpals all have much more greatly expanded proximal heads than those of the type of *Hupehsuchus*. The metacarpals and most of the phalanges of V4070 are approximately the same length as those in the type, but the proximal elements are wider and the distal ones more narrow. None of the preserved phalanges are circular as are some in the type of *Hupehsuchus*. None of the terminal phalanges are preserved in their entirety, but the phalangeal count is at least 4, 4, 4, 4, 4, not counting the medial and lateral supernumerary digits. The second and third digits might have five phalanges, as do those of the foot.

In contrast with the crus of the type of *Hupehsuchus*, the distal end of the tibia is much narrower than that of the fibula in V4070. The proximal end is much broader. The differences in the carpus and manus of the two animals are in many ways paralleled by those of the tarsus and pes. There appear to be four proximal tarsals. Those distal to the fibula are clearly the astralagulus and calcaneum, since they surround the perforating foramen in the manner of all primitive amniotes. More medial is a large bone that may be the homologue of the centrale in primitive reptiles (or a completely new element), and a second, considerable smaller unit. There are five distal tarsals, but the position and size of the most lateral indicates that it is the fourth not the fifth distal tarsal. The most medial bone is a supernumerary element, as in the carpus, that supports a single more distal bone. The heads of the metatarsals are greatly expanded. The third articulates with three distal tarsals. The third distal tarsal is a tiny element wedged in between the second and forth. The fifth metatarsal articulates with the calcaneum and the fourth distal tarsal. The head is inturned, rather like that of lepidosaurs, and it might be termed 'hooked'. As in the manus, the size of the phalanges decreases distally, but none are flattened and rounded as are those of the type of *Hupehsuchus*. The phalangeal count is 4, 5, 5, 3+, 3+. The lateral digits are disrupted in the left foot, but some details of the right can be seen beneath it.

Both the foot and the hand of this specimen are wider and more flipper-like than those of the type of *Hupehsuchus*, but the individual phalanges retain their primitive, cylindrical configuration. Because of the relative shortness of the neural and haemal spines, the limbs may have been more important in locomotion than in the other animal. It is surprising to find two obviously closely related genera in a particular locality, but it may be noted that several similar nothosaurs are present in the Middle Triassic of Monte San Giorgio in Switzerland, and many species of icthyosaurs in the Lower Jurassic of Holzmaden, Germany.

Although it is probable that this specimen represents a distinct species or genus, it is not thought advisable to give it a formal taxonomic designation. Although the configuration of the limbs is sufficiently distinct to recognize subsequently discovered specimens, the absence of a skull and the very poor preservation of the remainder of the skeleton render it a poor choice as a type. Until additional specimens are discovered, it seems advisable to leave this individual without a formal name.

NANCHANGOSAURUS

In addition to *Hupehsuchus* and V4070, a further genus has been described that may belong to the same group (figures 14 and 15). This is *Nanchangosaurus*, from the Daye Limestone, Hupei Province, Nanzhang County, Hsunjian District, village of Cold Water Spring, not far from the *Hupehsuchus* locality. It was

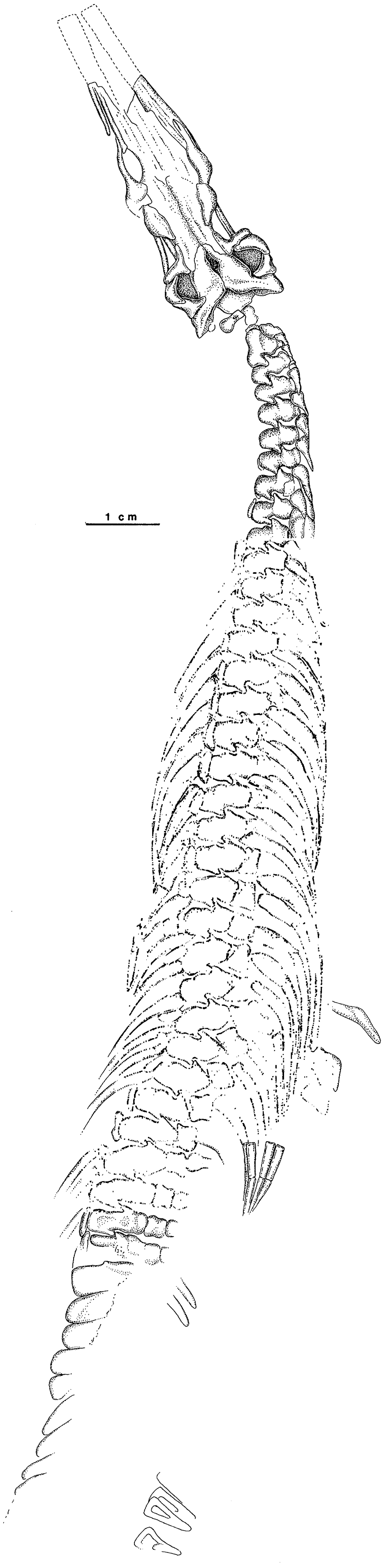

Figure 14. *Nanchangosaurus suni*. V646, Museum of Geology, Beijing. Skeleton of holotype.

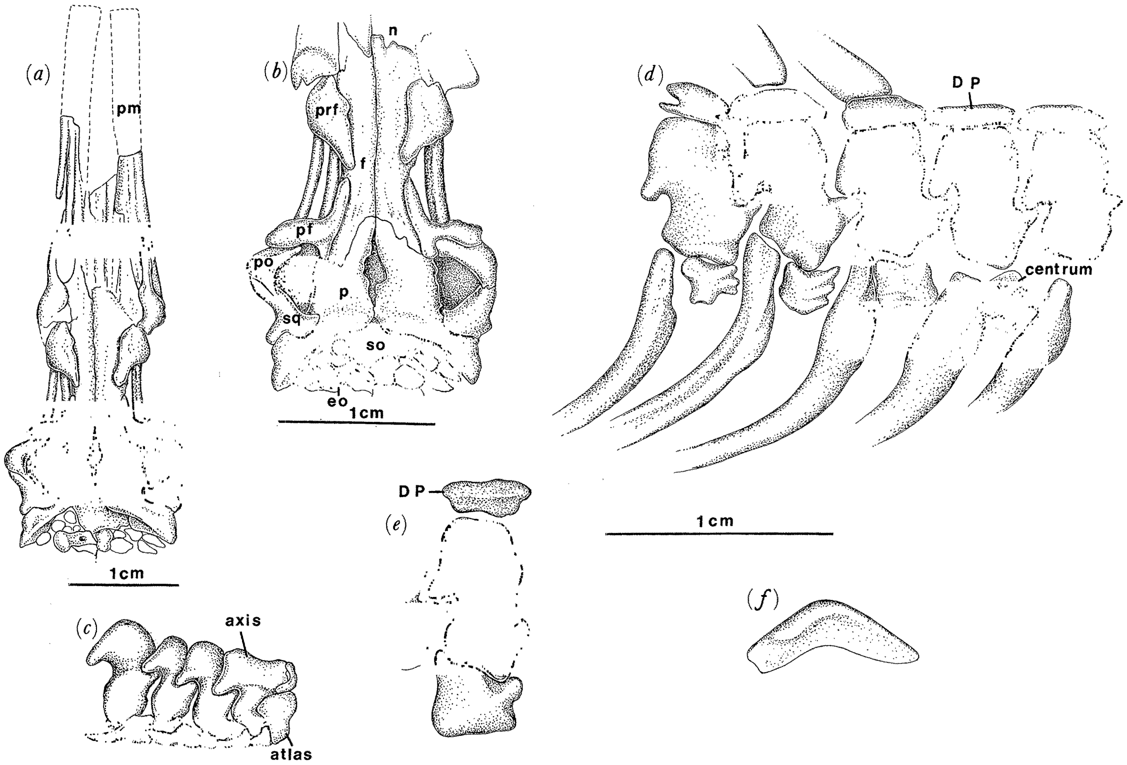

Figure 15. Details of *Nanchangosaurus*. V646. (*a*) Dorsal view of skull. (*b*) Dorsal view of skull table. (*c*) Lateral view of cervical vertebrae. (*d*) Lateral view of trunk vertebrae numbers 15–19. (*e*) Trunk vertebra 22. (*f*) Medial plate of ventral armour near middle of trunk.

originally described as being from the Lower Triassic, but it is now thought to be Middle Triassic in age, although somewhat older than *Hupehsuchus*. It is known from a single specimen (V646, Beijing Geological Museum) of an animal with a skull–trunk length of approximately 19 cm, preserved in dorsal view, with the vertebrae angled to show their lateral surface. The skull roof shows several features in common with *Hupehsuchus*. The snout is very long and flat. The anterior extremity is truncated at the end of the block, but the portion present indicates similar proportions to those of *Hupehsuchus*. The prefrontal overlaps the orbit, as in *Hupehsuchus*, but does not separate the frontal from the orbital margin. In contrast with *Hupehsuchus*, the postfrontal forms part of the anterior margin of the large upper temporal opening. A suture in front of the anterior extremity of the prefrontal in *Nanchangosaurus* indicates that the frontal was long, as in primitive diapsids, in contrast with that of *Hupehsuchus*. The large pineal opening is midway in the length of the parietals. As in *Hupehsuchus* there is a wide supraoccipital and a large displaced exoccipital bearing an opening for the XIIth nerve. A mosaic of small fragments in the occipital area may be remnants of the otic capsule.

Both genera have moderately long necks with short cervical ribs. One is definitely associated with the atlas in *Nanchangosaurus*, whereas this area is not well preserved in *Hupehsuchus*. Ribs 9–11 appear intermediate in length. The 11th is equal in length to three adjacent vertebrae. In *Hupehsuchus*, the 11th rib is the length of at least four vertebrae. It is not possible to determine the length of other posterior neck ribs in either genus, but the neck might be at least a single vertebra longer in *Nanchangosaurus*.

It is difficult to identify the position of the sacrum. Long trunk ribs are present at least as far back as the 28th presacral vertebra, with shorter trunk ribs adjacent to vertebrae 33 and 34. Four haemal arches are visible adjacent to the area of the 39th through the 41st vertebrae. If, as in *Hupehsuchus*, there are three caudal vertebrae anterior to the first haemal arch, this would indicate the presence of 34 presacrals, three less than in *Hupehsuchus*.

The most striking similarity with *Hupehsuchus* is the presence of dermal plates over the posterior cervical and trunk vertebrae. There is, however, no evidence for the division of the neural spines that characterizes the younger genus. The dermal plates are not sculptured, and there is only a single unit per segment that lies immediately above each spine.

The neural spines are approximately as long as the portion of the neural arch extending below the level of the zygapophyses. Although the neural spines are somewhat swollen, the basic pattern of the zygapophyses throughout the trunk region resembles that of primitive terrestrial reptiles, rather than being modified as are those of *Hupehsuchus*. The centra and neural arches are loosely sutured to one another. Transverse processes are not clearly defined. An articulating surface on the ventrolateral margin of the arch that received the tuberculum appears to be continuous with one on the lateral surface of the centrum, as in

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Hupehsuchus. The trunk ribs are thickened proximally. A single large element of the ventral gastralia is visible; it resembles scales of the medial row in *Hupehsuchus* in its size and proportions.

This specimen is not nearly as complete as the type of *Hupehsuchus*, but it probably belongs to the same order. It was originally described by Wang (1959) as a possible sauropterygian, but it shows no significant similarities with either nothosaurs or plesiosaurs. Unfortunately, the species does not show the structure of the shoulder girdle, which would provide the strongest evidence of affinities with that group. The relative shortness of the neck and the greatly elongate and flattened skull are features never encountered in sauropterygians. Nor do any sauropterygians have dermal armour, but all have more conspicuous transverse processes.

Dong (1979) recognized that the skull table of *Nanchangosaurus* was nearly identical with that of *Hupehsuchus* and suggested that both animals might belong to the same genus. The type of *Nanchangosaurus* is substantially smaller than any of the specimens of *Hupehsuchus*, but it is difficult to establish how much change might occur as a result of extensive size increase. The fact that the orbital opening is usually larger in juveniles might account for the contact between the pre- and postfrontal in *Hupehsuchus*, but not in *Nanchangosaurus*. The number of dermal plates is different, but additional pieces might be added during growth. The elaboration of the distal portion of the neural spines might also be size related, but this seems unlikely. It is not likely that the radical differences in the configuration of the zygapophyses of the posterior trunk vertebrae could be accounted for by growth, nor could the relative size of the frontal. It seems logical to identify *Nanchangosaurus* as a member of a primitive sister group of *Hupehsuchus*, although some of the features exhibited by the older genus would be expected in juvenile individuals of *Hupehsuchus*.

What is perhaps the most important difference is the attitude of the fossil. In contrast with all the specimens of *Hupehsuchus*, the only specimen of *Nanchangosaurus* is preserved in primarily dorsal rather than in lateral view. This can be attributed primarily to the shape of the trunk region and the relatively shorter ribs; the longest ribs in *Nanchangosaurus* are only about 60% the length of those in *Hupehsuchus*, relative to the length of the vertebral centra. Although the long neural spines may contribute to the lateral orientation of the skeletons of *Hupehsuchus*, they alone are not responsible for the lateral orientation because the vertebrae are also exposed laterally in *Nanchangosaurus*, although the rib cage is exposed in dorsal view. Clearly, *Hupehsuchus* had a deeper, more laterally compressed body. This may be attributed to greater specialization for lateral undulatory locomotion than *Nanchangosaurus*.

The long flattened rostrum and the combination of vertebral features, with dermal plates and very short transverse processes, are derived features otherwise encountered only in *Hupehsuchus* that give strong evidence of the sister-group affinity of the two genera. The generally less derived aspect of other features of the skeleton of *Nanchangosaurus* indicate that the deepening of the trunk and the implied increased facility for aquatic locomotion in *Hupehsuchus* were achieved within this monophyletic group.

DISCUSSION

Biology

Hupehsuchus is unique among Triassic reptiles in many aspects of the skeleton. The most conspicuous features reflect adaptation to aquatic locomotion. The body outline is fusiform to spindleshaped and laterally compressed; the limbs have the shape of paddles. The great elongation of the neural spines may be associated with the elaboration of the epaxial musculature to accentuate lateral undulation. The articulating surfaces between the neural arches are progressively modified to concentrate the greatest amount of lateral movement in the area of the posterior trunk and tail. The tail resembles that of Triassic ichthyosaurs in being long and nearly straight. It shows no evidence of the downturning encountered in Jurassic and Cretaceous ichthyosaurs which have lunate tails such as rapid swimming thunniform fish (Webb 1982). Swimming would be expected to conform with the axial subundulatory mode discussed by Massare (1988).

The greatly thickened ribs, elaboration of the ventral gastralia, and dermal plates associated with the neural spines would have increased the weight, thus countering the natural buoyancy that would have interfered with underwater swimming. However, the position of the dermal plates, well above the centre of gravity, would have made the body unstable around the long axis.

The great mass and the lateral compression of the body would have made it very difficult for *Hupehsuchus* to move about on land to lay eggs. It is conceivable that this genus gave birth to live young, but no evidence is provided by the specimens currently available. Ichthyosaurs and some sea snakes are the only groups among the many lineages of secondarily aquatic reptiles that are known to give birth to live young.

It is difficult to explain the function of the dorsal plates. Judging by the disarticulated tail section (V4069a), adult specimens of *Hupehsuchus* were among the largest marine vertebrates of their time. Hence the selective advantage for a protective role is not obvious. Neither is the distribution of the plates effective for this role. If *Nanchangosaurus* can be accepted as representative of the morphological pattern that led to *Hupehsuchus*, the elaboration of the dermal plates and the development of the distal portion of the neural spines occurred within the Hupehsuchia, subsequent to its initial aquatic adaptation. The presence of dermal plates might be attributed to inheritance from terrestrial ancestors in which they served to a degree for protection and possibly to provide additional rigidity to the vertebral column. The dorsal portion of the neural spines may have originated by downward growth from the base of the most proximal row of dermal plates. It is more difficult to explain why additional rows of plates were elaborated. They might have extended from the dermis as a nearly rigid dorsal fin, but this does not explain why there were three rows of plates. They presumably contributed to the rigidity of the central trunk region, whereas their lesser development in the posterior trunk and anterior tail would have allowed more flexibility for swimming. The plates would presumably have greatly restricted dorsoventral flexion, but this would also have been greatly limited by the anteroposterior width of the neural spines and the elaboration of the ventral armour. This problem remains unresolved.

The complete absence of teeth suggests some specialized mode of feeding. The appearance of the bone surface does not indicate the presence of a turtlelike beak, although a horny bill of an avian pattern cannot be ruled out. The general configuration of the rostrum resembles the pattern of modern whalebone whales. This raises the possibility that *Hupehsuchus* might have possessed a material resembling baleen. Size is not a major basis for distinguishing *Hupehsuchus* from the habitus of baleen whales, since early baleen whales were only about 3–4 m in length (Pivorunas 1979).

Sanderson & Wassersug (1990) recognized two categories of mobile suspension feeders, continuous ram feeders and intermittent ram feeders. *Hupehsuchus* corresponds with continuous ram feeders in the possession of a large skull and mobile lower jaws without a fixed symphysis. On the other hand, the skull is not relatively larger than that of Triassic ichthyosaurs, all of which have teeth, and the skull is narrow, in marked contrast with baleen whales. A more serious difficulty in accepting the hypothesis of continuous ram feeding is that *Hupehsuchus* has a relatively long neck, in contrast with the very short necks of whales, especially baleen whales, in which the head functions as an extension of the trunk. It would be difficult for *Hupehsuchus* to avoid bending the neck if it sped through the water with its large mouth agape. Significantly, there is little if any shortening of the neck from the condition in the otherwise more primitive genus *Nanchangosaurus*. It is possible that these genera were intermittent suspension feeders, and opened their mouths to feed only when stopped or at slow speeds. The very long retroarticular process indicates the capacity to open the mouth with considerable force against the resistance of the water. Unfortunately, the area of the jaw articulation is not sufficiently well preserved to establish the degree of jaw opening that was possible.

Phylogenetic position

The monophyly of the Hupehsuchia is established by the characters cited in the ordinal diagnosis. As nearly all aspects of the skeleton are known in *Hupehsuchus*, it should be easy to establish its phylogenetic position. Knowledge of *Nanchangosaurus* should facilitate recognition of the primitive anatomical pattern of this group.

Hupehsuchus can be recognized as a member of the subclass Diapsida on the basis of all the osteological criteria established by Benton (1985). (1) Presence of a superior temporal fenestra. (2) Presence of an upper temporal arch formed by a triradiate postorbital and a triradiate squamosal which have a small contact with each other; the parietal has small contacts with the postorbital and quadrate and it has a lateral process. (3) Presence of a well-developed suborbital fenestra. (4) Maxilla, palatine, ectopterygoid and jugal bones and their interrelationships modified as a result of the presence of the suborbital fenestra. The maxilla–palatine suture is reduced in length; the ectopterygoid is reduced and the contact between the ectopterygoid and the cheek is reduced; there is no ectopterygoid–maxilla contact.

Evans (1988) cited an additional character, a lateral temporal opening, which was probably present in the most primitive diapsids. This opening is missing in many groups of aquatic diapsids and in the terrestrial Araeoscelidae and Trilophosauridae. She also cited the greater length of the cervical vertebrae, but this feature is only known in otherwise highly derived genera.

Although membership in the Diapsida is well supported, it is difficult to establish more specific affinities within this group. Benton recognized two grades of diapsids, the stem Diapsida, including the Petrolacosauridae, Araeoscelidae and several less well-known families, and the Neodiapsida, including the Archosauromorpha and the Lepidosauromorpha. The Neodiapsida is recognized on the basis of the following derived characters: reduced lacrimal, ventromedial flanges on parietal, absence of caniniform maxillary teeth, reduced quadratojugal, quadrate exposed in lateral view, quadrate notched posteriorly, stapes slender, reduced number of teeth on pterygoid, no teeth on parasphenoid, retroarticular process, ulna lacks good olecranon and sigmoid notch, acetabulum rounded, femur sigmoidal and slender, distal articular surfaces on femur level, femur more than 10% longer than humerus. Although numerous characters are listed, many are difficult to compare with the condition in the Hupehsuchia. None of the characters of the appendicular skeleton can be compared in detail because the girdles and limbs are highly modified for aquatic locomotion. Similarly, the complete absence of teeth make it uncertain that specific changes in the dentitions are really homologous. The check, quadrate and middle ear region are not well-enough preserved for comparison. It is probable that the lacrimal was reduced, but the antorbital region is so specialized that specific comparison is difficult. The parietals appear to bear flanges. The retroarticular processes are very long. The last three characters suggest inclusion of *Hupehsuchus* within the Neodiapsida, but with some hesitation.

Similar problems arise in evaluating possible relationships with either the Archosauromorpha or the Lepidosauromorpha. Benton listed six synapomorphies of the Lepidosauromorpha. (1) Postfrontal enters border of upper temporal fossa. This is true of *Nanchangosaurus*, but not for *Hupehsuchus*. This characters is otherwise variable among both groups. (2) Accessory intervertebral articulations present on the midline of the neural arch between the zygapophyses. Accessory articulations appear to be present in *Nanchangosaurus*, although confirmation would require partial disarticulation of the vertebrae. The bases of the neural spines resemble most closely those of the early aquatic lepidosauromorph *Hovasaurus*, which probably swam by lateral undulation of the trunk and tail (Currie 1981). (3) Cervical centra shorter than average mid-dorsal centra. This is true, but might be related to aquatic adaptation rather than being indicative of relationship. (4) Dorsal ribs single-headed. This is certainly the case. Characters 5 and 6 refer to the sternum, which is certainly absent. Of Benton's list, three characters are shared with lepidosauromorphs. A fourth might be added: the shortness of the transverse processes in the trunk region.

Benton listed 14 archosauromorph synapomorphies. Characters 1, 2, 3 and 5, cannot be compared, either because of the lack of resolution of the character in the known specimens of the Hupehsuchia, or because the skull is too modified to establish homology. Loss of tabular (character 4), loss of cleithrum (8), and loss of entepicondylar foramen (9) occur in too many groups to be reliable indicators of relationship. Character 6, vertebrae not notochordal, occurs in the Hupehsuchia, but also in sauropterygians, which are excluded from the Archosauromorpha. Character 7, transverse processes on dorsal vertebrae project as distinctive narrow elongate processes, is contradicted by the condition in the Hupehsuchia in which they are extremely short. Character 10, loss of foramen in carpus between ulnare and intermedium, is true of the Hupehsuchia, but also of many other aquatic diapsids. Characters 11, 12 and 14 are very important features of the tarsus and foot. None are found in the Hupehsuchia, but may have been lost in relationship to aquatic specialization. The fifth distal tarsal is lost (character 13), but this occurs in many other aquatic forms as well. Six of the derived characters cited by Benton are shared by archosaurmorphs and the Hupehsuchia, but none are unique to these two groups. There is not strong evidence for the affinity of the Hypehsuchia with either group of advanced diapsids.

Most recent efforts to establish relationships among the diapsids have concentrated on the terrestrial groups. On the other hand, several authors have discussed the possible relationships of particular aquatic groups to the Diapsida (Carroll & Gaskill 1985; Massare & Callaway 1990; Mazin 1982; Rieppel 1987, 1989; Sues 1987*a*, *b*). It is not the purpose of this paper to undertake yet another review of diapsid classification. Rather, we wish to consider possible relationships of the Hupehsuchia within this assemblage. With this limited goal in mind, we have listed all the derived features by which *Nanchangosaurus* and *Hupehsuchus* differ from primitive diapsids, and compared them with the derived characters of other aquatic diapsids (table 1). Comparison was initially limited to contemporary groups known from Triassic fossils: nothosaurs, placodonts, thalattosaurs, ichthyosaurs and *Helveticosaurus*, as well as stem lepidosauromorphs and archosauromorphs.

According to the principles of phylogenetic systematics (Hennig 1966; Wiley 1981; Ax 1987), the probability of sister-group relationship may be judged by the relative number of derived features groups share in common. The largest number of characters are shared with the highly specialized marine groups – the ichthyosaurs and nothosaurs – whereas the less-specialized aquatic groups – the placodonts, thalattosaurs and the genus *Helveticosaurus* – occupy an intermediate level of similarity.

Accepted literally, this pattern of character distribution would suggest a sister-group relationship between the Hupehsuchia and the ichthyosaurs or nothosaurs, with the placodonts, *Helveticosaurus*, and thalattosaurs occupying a more distant position. These data might be interpreted as indicating that all early Mesozoic aquatic reptiles shared a common ancestry, distinct from that of the lepidosauromorphs and archosauromorphs. This seems unlikely, however, because ichthyosaurs, nothosaurs, placodonts and thalattosaurs exhibit very different proportions of the trunk and limbs, indicating divergent modes of aquatic locomotion, as well as having very different patterns of skull and vertebral morphology.

The problem is to establish whether or not the large number of derived characters shared by these groups are actually homologous. Ichthyosaurs share the largest number of derived characters in common with *Hupehsuchus*, but nearly all of these characters are also shared with other aquatic groups. Only three derived characters are uniquely shared by Triassic ichthyosaurs and *Hupehsuchus*: relatively long antorbital region, short transverse processes for the ribs, and laterally compressed trunk region. However, the degree of lateral compression is not as great in the more primitive genus *Nanchangosaurus*.

Adequately known Triassic ichthyosaurs share the following unique derived characters (J. M. Callaway, personal communication): very large orbits, short cheek region, absence of a clearly defined neck region, length of ribs increasing progressively from neck into trunk region, ribs articulate primarily with centrum, not with arch. None of these characters are expressed in the Hupehsuchia. This does not preclude their having evolved in early ichthyosaurs from an ancestry among the Hupehsuchia, but there is no evidence that this did happen.

The basic structure of the vertebrae in *Hupehsuchus* seems very distinct from that of all adequately known ichthyosaurs, in which the centra dominate the column at the expense of the arches. Most ichthyosaurs are characterized by centra that are much higher than long and deeply amphicoelous. However, in the early Triassic genera *Utatsusaurus* (see Shikama *et al.* 1978) and *Chaohusaurus* (Young & Dong 1972) the centra are at least as long as they are high, and not deeply amphicoelous.

Leaving aside the many similarities also shared with other groups of marine reptiles, there are no more unique derived similarities shared by ichthyosaurs and the Hupehsuchia than those shared by the Hupehsuchia and primitive terrestrial lepidosauromorphs and archosauromorphs.

The difficulty of identifying unique derived characters uniting the Hupehsuchia with ichthyosaurs, despite the great number of derived similarities, raises the possibility that skeletal features that are common to

Table 1. *Derived character states in* Hupehsuchus (*using primitive diapsids as an outgroup*) *compared with the distribution of similar characters in primitive members of other groups of diapsid reptiles*

(0 = primitive features of neodiapsids. 1 = derived condition seen in *Hupehsuchus*.)

	Primitive lepidosauromorphs	Primitive archosauromorphs	Triassic ichthyosaurs	nothosaurs	*Helveticosaurus*	placodonts	Thalattosauria	Mosasauridae	Plesiosauria
skull									
elongate rostrum	0	0	1	0	0	0	0	0	0
absence of lateral temporal opening	0	0	1	0	0	1	0	0	0
elaboration of quadratojugal	0	0	1	0	?	1	0	0	0
posterior position of narial opening	0	0	1	1	0	1	1	1	1
loss of palatal dentition	0	0	1	1	?	0	0	0	1
orbit overlapped by prefrontal	0	0	1	0	0	1	0	1	0
loss of tabular	0	1	1	1	?	1	1	1	1
loss of supratemporal	0	0	0	1	?	1	0	1	1
loss of postparietal	0	0	1	1	?	1	1	1	1
lower jaw									
retroarticular process more than 10% of total jaw length	0	0	0	1	1	1	1	1	1
body form									
fusiform	0	0	1	1	0	0	1	1	1
laterally compressed	0	0	1	0	0	0	0	0	0
vertebrae									
dermal plates above neural spines	0	0	0	0	0	1	0	0	0
cervical centra shorter than trunk centra	1	0	0	1	1	1	0	0	0
centra not deeply amphicoelous	0	1	0	1	0	0	0	1	1
arch and centra not fused in adult	0	0	1	1	0	0	0	0	0
at least 9 cervical vertebrae	0	0	?	1	1	0	0	0	1
at least 35 resacral vertebrae	0	0	1	1	1	0	0	0	1
less than two sacral vertebrae	0	0	1	0	?	0	0	1	0
reduction or loss of distinct transverse processes	1	0	1	0	0	0	0	1	0
modification of posterior trunk and caudal zygapophyses	0	0	0	0	0	0	0	1	0
ribs									
trunk ribs with confluent heads	1	0	0	1	1	1	1	1	1
trunk ribs pachyostotic	0	0	0	1	0	0	0	0	0
no clearly defined sacral ribs	0	0	1	0	?	0	0	1	0
appendicular skeleton									
absence of cleithrum	0	1	1	1	1	1	1	1	1
scapulocoracoid not coossified in adult	0	1	1	1	1	1	1	1	1
forelimb longer than rear	0	0	1	1	0	0	0	1	0
humerus flattened, shaft not well defined	0	0	1	0	0	0	0	1	0
humerus lacking entepicondylar foramen	0	1	1	0	1	1	1	1	1
humerus lacking ectepicondylar foramen and groove	0	0	1	0	1	0	1	0	1
articulating surfaces for ulna and radius terminal	0	0	1	1	1	1	0	1	1
ulna and radius flattened	0	0	1	0	0	0	0	1	1
ulna lacking olecranon	0	0	1	1	1	1	1	1	1
loss of pisiform	0	1	1	0	1	1	1	0	0
no centralia	0	0	1	1	1	1	1	?	1
loss of distal carpal 5	0	0	0	1	1	1	1	1	1
polyphalangy (manus)	0	0	1	0	1	0	0	1	1
all of pelvis reduced in size	0	0	1	0	0	0	0	1	0
ilium narrow and anteriorly directed	0	0	1	0	0	0	0	1	0
femur lacking ventral groove and ridge system	0	0	1	0	?	0	0	1	1
tibia and fibula flattened	0	0	1	0	0	0	0	1	1
centrale in proximal tarsal row	0	0	?	0	0	0	0	?	1
fifth distal tarsal lost	0	1	?	1	?	?	1	1	0
fifth metatarsal articulates with fourth distal tarsal	0	1	?	?	?	?	1	?	1
polyphalangy (pes)	0	0	1	0	1	0	0	1	1
total	3	8	32	22	16	19	16	29	26

secondarily aquatic reptiles might have evolved convergently in each of these groups. To test this hypothesis, further comparisons were made with two other groups of secondarily aquatic diapsids: the plesiosaurs and the mosasaurs. Much recently reported evidence supports the derivation of plesiosaurs from Triassic nothosaurs (Carroll & Gaskill 1985, Sues 1987*a*), but the specialized body plan that characterizes plesiosaurs is not known before the Lower Jurassic, making it extremely unlikely that the derived character states they exhibit are homologous with those of *Hupehsuchus*. It has long been recognized that mosasaurs are the sister-group of terrestrial varanoid lizards. This is amply demonstrated by a host of varanoid synapomorphies (Russell 1967; Estes *et al.* 1988). Most of the derived features in which mosasaurs resemble *Hupehsuchus* only evolved in the middle to late Cretaceous. yet, plesiosaurs share 26 derived features of the skeleton with *Hupehsuchus*, and mosasaurs share 29. It is obvious from these examples that skeletal features specifically associated with adaptation to an aquatic way of life must be used with caution in evaluating relationships among major groups of diapsid reptiles.

According to the usual approach of phylogenetic analysis, homoplastic (convergent) characters should be identifiable by application of the principle of parsimony (Patterson 1982). If two groups are united by many similar derived characters, but fewer characters support an alternative relationship, the smaller number of characters are assumed to have resulted from convergence. Comparison of *Hupehsuchus* and mosasaurs, however, suggests that **most** of the derived characters exhibited by *Hupehsuchus* were convergently acquired by mosasaurs. How could this be recognized if we did not know from other evidence that mosasaurs evolved separately from terrestrial ancestors that retained the primitive character state for these features? The principle of parsimony cannot be directly applied in this situation.

In some cases it may be possible to recognize that similar characters are not homologous by detailed anatomical comparison. For example, although both ichthyosaurs and mosasaurs have posteriorly located external nares, their relationships with the surrounding bones are different, suggesting that their posterior position is not strictly homologous. On the other hand, many of the changes related to an aquatic way of life are of such a general nature that it is not possible to refute the possibility of their common origin by direct observation. For example, many groups of secondarily aquatic reptiles have a loose articulation between the neural arches and the centra. In a general sense this is the 'same' character in all groups, although it may have evolved independently many times. Similarly, many groups, including aquatic mammals, have independently reduced the degree of ossification of the ends of the limb bones, the carpals and tarsals. The same tissues, the same developmental processes, and the same functional explanations may be involved in all groups, but the changes are not strictly homologous because they have occurred independently in each group. Rieppel (1989) noted that many of the similarities between *Helveticosaurus* and other marine diapsids may be attributed to paedomorphosis. This is clearly evident in the reduction in the degree of ossification in the girdles and limbs, which can readily be seen as the retention of a juvenile condition. A common mechanism does not, however, indicate a common ancestry.

Another way to assess the homology of characters is to consider the basic adaptive modes of the groups in question. If, as in the case of ichthyosaurs and plesiosaurs, their basic modes of locomotion are very different, is it likely that specific similarities, such as the complex mosaic pattern of the carpals and tarsals, are strictly homologous? Even if such groups did share a common ancestry, it is not likely that the derived characters shared by their primitive aquatic ancestors would be retained in their highly divergent descendants.

We might choose not to use characters associated with aquatic locomotion in attempting to establish relationships among these groups. Unfortunately, other characters expressed in this assemblage might also have been subject to convergence. Might the relatively massive cheeks in placodonts, ichthyosaurs and *Hupehsuchus* have evolved separately in each group in order to accommodate the force of augmented jaw musculature necessary for aquatic feeding? The plesiosaurs also have a relatively solid cheek structure, although the cheek region in their plesiomorphic sister group, the nothosaurs, was much more lightly built. Or, can we safely assume that the loss of the tabular, supratemporal and postparietal support the monophyly of placodonts, nothosaurs and the Hupehsuchia? All are known to have been lost independently in archosauromorphs and lepidosauromorphs (Carroll & Currie 1991). In fact, is there any category of characters that is not commonly subject to convergence? Is it ever possible to establish phylogenetic relationships without some specific information regarding the strict homology of the characters in question? The problem of establishing the relationships among the aquatic diapsids suggests that it is not.

The concept of homology rests ultimately on the genealogical continuity of the characters in question from common ancestors through their descendants. The actual distribution of character states in potential ancestors can only be established from the fossil record. The problem of establishing the homology of characters among aquatic diapsids would presumably be lessened if we knew more of the primitive representatives of these groups. Many divergent opinions regarding the taxonomic position of the plesiosaurs were proposed on the basis of the Jurassic and Cretaceous members of this group (see Williston 1907; Romer 1974). Their affinities with primitive diapsids were only recognized on the basis of the cranial anatomy of their Triassic relatives, the nothosaurs (see Kuhn-Schnyder 1962; Carroll 1981; Carroll & Gaskill 1985). Massare & Callaway (1990) point out a similar situation regarding the relationship of the ichthyosaurs. Their affinities remained a complete mystery when only the Jurassic and Cretaceous genera were considered. Extension of comparison to the Triassic genera suggests divergence from the base of the lepidosauromorph assemblage. A robust hypothesis of the affinities of the Hupehsuchia requires knowledge of the homology of their derived characters that can only be gained through knowledge of fossils of more primitive members of this group.

Without casting doubt on the utility of the methodology of phylogenetic systematics to recognize relationships where there are sufficient data to characterize all the relevant groups, it is yet necessary to question whether this methodology can yield valid phylogenies when significant portions of the data are not available.

The neodiapsid radiation leading to nothosaurs, placodonts, *Helveticosaurus*, ichthyosaurs, thalattosaurs and the Hupehsuchia might have occurred over the entire space of the Permian, some 38 million years. Aquatic adaptation may have occurred separately in each group, or some of these groups might have a unique sister-group relationship to one another, but all of the actual evidence (in terms of original synapomorphies) might be lost in their known descendants. It is possible that none of the character states exhibited in the known genera provide evidence of the pattern of their radiation.

If the ancestors of the Hupehsuchia evolved from primitive terrestrial diapsids, separate from any other recognized group, the earliest members of these two lineages would be expected to share some unique features in common with one another. The known member of the Hupehsuchia, in contrast, are so specialized for an aquatic way of life that any synapomorphies that their primitive ancestors may have shared with their specific terrestrial antecedents were apparently lost. Their specific sister-group affinities are potentially knowable, but they are not necessarily determinable on the basis of currently available evidence.

It is clear from the problems of establishing the phylogenetic position of the Hupehsuchia that simple tabulation of the total number of derived characters shared with other groups of contemporary diapsids is not sufficient to establish relationships. Most of derived characters appear to be subject to convergence among secondarily aquatic reptiles. Systematists should recognize that there are situations in which strict application of parsimony may give misleading results. This problem is particularly serious in cases where we have little knowledge of the fossil record. Computer programs are designed to produce cladograms that demonstrate relationships. None are capable of recognizing situations in which the specification of sister-group relationships cannot be justified.

SUMMARY

The fossils of *Hupehsuchus* and *Nanchangosaurus* provide knowledge of a previously unrecognized assemblage of Triassic aquatic reptiles. Most features of *Hupehsuchus* demonstrate a high degree of adaptation for rapid swimming. The function of the multiple rows of dermal plates above the neural spines remains enigmatic. The Hupehsuchia are definitely members of the Diapsida, but their specific affinities to other groups of primitive diapsids remain unknown. The great degree of convergence shown by secondarily aquatic reptiles makes it very difficult to apply cladistic methodology to establish their phylogenetic position. The extensive gap in the fossil record of the neodiapsids during their period of initial radiation makes it difficult to discover synapomorphies that unite the major groups. The mode of swimming by lateral undulation and the reduction of the transverse processes suggest the possibility that ichthyosaurs and the Hupehsuchia might share a common aquatic ancestry, but this is not firmly established.

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KEY TO ABBREVIATIONS USED IN FIGURES

a, angular
art, articular
Ast, astragalus
at, atlas
ax, axis
axi, axis intercentrum
Cal, calcaneum
Cen, centrale
cb, ceratobranchial
clav, clavicle
d, dentary
DP, dermal plate
dto, dorsal temporal opening
ect, ectopterygoid
en, external naris
eo, exoccipital
F, femur
f, frontal
FI, fibula
H, humerus
I, ilium
ic, interclavicle
In, intermedium
ISC, ischium
m, maxilla
n, nasal
P, pubis
p, parietal
pal, palatine
pf, postfrontal
pm, premaxilla
po, postorbital
prf, prefrontal
ps, parasphenoid
pt, pterygoid
q, quadrate

qj, quadratojugal
qr pt, quadrate ramus of pterygoid
R, radius
Ra, radiale
rt art p, retroarticular process
sc cor, scapulocoracoid
so, supraoccipital
sof, suborbital fenestra
sq, squamosal
T, tibia
U, ulna
Ul, ulnare
v, vomer
1–4, distal carpals and tarsals
i–v, metacarpals and metatarsals

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Figure 3. The holotype of *Hupehsuchus nanchangensis*, V3232, in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. Photograph of cast. Specimen 73 cm in length.

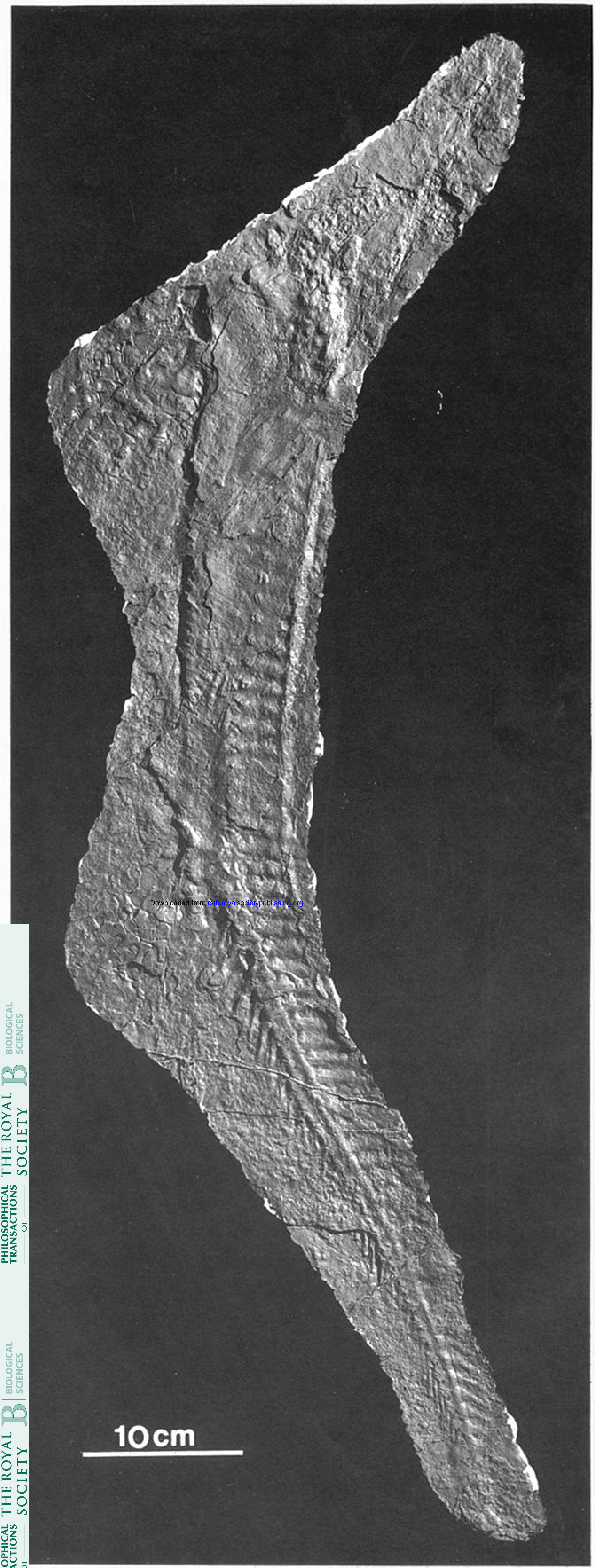

Figure 12. V4070. Unnamed species. Photograph of latex cast of entire specimen. Little detail can be seen except for the fore- and hindlimbs. Approximately one third life size.