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Functional Morphology and Ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia)

Kebang Lin
Olivier Rieppel

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Functional Morphology and Ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia)

Kebang Lin

Olivier Rieppel

Abstract

Keichousaurus hui Young, 1958, from the Middle Triassic of Guizhou, China, is a small sauropterygian reptile. It has a short snout and elongated temporal openings, resembling the European pachypleurosaurid *Dactylosaurus*. Unlike all other stem-group eosauroptrygians, the parietal foramen is displaced anteriorly. The neck is long and flexible. The body is rigid and the bones pachyostotic. There are two or three sacral vertebrae. There is distinct sexual dimorphism, as in Alpine pachypleurosaurids. The broad ulna is autapomorphic for *Keichousaurus*. The growth of the humerus is highly positively allometric, reflecting the principal role of the forelimb in locomotion. The overall horizontal orientation of the pectoral girdle indicates that *Keichousaurus* was not a subaquatic flyer. Instead, a drag-based regime was used in locomotion.

Introduction

Reinvasion of the aquatic environment occurred repeatedly in the history of tetrapod evolution. In every major tetrapod clade there have been lineages that were adapted to a life in the water. The Mesozoic Sauropterygia is one of such lineages among reptiles. Three major clades are traditionally recognized within Sauropterygia. The Placodontia, sister clade of the Eosauroptrygia (Rieppel, 1994), is characterized by a massive and well-consolidated skull, crushing teeth, and heavy limbs, indicating a bottom-dwelling, mollusc-eating mode of life. The distribution of placodonts is restricted to the Middle and Upper Triassic of the western Tethyan realm. Stem-group Eosauroptrygia ("nothosaurs") of the Triassic ranged from small to large size (20 cm to 4 m), and their occurrence is restricted to a lagoonal or continental shelf environment, or to shallow epicontinental seas. Their limb structure, although modified somewhat from the primitive condition in advanced forms, is still closely comparable to terrestrial forms. Crown-group Eosauroptrygia, plesiosaurs, pliosaurs, and elasmosaurs, were a prominent faunal element in Jurassic and Cretaceous open seas, reaching up to 15 m in length.

Their specialized body proportions and limb structure indicate an obligatory aquatic mode of life. Their trunk region was rigid, the limb girdles and limbs were massive, and the manus and pes were transformed to hydrofoils.

The monophyly of the Sauropterygia is supported by a number of synapomorphies, including the loss of the lower temporal bar and lacrimal, the scapula located partially lateral to the clavicle, and the interclavicle located ventral to the clavicles. The phylogenetic interrelationships of Triassic stem-group Eosauroptrygia were recently reviewed by Rieppel (1997). They comprise two clades, an unnamed clade here referred to as "nothosaurs" (pachypleurosaurids, *Simosaurus*, *Germanosaurus*, *Nothosaurus*, and *Lariosaurus*) and the Pistosauria. The "nothosaurs" appear at the transition from the Lower to the Middle Triassic, peak in diversity during the Middle Triassic, and disappear with the Upper Triassic eustatic sea level drop: they are never found above the Norian-Rhaetian boundary. Among "nothosaurs," two morphological groups are traditionally recognized on the basis of size and skull proportions: nothosaurids and pachypleurosaurids. Nothosaurids are the larger of the two (adult size usually longer than 2 m). Their

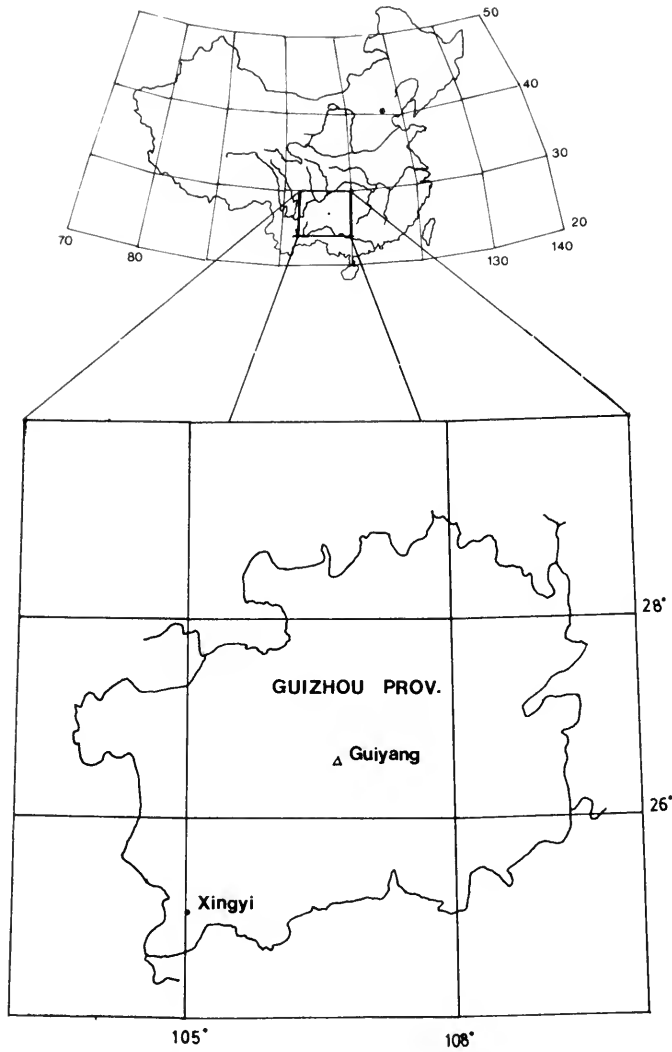


FIG. 1. Geographical occurrence of *Keichousaurus hui* (Middle Triassic, Anisian). The locality is about 200 km south-southwest of Guiyang, the capital city of Guizhou Province.

skull is relatively larger compared to their body, and the upper temporal fenestrae are larger than the orbits. Pachypleurosaurids, by contrast, are generally small. They have a relatively small skull, and their upper temporal fenestrae are smaller than the orbits. Indeed, the upper temporal openings of pachypleurosaurids are either much smaller than or have a different shape from those of more basal diapsids, rendering the small upper temporal fenestrae a synapomorphy of the group (Rieppel & Lin, 1995). Another unique feature of pachypleurosaurids is the quadrate fossa behind the articular facet in the retroarticular process, which might have participated in forming the middle ear cham-

ber. The quadrate of pachypleurosaurids is concave posteriorly and may have supported a tympanum (Rieppel, 1989).

Pachypleurosaurids are abundant from the Anisian–Ladinian boundary through the Ladinian of the Alpine Triassic, an intraplatform basin habitat extending along the northern shore of the developing Neotethys ocean. The study of European pachypleurosaurids goes back to the beginnings of vertebrate paleontology in Italy in the 1850s (Rieppel, 1987). By far the largest number of specimens have been found at Monte San Giorgio, Switzerland. Four species of pachypleurosaurids are recognized there: *Serpianosaurus mirigiolen-*

sis (Rieppel, 1989), *Neusticosaurus pusillus*, *Neusticosaurus peyeri* (Sander, 1989), and *Neusticosaurus* ("Pachypleurosaurus") *edwardsii* (Carroll & Gaskill, 1985; Sander, 1989).

In 1957, a field team from the Museum of Geology, Chinese Ministry of Geology, led by C. C. Hu, collected a number of primitive sauropterygian fossils in Middle Triassic deposits of the province of Guizhon, China. These sediments represent a shallow epicontinental sea within the western part of the Pacific faunal province. The specimens were sent to the Institute of Vertebrate Paleontology of the Chinese Academy of Sciences and formed the basis of a preliminary description by Young (1958), which included additional specimens collected by T. T. Ts'ao of the Guizhou Museum on behalf of the Institute. The pachypleurosaur was named *Keichousaurus hui*, but because the specimens were not adequately prepared at the time and the illustrations were crude, comparison with the European genera by later workers met with great difficulties. During the past 30 years, more material was collected from the same locality. Most of the specimens can be referred to *Keichousaurus hui* on the basis of general body proportions and configuration of the individual skeletal elements. The present study is based on some of the new specimens collected by Mr. Huiyang Cai of Guizhou Museum and by the senior author in 1984, as well as on the specimens studied by C. C. Young (1958), which are kept in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing. The purpose of this paper is to give a detailed description of the osteology of *Keichousaurus hui*, so that a detailed comparison with other pachypleurosaurids and nothosaurids can be made. The paper concludes with a discussion of the functional morphology of this pachypleurosaur.

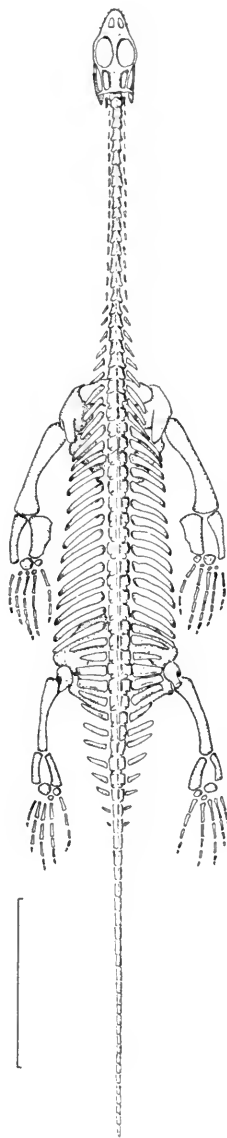


FIG. 2. Skeletal reconstruction of *Keichousaurus hui*. Scale bar = 50 mm.

Systematic Paleontology

Diapsida Osborn, 1903

Neodiapsida Benton, 1985

Lepidosauromorpha Benton, 1985

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994

Pachypleurosauroidea Huene, 1956

***Keichousaurus* Young, 1958**

TYPE SPECIES—*Keichousaurus hui* Young, 1958.

DIAGNOSIS—Small to medium-sized pachypleurosaur. There are 25–26 cervical and 18–19 dorsal vertebrae. The cervical region is longer than the trunk region. The rostrum is short and blunt. The following characters differentiate *Keichousaurus* from other pachypleurosaurids: the upper temporal openings of *Keichousaurus* are elongated, only slightly shorter than the orbit; the parietal opening is anteriorly positioned and tends to close in maturity; the humerus is stronger and longer than the

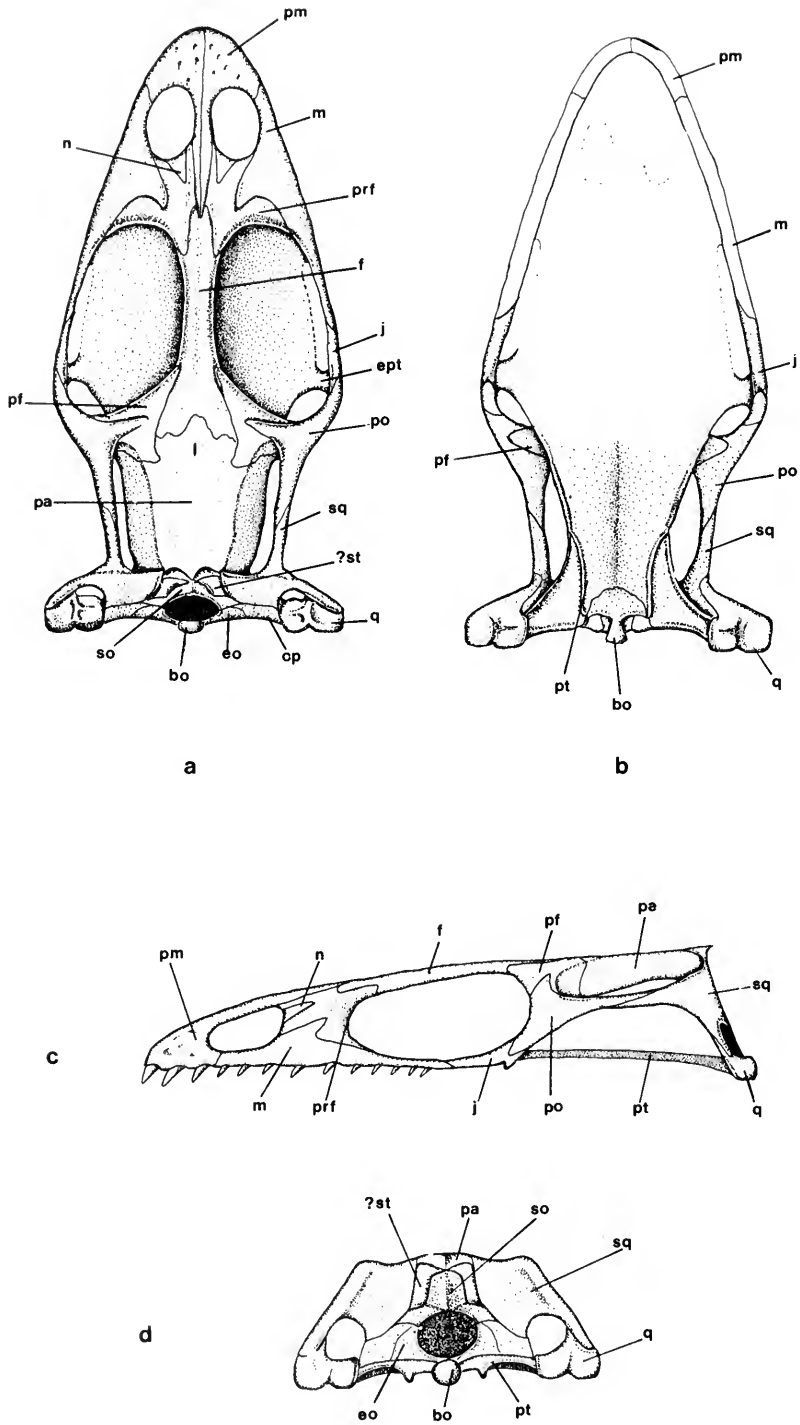


FIG. 3. Reconstruction of the skull of *Keichousaurus hui*; **a**, dorsal view; **b**, palatal view; **c**, lateral view; **d**, occipital view. Abbreviations: a, angular; ar, articular; ast, astragalus; bo, basioccipital; c, centrum; ca, caudal vertebra; cal, calcaneum; cb, ceratobranchial; cl, clavicle; cor, coracoid; d, dentary; dc, distal carpal; dt, distal tarsal; eo, exoccipital; ept, ectopterygoid; f, frontal; fi, fibula; ic, intercentrum; icl, interclavicle; il, ilium; im, intermedium; isc, ischium; j, jugal; m, maxilla; n, nasal; na, neural arch; op, opisthotic; pa, parietal; pc, centrum; pf, postfrontal; pm,

femur, and the ulna is broad; two or three sacral vertebrae; slight hyperphalangy.

DISTRIBUTION—Middle Triassic. Southwestern China (Fig. 1).

Keichousaurus hui Young, 1958

HOLOTYPE—V952 in IVPP.

DIAGNOSIS—Same as for genus.

REFERRED MATERIAL—The specimens whose numbers have the prefix GXD are from the collection of Guizhou Province Museum; those with prefix V are from the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; and the one with BPV is from the Beijing Natural History Museum.

1. V952. The type specimen of *Keichousaurus hui* designated by Young (1958); an adult skull in dorsal view with 21 cervical vertebrae.
2. GXD7601. An extremely well-preserved skull in dorsal view with 14 cervical vertebrae. Judged by its size and structure, this specimen represents a somewhat earlier development stage than V952.
3. GXD7613. An adult individual in dorsal view. The skull and the first six or seven cervicals are missing, as is the tip of the tail. The remainder of the skeleton, including the rear portion of the right lower jaw, is extremely well preserved.
4. GXD7621. A well-preserved individual in dorsal view. The skull, anterior cervicals, left epipodial of forelimb, left hind limb, and most of tail are missing.
5. GXD7603. This specimen is smaller, presumably younger, than the last two. It is exposed in dorsal view. The left hind limb and tail are missing. The skull is not well preserved.
6. GXD7602. A young individual exposed in dorsal view. The left hand, left hind limb, and tail are missing. The right hind limb is very well preserved.
7. GXD838028. A fully grown individual in ventral view. The rear portion of the skull is

preserved. The size of the skull is comparable to that of V952.

8. V953. A young specimen in ventral view. Only the right limbs are well preserved.
9. V7919. A young specimen in ventral view. Only part of the tail is missing. (The pectoral girdle was originally buried in very hard matrix. Dental drill and compressed-air-powered vibrating tools were used to remove this matrix. The work was rewarded by uncovering the clavicles that are superficial to the scapulae, a reverse of the relationship of the two bones in other sauropterygians.)
10. GXD835002. An embryo in dorsal view. This specimen has a relatively large skull, small limbs, and a short tail. (This is the only specimen with a complete tail.)
11. V7917. A very young specimen in dorsal view. This specimen is virtually complete from the snout to the tip of the tail.

Morphological Description

The specimens are embedded in thin layers of gray pelitic limestone. Most of the specimens were preserved dorsoventrally flattened. The limbs usually lie close to the body. The forelimbs are kept more or less straight, while the epipodials of the hind limbs bend toward the base of the tail. Postmortem disturbance appears to be minimal. Only the manus and pes are affected. Preparation was performed under a Wild M7 microscope with pin vice and fine needles. Reconstructions are based on all available material (Fig. 2).

The Skull

A reconstruction of the skull is shown in Figure 3. Description of the dorsal aspect of the skull of *Keichousaurus* is based mainly on GXD7601 and V952 (Fig. 4). There is only one specimen (GXD838028) in which the rear part of the palatal elements can be observed (Fig. 5).

Among known pachypleurosaurids, the general

←

premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; pub, pubis; q, quadrate; ra, radius; sa, sacral; sc, scapula; so, supraoccipital; sq, squamosal; st, supratemporal; ti, tibia; ul, ulna; ulr, ulnare.

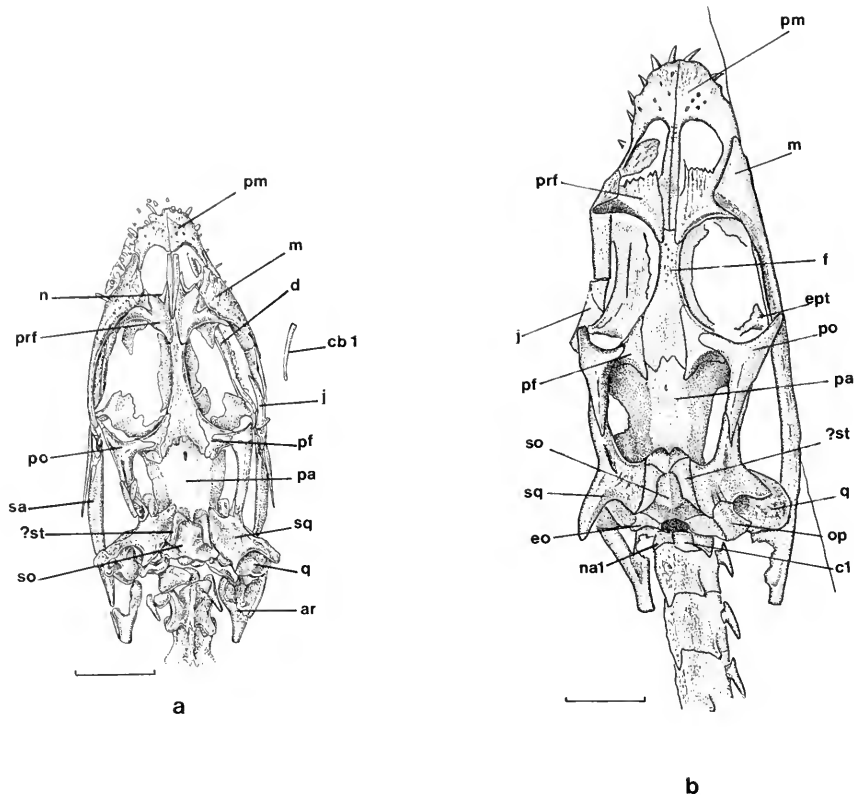


FIG. 4. The skull of *Keichousaurus hui* in dorsal view (a, GXD7601; b, V952). Scale bar = 5 mm. Abbreviations as in Figure 3.

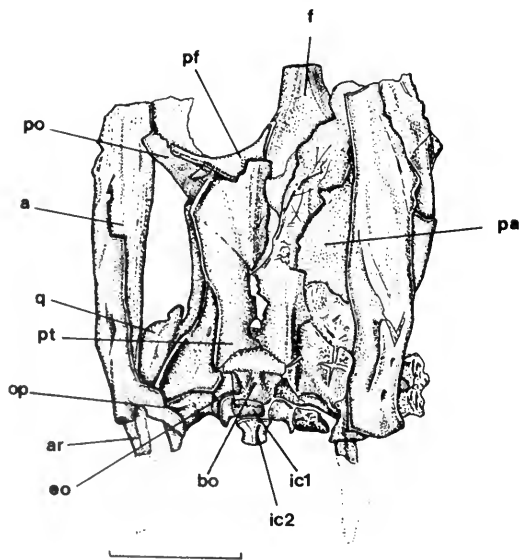


FIG. 5. The skull of *Keichousaurus hui* (GXD838028) in palatal view. Scale bar = 5 mm. Abbreviations as in Figure 3.

proportions of the skull of *Keichousaurus* are most similar to those of *Dactylosaurus* (Sues & Carroll, 1985; Rieppel & Lin, 1995). The snout is short and broad. The orbits are large, situated at the middle one-third of the skull. The external nares are situated at the middle one-third of the antorbital region of the skull. The skull is widest at the midpoint of the lower rim of the orbit. As in *Dactylosaurus*, the upper temporal openings are long and narrow, extending to the rear end of the skull table, while in other pachypleurosaurids they are round or keyhole shaped. Cheek emargination, resulting from the loss of the lower temporal bar, is more pronounced than in other pachypleurosaurids, except for *Dactylosaurus*. The skull is quite shallow, less than 30% of the skull width, with the highest point at the rear end of the skull table.

The premaxilla has a long medial process that extends back to contact the frontal. Unlike in other pachypleurosaurids, the anterior part of the premaxilla is short and broad, so that the snout anterior to the external nares is wider than it is long.

The lateral process of the premaxilla meets the maxilla at the midpoint of the outer rim of the external nares. The surface of the bone is irregularly pitted. There are five conical teeth in each premaxilla.

The very short and triangular nasals are situated in shallow grooves in the prefrontal. They are separated from one another by the posterior process of the premaxilla. The posterior end of the nasal does not extend beyond that of the premaxilla. In *Serpianosaurus mirigiolensis*, *Neusticosaurus edwardsii*, and *Neusticosaurus peyeri*, the nasals are large, extending to a level well behind the anterior margin of the orbits (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989). The skull configuration of *Neusticosaurus pusillus* varies considerably. Nevertheless, the nasals are always longer than those in *Keichousaurus* (Sander, 1989).

In all adult specimens of *Keichousaurus*, the frontals are fused along the midline without any trace of a suture. Anteriorly, the bone is very narrow, but it gradually broadens posteriorly. The anterior end of the frontal is partially covered by the prefrontals on both sides. The cross-section of the bone between the orbits is triangular. The posterior wings of the frontal are grooved dorsolaterally to accommodate the postfrontals. The frontoparietal suture curves forward at the midline so that the parietal reaches the level of the posterior margin of the orbits.

The parietals are fused along the midline. The skull table is flat. The laterally descending flanges of the parietal extend along the medial margin of the upper temporal opening, providing a surface for the attachment of the jaw adductor musculature. This character is also seen in *Youngina*, *Claudiosaurus*, and other advanced diapsids (Carroll, 1981), but not in primitive diapsids or in *Serpianosaurus* or *Neusticosaurus* (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989). The pineal foramen is smaller and situated more anteriorly than in any other pachypleurosaurid, right between the posterior tips of the frontal. An anteriorly situated parietal opening is thought to be a typical plesiosaur character and is also observed in *Pistosaurus* (Sues, 1987). In contrast, the pineal foramen in "nothosaurs" tends to be displaced posteriorly. In the eosuchian *Youngina* and in *Claudiosaurus*, the pineal foramen is large and is situated at the middle of the parietal skull table (Carroll, 1981).

At the back of the skull table, the midline of the parietal extends a short distance beyond the sharp ridge that separates the skull table from the

occipital surface, forming a wedge-shaped protrusion. On both sides of the wedge, the parietal turns downward and somewhat inward, forming two notches for the attachment of the epaxial muscles.

On the occipital surface, just medial to the squamosals, there is a pair of columnar bones (?supratemporals). The upper end of the bone turns sharply inward toward the midline, forming a beak-shaped projection. The points of the beaks meet in the midline, separating the occipital portions of the parietal and supraoccipital. Bones occupying this position have never been reported in other nothosaurs. Since this structure can be observed in all skulls exposed dorsally, it is unlikely that it is a fragment of another, adjacent bone.

The squamosals are large bones mainly confined to the occipital surface of the skull. The long anterior ramus of the bone extends forward underneath the postorbital, entering the upper temporal bar. The quadrate ramus of the squamosal is slender and extends posteroventrolaterally. In the occipital region, the body of the squamosal expands considerably medially as in other pachypleurosaurids. Medially, it makes contact with the parietal, ?supratemporal, supraoccipital, and opisthotic successively, forming a continuous occipital wall. The posttemporal fenestra, present in *Claudiosaurus* and primitive diapsids, is either very small or lost. Whether there is a quadratojugal is not certain. If present, it must be very small.

The postorbital of *Keichousaurus* is a triradiate bone, while in *Serpianosaurus* and *Neusticosaurus*, this bone is triangular rather than triradiate. The posterior ramus extends back to the occipital margin above the postorbital ramus of the squamosal. The two bones interdigitate with each other to form the upper temporal bar. The upper temporal bar is slender as in *Anarosaurus* and *Dactylosaurus* (Rieppel & Lin, 1995) and differs considerably from that of *Serpianosaurus* and *Neusticosaurus*, where the upper temporal arch is broad and the temporal emargination is less pronounced. The other two rami of the postorbital are short. The superior ramus fits into a groove in the postfrontal; the inferior ramus points anteroventrally, making contact with the small jugal along the posterolateral margin of the orbit. The jugal is reduced to a slender bar. The bone is partially covered laterally by the maxilla. The posterior end thickens slightly and makes contact with the postorbital and ectopterygoid. In GXD7601, there

seems to be a small downward extension at the posterior end of the jugal.

The postfrontal is triangular. Its anterior edge contacts the frontal, and the lateral apex has a groove to accept the postorbital. The anterior edge forms the posteromedial rim of the orbit. The posterior edge participates in the formation of the upper temporal fenestra.

The prefrontal is very large. It occupies the region between the external nares and the orbits. The orbital margin of the prefrontal is considerably thickened to form a ridge, and it turns steeply downward along the anterior margin of the orbit, reaching the level of the palate. As in other sauropterygians, there is no trace of the lacrimal.

The maxilla is a large element. It has an elongated triangular shape. Anteriorly, it reaches the premaxilla and forms the posterolateral margin of the external nares. Dorsally, the maxilla has a fingerlike median protrusion fitting into a shallow groove on the prefrontal. The posterior extension of the maxilla forms the lateral rim of the orbit.

The supraoccipital is a large element. A ridge runs along the midline, confluent with the ridge on the parietal. Underneath the questionable supratemporal, the supraoccipital makes contact with the squamosal. Two shallow depressions are apparent just above the rim of the foramen magnum, presumably to accommodate the insertion of the epaxial neck muscles.

The suture between the exoccipital and opisthotic can be discerned in GXD7601 in dorsal view and in GXD838028 in ventral view. The exoccipital is thin and lies superficial to the opisthotic. The opisthotic extends laterally and contacts the supraoccipital and squamosal. The paroccipital process extends further beyond the contact with the squamosal. The distal end of it bears a slightly expanded articular facet. It probably articulated with the quadrate. The body of the paroccipital process is broad. The space between the lower margin of the paroccipital process and the posterior margin of the pterygoid is closed by an extension of the paroccipital process.

The monimostylic quadrate is short and broad. Its body is essentially horizontal. An ascending process articulates in a shallow groove on the anterior surface of the squamosal's quadrate ramus. The posterior aspect of the quadrate is concave, a trait that is associated with the suspension of a tympanum. The medial surface of the quadrate is intimately sutured to the quadrate ramus of the pterygoid and to the paroccipital process.

The middle ear chamber is formed by the me-

dial part of the quadrate, the squamosal, the paroccipital process, and possibly the quadrate fossa in the retroarticular process of the lower jaw. The stapes could not be identified, but it is reported in *Neusticosaurus edwardsii* (Carroll & Gaskill, 1985). The posterior concavity of the quadrate and the middle ear chamber indicates the presence of an impedance-matching middle ear.

The whole occipital surface is well consolidated. In sauropterygians, both pachypleurosaurids and "nothosaurs" have a closed occiput (Schultze, 1970), while plesiosaurs retain a wide-open occiput. Since it is a complex modification involving more than one bone to change shape, the closed occiput is an important synapomorphy uniting pachypleurosaurids and "nothosaurs."

The palate is not well preserved, and only its posterior part is exposed. Through the left orbit of V952, we can see that the palatine extends back to the level of the jugal, and the suborbital fenestra appears to remain as a narrow slit. In Alpine pachypleurosaurids, the suborbital fenestra is confluent with the subtemporal fenestra (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989). The condition in *Keichousaurus hui* may be more primitive: related to the seemingly separated suborbital fenestra is the presence of the ectopterygoid. The ectopterygoid appears to be present in specimens GXD7601, V952, and GXD838028, although the suture is not always clear. The ectopterygoid appears to make contact with the jugal. As in all other nothosaurs, the interpterygoid vacuity is completely closed, and the pterygoid extends back to the level of the basioccipital. The basisphenoid appears to have been completely covered by the pterygoid. The quadrate ramus of the pterygoid extends directly laterally rather than posterolaterally. As in all sauropterygians, the transverse flange of the pterygoid has disappeared. A marked longitudinal ridge separates the quadrate ramus from the medial portion of the pterygoid, as in other pachypleurosaurids. The occipital condyle is formed solely by the basioccipital. The base of the condyle is constricted such as to form a neck.

The Lower Jaw

The anterior part of the lower jaw is not well exposed. From what can be seen through the orbits, the dentary extends to the level of the back of the orbit. The teeth are conical in shape.

The coronoid is not observable. A thin splenial

can be discerned along the inner wall of the dentary. The surangular is located immediately behind the dentary. There is a shallow groove on the lateral surface of the surangular to accommodate the wedge-shaped angular. The remainder of the suture between the surangular and the articular could not be discerned. The articular expands dramatically inward to form the articulating surface. Posterior to the jaw joint is a prominent retroarticular process. A medial expansion extends back two-thirds of the length of the retroarticular process, forming a large quadrate fossa. A similar structure was found in European pachypleurosaurids, and it was believed to be part of the articulating surface that received the posterior extension of the quadrate when the jaws are open (Rieppel, 1989; Sander, 1989). In *Keichousaurus hui*, however, this fossa is considerably larger and deeper than in Alpine pachypleurosaurids. In addition to accommodating the quadrate, the function of this quadrate fossa may be to form part of the middle ear chamber and to support the tympanum. Behind the quadrate fossa, the retroarticular process tapers to a robust bony bar for the insertion of the depressor mandibulae.

Tooth Implantation

In the lower jaw of *Keichousaurus hui*, the teeth are set in individual sockets along a longitudinal groove, as in generalized diapsids. However, *Keichousaurus hui* (as well as *Neusticosaurus pusillus*; see Fig. 13 in Sander, 1989) is peculiar in that, in contrast to generalized diapsids, the inner wall of the lower jaw is thicker and higher than the outer wall (see GXD7601). This condition could be derived from a thecodont condition by lowering the outer wall. Since the upper jaw is not exposed in ventral view in any of the specimens, the exact nature of tooth implantation in the maxilla and premaxilla is not clear.

Vertebrae and Ribs

The vertebral count, especially the number of cervical versus dorsal vertebrae, is considered important in the classification of pachypleurosaurids. However, an accurate count is difficult to establish (Figs. 6, 7), because the distinction between the cervical and dorsal regions cannot be clearly established in reptiles (Hoffstetter & Gasc, 1969). Carroll and Gaskill (1985) and Rieppel (1989)

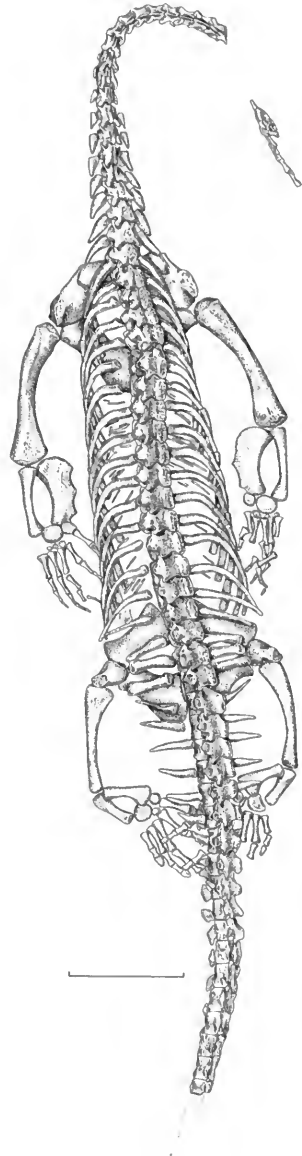


FIG. 6. *Keichousaurus hui* (GXD7613) in dorsal view. Scale bar = 20 mm.

used the transition from double-headed cervical ribs to the single-headed dorsal ribs as a mark to differentiate the two regions in *Neusticosaurus edwardsii* and *Serpianosaurus*, respectively. Sues and Carroll (1985) used the change in the rib heads as well as the modification of the zygopophyses to distinguish the cervical and dorsal vertebrae of *Dactylosaurus*. Among the specimens under study, none shows the nature of the rib articulation in the cervical-to-dorsal transition

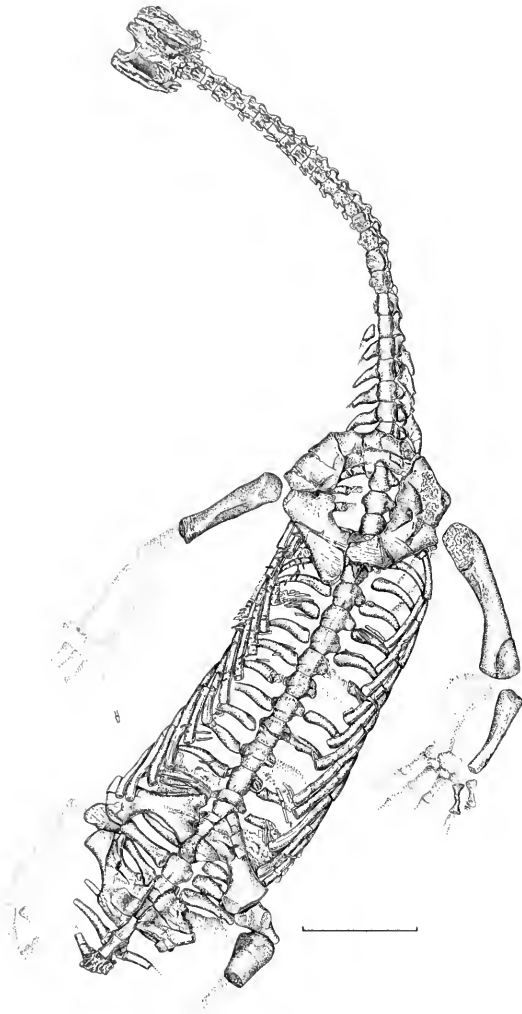


FIG. 7. *Keichousaurus hui* (GXD838028) in ventral view. Scale bar = 20 mm.

area. The neural arch configuration, however, can be observed in all the specimens that are exposed in dorsal view. In the cervical region, the transverse process does not project beyond the zygopophysis. The neural arch is constricted in the middle. In the dorsal region, pachyostosis (thickening of the ribs and vertebrae) is apparent, and the transverse processes extend beyond the zygopophyses. It can also be observed that the last cervical ribs are much shorter and stouter than the first dorsal ribs. This coincides perfectly with the change in the neural arches.

There is, however, variability in the vertebral count. Among the specimens studied, the count of preserved vertebrae ranges from 43 to 45. Of

these, 25–26 are cervical and 18–19 are dorsal vertebrae. The ratios of cervical/dorsal vertebrae of European species are: *Serpianosaurus* 15–18/20–23 (Rieppel, 1989), *Neusticosaurus edwardsii* 17/19–20 (Carroll & Gaskill, 1985), *Neusticosaurus peyeri* 15–16/19–20, and *Neusticosaurus pusillus* 18–20/22–24 (Sander, 1989). *Dactylosaurus* has the same vertebral count as *Neusticosaurus edwardsii* (Sues & Carroll, 1985). Since the length of vertebrae does not vary much from cervical to dorsal region, a higher count of cervical vertebrae translates into a longer neck for *Keichousaurus hui* compared with other pachypleurosaurids (Rieppel & Lin, 1995).

The number of sacral vertebrae varies from two to three. In GXD7621, two pairs of sacral ribs are drastically thickened, differentiating them from anteriorly and posteriorly adjacent ones. In GXD7613, the last pair of dorsal ribs is also thickened distally, although not as much as in the sacral ribs. In GXD7602, the ribs in the sacral region do not thicken noticeably, but there are three pairs of ribs converging on the ilium. In GXD7603, the distal ends of three pairs of ribs in the sacral region are expanded, but the proximal ends are not. Compared with other pachypleurosaurids, in which there are three sacral vertebrae, the condition in *Keichousaurus* is more closely comparable to that of generalized diapsids.

No specimen except the smallest one (GXD835002) preserves the whole length of the tail. The count of caudal vertebrae is at least 25 (GXD7613) and might well be more than 30. The count of caudal vertebrae for European pachypleurosaurids is: *Neusticosaurus edwardsii* 42 (Carroll & Gaskill, 1985), *Neusticosaurus pusillus* 51–58, *Neusticosaurus peyeri* 40–48 (Sander, 1989), and *Serpianosaurus* at least 47 (Rieppel, 1989). Sander (1989) showed that the counts of caudal vertebrae are positively correlated with ontogenetic growth.

The elements of the atlas–axis complex remain discrete (Fig. 8). As in other generalized sauropterygians, no proatlas was found. An oblong proatlas was reported for *Claudiosaurus* (Carroll, 1981). In GXD838028, the first and second intercentra are in contact ventrally so that the first centrum cannot be seen in ventral view. It is exposed in dorsal view in GXD7601. The first pair of neural arches can be seen in GXD7602. They are paired triangular elements. The front edge of the atlas arch is straight. Whether the arches articulate with the occiput, and the nature of their articulation with each other, is not clear. The postzyg-

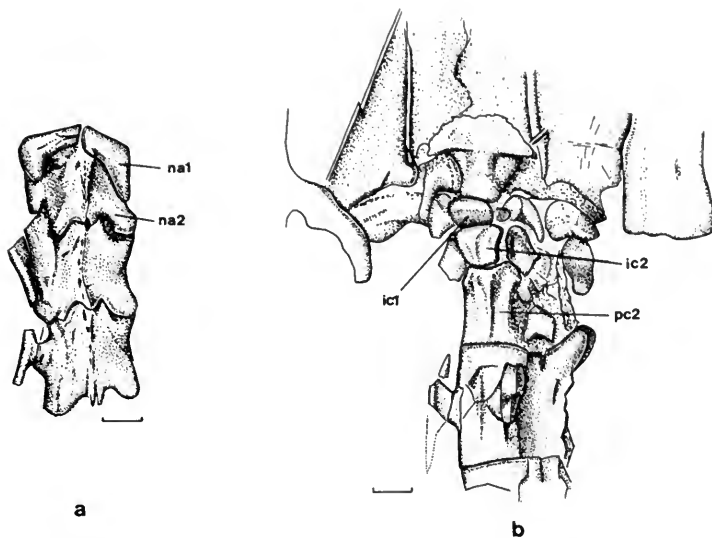


FIG. 8. The atlas-axis complex of *Keichousaurus hui*; A, GXD7602, dorsal view; B, GXD838028, ventral view. Scale bar = 1 mm. Abbreviations as in Figure 3.

apophyses extend across the second neural arch. The neural spine was not developed on the atlas arch. The axis is larger than the third cervical, as is the case in most reptiles. As in other generalized reptiles, the axis intercentrum and centrum are not fused. The intercentrum is about half the length of the centrum. Both are constricted laterally. The parapophysis, which is formed jointly by the intercentrum and centrum, is close to the ventral surface of the column. A pronounced keel is present on the ventral midline of both intercentrum and centrum. The axis neural arch has essentially the same shape as the rest of the cervical vertebrae, except for the neural spine, which is thicker and longer.

The vertebral centra of the cervical region are longer than they are broad. The middle of the centra is constricted laterally. The length of the cervical vertebrae does not increase much from the third to the last, but approaching the dorsal region, the vertebrae become broader. In the dorsal region, the diameter of the centra is subequal to their length, and the midportion is expanded both ventrally and laterally instead of being constricted, giving the centra a barrel-like appearance. In the anterior caudal region, the centra are constricted again.

In all the specimens, the vertebral column is well articulated. In specimens GXD7603 and GXD838028, a slight displacement of the vertebral column occurred in the area of the sacral re-

gion. These two specimens demonstrate that the vertebral centra are weakly amphicoelous, as is the case in other pachypleurosaurids.

The outline of the neural arch in the cervical region, as exposed in dorsal view, is bell-shaped. The articulating surfaces between the zygapophyses slant ventromedially, indicating that lateral and rotational movements of the neck are coupled (to be discussed later). Pachyostosis of the neural arch begins at the 15th or 16th cervical.

In the dorsal region, the outline of the neural arch is pentagonal, as in *Dactylosaurus*. The transverse processes are more inflated in *Keichousaurus* and *Dactylosaurus* than in *Neusticosaurus* and *Serpianosaurus*, where the outline of the neural arch is rectangular. The articular facet on the transverse processes of the dorsal vertebrae is elongated dorsoventrally, and it has a shallow saddle-shaped contour. This is reflected in the capitulum of the dorsal ribs, which seems to be quite free to move. In the sacral region and in the first few caudal vertebrae, where the ribs are still distinct, the articulating facet is round and concave. This may indicate a more rigid connection between vertebrae and ribs. In ventral view, the transverse process is anteriorly positioned on each vertebral segment.

The plane of the articulation surface of the prezygapophyses faces ventromedially in the dorsal, sacral, and anterior caudal regions. Also, to a lesser degree, they tilt up anteriorly. Thus, the suc-

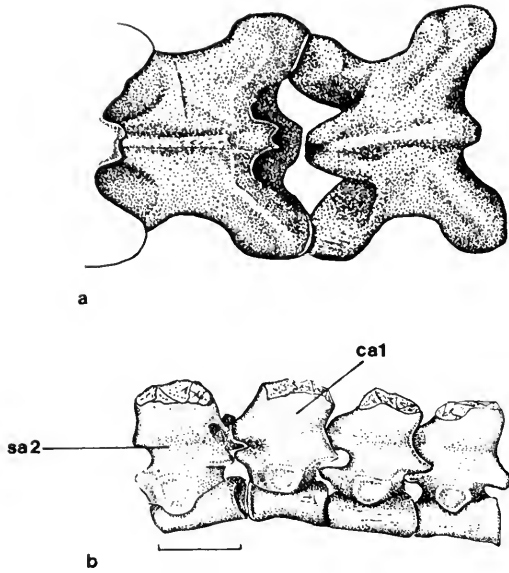


FIG. 9. a, Accessory intervertebral articulation in *Keichousaurus hui* (GXD7601); b, proximal caudal vertebrae of *K. hui* (GXD7613). Scale bar = 2 mm.

cessive vertebrae are interlocked together, severely restricting lateral bending as in *Dactylosaurus* (Sues & Carroll, 1985).

An accessory articulation complex can be seen between successive neural arches in the cervical region (Fig. 9a), as is observed in all other pachypleurosaurids (Kuhn-Schnyder, 1959; Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989). At the rear end of the neural arch, a medial extension of the postzygapophysis forms a shelf at the midline at a deeper level than the primary articulating surface. At the base of the following neural spine, a tongue-like process fits onto this shelf. The front edge of the lower part of the neural spine fits into a vertical groove at the rear end of the more anterior neural spine. This articulation further restricts the rotational movement of the vertebral column.

The neural spines of the cervical region are narrow and very low, except for the second cervical. In the dorsal region, they become significantly thickened. The height is also increased but does not exceed the length. The tip of the dorsal neural spine is usually slightly expanded laterally and typically unfinished at the top, suggesting that there might have been a portion that remained unossified. The dorsal and the first five or six caudal neural spines are very long, fitting tightly with their neighbors. Dorsoventral flexion was proba-

bly impossible in this area. The densely packed rib cage in the dorsal region and the long and laterally pointing proximal caudal ribs make lateral movement equally difficult. The highest neural spines along the vertebral column are in the sacral region. From the 6th to the 10th caudal vertebrae, the front edge of the neural spine tilts back (Fig. 9b), forming a triangular gap between the successive spines. This may indicate an increase in dorsoventral mobility.

The hemal arches can be observed only in GXD7613. The first hemal spine is associated with the 6th and 7th caudal vertebrae. The 5th caudal bears an area of unfinished bone on the ventral surface, but whether it supported a hemal spine is not certain. About 8 hemal spines are present. In contrast with their counterparts in *Neusticosaurus* and *Serpianosaurus*, there is no distinct pedicel on the hemal spines of *Keichousaurus*. The last few hemal spines diminish rapidly in size and transform to small chevrons pointing backward.

In GXD838028, only a single rib articulation can be observed for each cervical vertebra. The parapophyses are prominent, extending laterally from the centrum. From the 3rd to the 7th cervical, the parapophyses are in the anterior half of the centrum. From the 8th cervical, the parapophysis starts to shift backward and upward, and the neural arch participates in the formation of the facet, but there is no transverse process per se. In the last few cervical vertebrae of GXD838028, the suture between the centra and neural arches runs through the articulating facet, and the transverse process becomes prominent. The same condition is also reported for *Neusticosaurus edwardsii* (Carroll & Gaskill, 1985). Sander (1989) reported double-headed cervical ribs in both *Neusticosaurus pusillus* and *Neusticosaurus peyeri*. In *Serpianosaurus*, the cervical ribs are also double-headed (Rieppel, 1989). In the dorsal region, the prominent, dorsoventrally elongated transverse process is located high on the neural arch. The suture between the centra and neural arches remains open, even in the largest specimen, GXD838028. In the tail region, the articulating facet starts to migrate down again; in GXD7613, the suture runs through the articulating facet of caudal vertebrae 6, 7, and 8.

GXD838028 shows the first pair of cervical ribs to be single-headed, curved, and articulating with the atlas intercentrum (Fig. 8). In V952, the anterior cervical ribs up to the 13th show the double process noted in *Serpianosaurus* by Rieppel

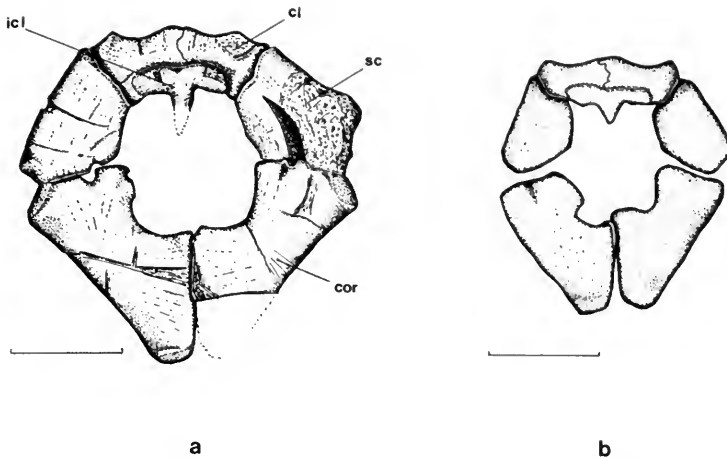


FIG. 10. The pectoral girdle of *Keichousaurus hui* (a, GXD7601; b, V7919). Scale bar = 10 mm. Abbreviations as in Figure 3.

(1989). No trace of an anterior process can be seen on the last eight or so cervical ribs of GXD7613. These ribs are straight and pointed. They show a gradual increase in length caudally, with successive ribs about 20% longer than more anterior ribs. An abrupt increase in length appears at the transition between cervical and dorsal regions. The first dorsal rib is more than twice the length of the last cervical rib. It is also thinner than the last cervical rib. The typical dorsal ribs are five to six times the length of the corresponding centrum. They bend backward, extending to the level of 4th or 5th vertebra behind. When restored, these ribs may point posteroventrally. The distal end of the typical rib expands slightly, suggesting that there might be a cartilaginous link between the rib and the gastralia. The last two or three ribs in front of the sacral region differ significantly from the typical dorsal ribs. They are shorter and almost straight.

The sacral ribs never co-ossify with their respective vertebrae or with one another, but there is some rugosity on their proximal surface, indicating strong muscle attachment. One pair of sacral ribs (the first pair of the two, or the second pair of the three) bears a recess at the distal end, which receives a small projection of the ilium.

Eight or nine pairs of caudal ribs are present. The first five pairs are almost as long as the sacral ribs, and like the sacral ribs, they point laterally. The last four pairs are slightly bent and shorten rapidly. They never fuse with their respective vertebrae.

Gastralia are present from the posterior end of

the pectoral girdle to the anterior end of the pelvic girdle. In ventrally exposed specimens, the gastralia are either completely eroded or only some broken fragments are left. Gastral ribs can be observed only through the gap between the dorsal ribs of the specimens prepared in dorsal view. The gastralia are thin and densely packed. There is more than one row of gastralia to each dorsal segment, but the exact number is not certain. There is one central V-shaped element and two collateral elements on each side of it in each row of gastralia. The lateral elements partially overlap the central element and adhere to the anterior side of it. *Neusticosaurus* has three elements per segment, one central and one collateral on each side (Carroll & Gaskill, 1985; Sander, 1989), whereas *Serpianosaurus*, like *Keichousaurus*, has five elements (Rieppel, 1989).

Pectoral Girdle and Forelimb

The configuration of the pectoral girdle of *Keichousaurus hui* (Fig. 10) conforms to the general pattern seen in other pachypleurosaurids. It forms a ventrally placed circle with a short dorsal extension of the scapular blade. The elements involved in forming the pectoral girdle are a single interclavicle, paired clavicles, scapulae, and coracoids.

The interclavicle is a small, thin, T-shaped element. It fits in a groove at the posterior edge of the ventral surface of the clavicles. The posterior edges of the bones are confluent. The transverse

bar of the interclavicle is one-half to two-thirds the length of the total length of the clavicles. There is a short stem of the interclavicle, about one-half the length of the transverse bar, pointing posteriorly. The interclavicle and clavicles are always firmly attached to one another.

The clavicles form the anterior margin of the pectoral girdle. This margin is basically straight, unlike in European pachypleurosaurids, where there is a lateral shank pointing posteriorly (Sander, 1989). The two clavicles meet each other at the ventral midline in an interdigitating suture. The length of the clavicular bar is about one-half to two-thirds the distance between the glenoids. There are three low projections on the anterior edge of the bar. One is in the middle where the clavicles meet, and the other two are situated near the corner of the clavicle–scapula articulation.

In sauropterygians, the normal relationship of the clavicle and the base of the scapula is reversed from the typical terrestrial tetrapod condition. Instead of being superficial to the scapula, the lateral portion of the clavicle lies deep to the anterior portion of the scapula, suggesting development of the clavicles in deeper tissues than in most primitive tetrapods. This is demonstrated in all the specimens of *Keichousaurus* where this articulation can be observed, except V7919. In the latter specimen, the clavicle and scapula show the primitive relationship with the scapula medial to the clavicle. Evidence of postmortal disturbance is minimal. Either the clavicular bar was accidentally dislocated in life or the peculiar relationship was caused by a developmental abnormality. The cause of this reversal is not clear. It has been proposed that the peculiar configuration in sauropterygians may have resulted from an extreme reduction of the extent of the shoulder girdle early in the evolution of the sauropterygians, followed by re-elaboration, with a reversal of the relationships (Carroll & Gaskill, 1985).

As in all other sauropterygians, the scapula and coracoid ossified separately. The dorsal process of the scapula is short and not at all blade-shaped. It is a low, tapering process arising from the base of the scapula and pointing posteriorly and almost horizontally. Its tip extends behind the level of the glenoid. The ventral portion of the scapula expands horizontally to form a ventral blade. Normally, the dorsal side of the anteromedial portion of the ventral portion bears a depression receiving the lateral process of the clavicle. Posteriorly, the long axis of the ventral portion of the scapula

forms a 30- to 45-degree angle with the longitudinal axis of the body.

The coracoid is the largest element of the pectoral girdle. The margin meeting the scapula is broad; the middle part of the bone is slightly constricted. Where the coracoids meet along the midline, they expand again, both anteriorly and posteriorly, to form a long symphysis, as is typical of nothosaurs. A coracoid foramen (or supracoracoid foramen) can be seen between the scapula and coracoid in most specimens. The position of the coracoid foramen is two-fifths to one-third the length of the line of contact between the scapula and coracoid. In the European pachypleurosaurids, the coracoid foramen is usually situated at the medial end of the scapula–coracoid suture. In some cases, the two notches on the scapula and coracoid do not even meet to form a foramen. Instead, they both open into the space surrounded by the pectoral girdle.

The glenoid cavity is formed by the scapula and coracoid at the lateral extremity of the shoulder girdle, facing mainly laterally. Both scapula and coracoid thicken considerably in this area. The free ends of the two bones are rough and form an angle of about 100 degrees. There must have been a largely cartilaginous joint capsule.

The humerus (Fig. 11) is the longest bone of adult individuals, being 28.8 mm long in GXD838028, about 31% of the trunk length. The proximal end is slightly expanded and has a rounded triangular outline in cross-section. The expansion of the dorsoventrally flattened distal end is more prominent. It bends slightly inward so that the anterior edge is straight. In contrast to all other pachypleurosaurids, but as in plesiosaurs, there is no trace of an entepicondylar foramen.

As in the European species, two morphotypes can be recognized in *Keichousaurus hui* based mainly on the structure of the humerus. This is interpreted as sexual dimorphism (Sander, 1989), and the two types are assigned sex *x* and sex *y*. In sex *x*, the humerus is smooth and featureless, whereas in sex *y*, muscle scars, processes, and crests are more prominent. The expansion of the distal end of the bone is more pronounced in sex *y*. The relative length of the humerus of sex *x* is shorter than in sex *y*. The overall appearance of the humerus of sex *x* retains the pattern of the juvenile stage.

The most conspicuous feature of *Keichousaurus hui* is the shape of its ulna (Fig. 12). In contrast to other pachypleurosaurids, the ulna of *Keichousaurus hui* is a broad, bladelike bone. It is

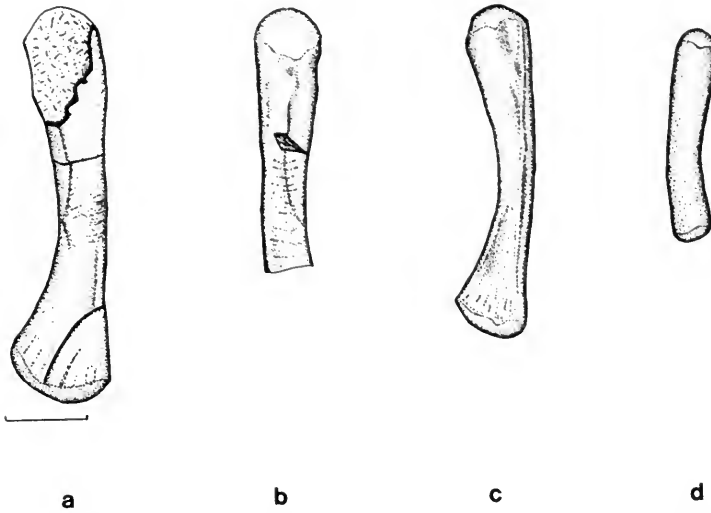


FIG. 11. The humerus of *Keichousaurus hui*. **a**, GXD838028, left humerus, ventral view; **b**, GXD838028, right humerus, ventral view; **c**, GXD7613, right humerus, dorsal view; **d**, V953, right humerus, ventral view. Scale bar = 5 mm.

much wider proximally than distally. The cross-section of the ulna is wedge-shaped, and the medial edge facing the radius is thicker. Only the “nothosaurid” *Lariosaurus* has a convergent configuration of the ulna (Mazin, 1985; Kuhn-Schnyder, 1987). There is no trace of an ossified olecranon. The most obvious functional advantage of the broad ulna is that it dramatically increases the surface area of the forelimb, turning the forelimb into a more effective oar.

The radius is a little longer than the ulna. It is slim, as is usually the case in pachypleurosaurids. The proximal end is wider than its distal end. The radius curves out slightly, and there is a wide space (spatium interosseum) between the radius and ulna at their distal ends (Fig. 12).

The number of ossified carpal elements is age dependent and corresponds to the pattern of stem-group diapsids (Carroll, 1985; Caldwell, 1994). In adult specimens, a total of five elements are os-

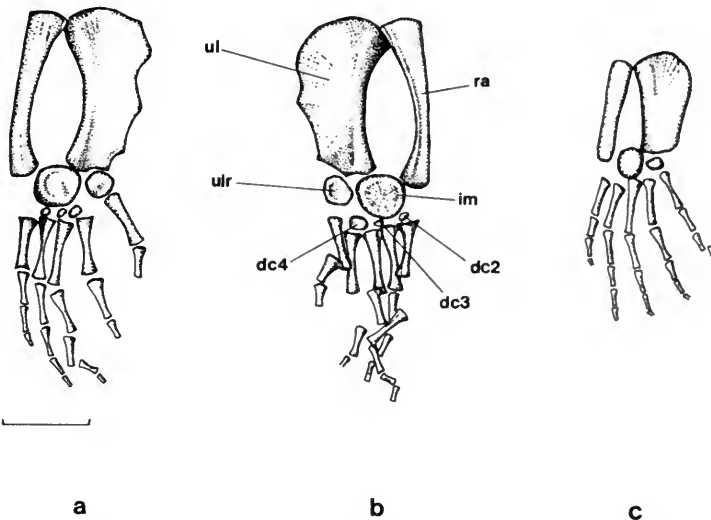


FIG. 12. The lower arm of *Keichousaurus hui*. **a**, GXD7613, left, dorsal; **b**, GXD7613, right, dorsal; **c**, V953, right, ventral. Scale bar = 5 mm. Abbreviations as in Figure 3.

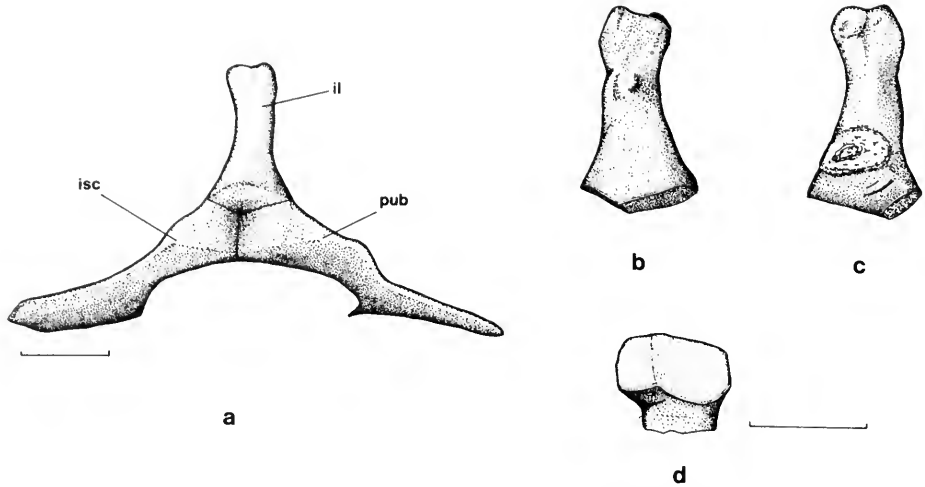


FIG. 13. The pelvic girdle of *Keichousaurus hui*. **a**, Reconstruction of the pelvis; **b**, GXD838028, left ilium, medial view; **c**, same in lateral view; **d**, same in ventral view. Scale bar = 5 mm. Abbreviations as in Figure 3.

sified. The intermedium is large and rounded, situated between the distal ends of the ulna and radius (Fig. 12). In some *Neusticosaurus*, the intermedium is more elongated and is situated at the end of the ulna, alongside the radius (see Fig. 17, Carroll & Gaskill, 1985). The diameter of the ulnare is only half that of the intermedium. Three tiny, round distal carpals are observed in mature specimens, situated at the proximal end of the second, third, and fourth metacarpals. Among European pachypleurosaurids, *Neusticosaurus edwardsii* and *Dactylosaurus* have three carpal elements: the intermedium, the ulnare, and the fourth distal carpal (Carroll & Gaskill, 1985; Sues & Carroll, 1985). *Serpianosaurus*, *Neusticosaurus peyeri*, and *N. pusillus* have only two, the intermedium and the ulnare (Sander, 1989). The number of carpal elements of *Keichousaurus hui* is the highest among well-known pachypleurosaurids, a plesiomorphic character.

The metacarpals and phalanges are reasonably well preserved in GXD7603 and GXD7613. As in Alpine pachypleurosaurids, the third metacarpal of *Keichousaurus hui* is the longest. The second metacarpal is only slightly shorter (in some cases, they are the same length). In fully grown individuals, the fourth metacarpal is shorter than the second, and the first and the fifth are about the same length. In *Neusticosaurus pusillus*, the relative lengths of the third and fourth metacarpals show a continuous spectrum, from the third longer than the fourth to the fourth longer than the third (Sander, 1989). As in Alpine pachypleurosaurids,

both ends of the metacarpals, especially the proximal end, expand, and they show a slight twist relative to one another. Unlike the condition in Alpine pachypleurosaurids, however, the proximal ends of the metacarpals do not overlap, resulting in a greater width of the manus, confluent with the contour of the lower arm. In undisturbed specimens, the first four metacarpals bow slightly toward the ulnar side, and the fifth bows toward the opposite direction.

The phalangeal formula is 3, 4, 4(?), 4, 3. The third digit is usually the longest. In other pachypleurosaurids, the fourth digit is always the longest (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989), as in primitive diapsids and lizards. Therefore, the hand of *Keichousaurus* is more symmetrical.

Pelvic Girdle and Hind Limb

The pelvic girdle of *Keichousaurus hui* (Fig. 13a) can be observed in GXD838028, V953, and V7919 in ventral view and in GXD7602, GXD7603, GXD7613, and GXD7621 in dorsal view.

The ilium (Fig. 13b) is small, as in other nothosaurs. The iliac blade is reduced to a slender vertical process. On the middle of the medial surface, there is a small projection that fits into the recess at the distal end of one of the sacral ribs. The base of the ilium is in the shape of a rounded triangle in ventral view. A triradiate keel divides the ven-

tral surface into three areas. The two medial areas are flat. The one in the front, which is smaller, articulates with the pubis; the larger one at the back articulates with the ischium. The lateral partition is slightly concave. It participates in the formation of the acetabulum. Above the acetabulum there is usually a scar on the ilium, suggesting the presence of a cartilaginous supraacetabular buttress base.

The pubis has an acetabular region, a narrow neck region, and a broad medial region. Three articulating facets are clearly distinguishable on the lateral end of the pubis: a posterior facet that articulates with the ischium; a dorsal facet that articulates with the ilium; and a lateral facet that forms part of the acetabulum. The pubis thins rapidly toward the neck region, where it also constricts posteriorly. It then widens into a broad and thin medial region. The medial region of the pubis forms a broad curve that is in contact with its counterpart on the other side. No pubic rim or process could be observed that would have been used to anchor the abdominal musculature or tendons (Romer, 1956). Rieppel (1989) reported such a structure in smaller specimens of *Serpianosaurus*, but he noted that it is not present in the larger specimens. In V953 and V7917, as in *Dactylosaurus*, the obturator foramen is enclosed in the pubis near the articulation with the ischium. In the largest specimen, GXD838028, the obturator foramen has completely disappeared. In Alpine pachypleurosaurids, the obturator foramen is open and slitlike.

The acetabular region of the ischium of *Keichousaurus hui* is structurally similar to that of the pubis. It bears three articulating facets: an anterior facet articulating with the pubis, a superior one articulating with the ilium, and a lateral facet forming the posterior part of the acetabulum. After a short, slightly narrowed neck region, the ischium expands posteromedially to form a flattened medial region. The posterior angle, for attachment of the caudal musculature, is not as well differentiated as in *Neusticosaurus pusillus* (Sander, 1989, Fig. 16) and *Neusticosaurus edwardsii* (Carroll & Gaskill, 1985, Fig. 18). The medial extremity of the ischium forms a more or less straight line in front but curves slightly laterally at the rear end.

The posterior margin of the pubis and the anterior margin of the ischium enclose a large space, the thyroid fenestra. The curved nature of the extremity of the pubis indicates that the symphysis probably was cartilaginous. The acetabular facet is a shallow socket facing ventrolaterally. Move-

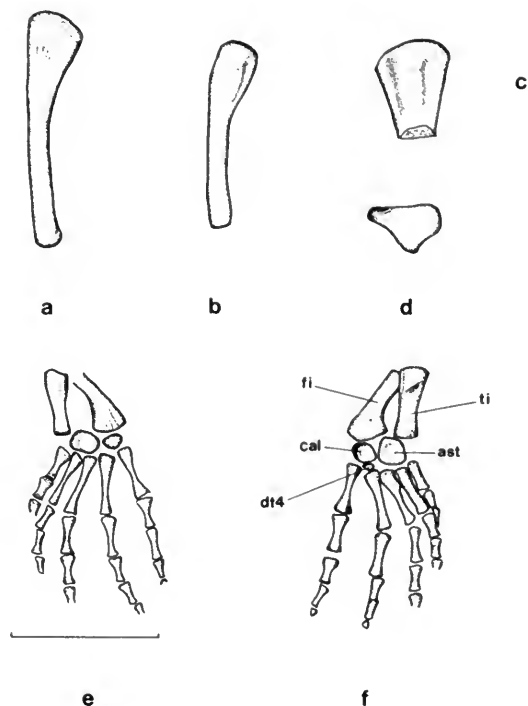


FIG. 14. The hind limb of *Keichousaurus hui*. a, GXD7613, left femur, dorsal view; b, V953, right femur, ventral view; c, GXD838028, proximal end of left femur, ventral view; d, GXD838028, proximal end of left femur, terminal view; e, V953, right lower leg, ventral view; f, V7919, left lower leg, ventral view. Scale bar = 10 mm. Abbreviations as in Figure 3.

ments of the femur are restricted to a plane below the acetabulum.

As is typical among pachypleurosaurids, the femur of adult *Keichousaurus hui* (Fig. 14) is less well developed than the humerus. It is shorter and more slender, and the surface of the bone is smoother than that of the humerus. The proximal end of the femur is as broad as that of the humerus. The distal end, however, is only about half as broad as the proximal end. The posterior side of the shaft is concave, whereas the anterior side is straight. The articulation surfaces at both ends are convex in contrast to *Neusticosaurus edwardsii*, in which they are concave (Carroll & Gaskill, 1985). In adult specimens, there is a shallow recess that might be comparable to the intertrochanteric fossa (Romer, 1956; see discussion on locomotion and muscle reconstruction below), located between a prominent posterior and a weaker ventral extension of the proximal head of the femur. The distal end of the femur is round and

TABLE 1. Measurements of *Keichousaurus hui*.

	GXD- 835002	V7917	V7918	GXD- 7602	BPV601	V953	GXD- 7603	V7919	GXD- 7601	V952	GXD- 7613	GXD- 7621	GXD- 838028	Max/ Min
1	9.0	10.9	—	15.5	16.5	—	18.0	19.1	17.5	24.4	—	—	—	—
2	9.5	—	—	18.8	—	—	23.0	23.7	22.6	27.8	—	—	—	—
3	4.7	6.4	—	8.1	—	—	9.3	10.0	9.4	—	—	—	12.7	2.70
4	3.2	4.2	—	4.9	—	—	6.6	6.0	6.0	6.5	—	—	—	—
5	11.3	30.5	—	56.5	65.9	—	69.3	60.7	—	—	83.2	—	85.2	7.54
6	13.9	29.6	43.7	52.9	61.2	—	67.4	66.4	—	—	77.1	81.6	90.5	6.51
7	13.5	36.9	—	—	—	—	—	—	—	—	—	—	—	—
8	9.4	23.3	33.7	41.9	—	53.4	56.4	51.2	—	—	62.1	64.5	71.2	7.57
9	34.2	71.0	—	124.9	143.6	—	154.7	146.2	—	—	—	—	—	—
10	3.7	7.1	9.7	13.3	—	20.8	17.4	18.4	—	—	26.0	27.2	27.7	7.49
11	5.0	9.5	12.9	17.4	—	24.8	24.3	23.3	—	—	26.8	30.8	34.8	6.96
12	0.5	—	—	2.3	—	—	2.9	—	—	—	3.3	3.5	3.8	7.6
13	1.3	—	—	3.5	—	—	—	—	—	—	—	—	—	3.2
14	0.5	—	—	2.5	—	—	3.0	—	—	—	4.0	3.5	4.5	9
15	1.3	—	—	3.9	—	—	—	—	—	—	—	—	3.5	2.69
16	0.7	—	—	—	—	—	3.0	3.2	—	—	4.3	3.8	4.8	6.86
17	1.3	—	—	—	—	—	—	—	—	—	—	—	—	4.2
18	0.6	—	—	—	—	—	2.8	—	—	—	4.0	4.0	4.8	8
19	1.3	—	—	—	—	—	—	—	—	—	—	—	4.5	3.46
20	—	—	—	—	—	—	3.5	—	—	—	4.0	4.1	4.5	—
21	—	—	—	—	—	—	—	—	—	—	—	—	2.4	—
22	2.6	7.2	10.5	11.0	—	14.3	13.0	13.9	—	—	16.2	16.5	19.2	7.38
23	2.0	5.9	9.3	10.1	14.5	16.3	15.0	20.0	—	—	25.0	25.6	28.8	14.4
24	0.6	1.0	2.0	2.8	—	3.4	3.2	4.2	—	—	5.1	5.2	5.4	9
25	0.5	0.9	1.1	2.0	—	2.8	2.8	2.8	—	—	3.4	3.0	3.7	7.4
26	0.6	1.1	2.2	2.5	—	3.8	3.9	5.0	—	—	6.4	6.5	8.0	13.33
27	1.0	2.9	4.5	5.0	—	7.5	7.0	9.2	—	—	11.5	11.8	13.1	13.1
28	0.6	1.5	2.1	2.6	—	4.1	3.0	5.3	—	—	5.7	5.5	7.4	12.33
29	1.2	3.0	5.0	4.7	—	7.5	7.1	10.0	—	—	12.1	12.9	14.2	11.83
30	—	—	—	—	—	0.9	1.0	1.2	—	—	1.6	2.0	2.5	—
31	—	—	—	1.2	—	2.0	2.0	2.0	—	—	3.0	3.1	4.0	—
32	0.4	—	—	—	—	2.5	2.3	3.3	—	—	4.0	4.1	4.0	10
33	0.5	1.1	—	—	—	3.2	3.1	3.7	—	—	5.2	5.0	5.3	10.6
34	—	1.5	—	—	—	4.0	3.3	4.0	—	—	4.5	5.2	5.5	—
35	—	1.4	—	—	—	3.1	3.1	3.7	—	—	4.4	4.7	5.2	—
36	—	1.1	—	—	—	2.9	2.7	3.1	—	—	3.9	4.0	4.8	—
37	—	—	—	—	—	5.5	—	4.7	—	—	—	—	—	—
38	—	2.0	—	—	—	6.0	7.0	7.0	—	—	—	—	—	—
39	—	3.1	—	—	—	5.7	7.2	7.5	—	—	—	—	—	—
40	—	3.5	—	—	—	5.9	6.0	7.3	—	—	—	—	—	—
41	—	2.5	—	—	—	4.2	4.5	—	—	—	—	—	—	—
42	2.5	6.2	9.5	11.3	13.0	15.5	14.1	16.5	—	—	18.8	20.9	21.6	8.64
43	0.5	1.6	2.3	3.5	—	3.5	3.9	4.1	—	—	5.1	6.0	6.9	13.8
44	0.2	0.6	1.5	1.6	—	1.2	2.0	1.5	—	—	2.5	2.5	3.0	15
45	0.7	0.8	2.0	1.9	—	2.1	3.1	2.2	—	—	2.8	3.5	4.8	6.86
46	0.8	2.2	3.4	4.0	—	5.1	5.0	6.0	—	—	7.5	7.5	8.0	10
47	1.1	2.5	4.2	4.7	—	5.5	6.0	7.0	—	—	8.0	8.2	9.9	9
48	—	—	—	1.0	—	1.1	1.5	1.5	—	—	1.9	1.7	—	—
49	—	—	—	1.7	—	1.8	2.3	2.3	—	—	2.5	2.8	—	—
50	0.4	1.0	—	2.0	—	3.0	2.3	2.5	—	—	3.3	3.3	—	—
51	0.6	1.7	—	2.5	—	4.5	4.1	4.5	—	—	5.3	5.5	—	—
52	0.7	2.0	—	3.2	—	5.0	4.6	5.0	—	—	5.9	6.5	—	—
53	0.7	2.0	—	4.2	—	5.0	4.8	5.0	—	—	5.9	6.5	—	—
54	0.7	1.5	—	3.4	—	4.3	4.2	4.2	—	—	5.2	6.0	—	—
55	—	—	—	2.5	—	3.6	3.5	3.0	—	—	3.8	4.0	—	—
56	—	3.1	—	4.6	—	5.8	4.7	5.0	—	—	6.8	—	—	—
57	—	4.0	—	6.5	—	7.5	6.0	8.5	—	—	—	—	—	—
58	—	6.5	—	7.5	—	8.8	8.0	8.5	—	—	—	—	—	—
59	—	5.0	—	6.5	—	7.2	—	9.0	—	—	—	—	—	—

TABLE 1. Continued

List of Measurements	
1 skull length at midline	31 length of intermedium
2 length of lower jaw	32 length of 1st metacarpal
3 width of skull	33 length of 2nd metacarpal
4 length of orbit	34 length of 3rd metacarpal
5 neck length	35 length of 4th metacarpal
6 trunk length	36 length of 5th metacarpal
7 tail length	37 length of 1st digit
8 glenoid-acetabulum distance	38 length of 2nd digit
9 snout-vent length	39 length of 3rd digit
10 width between glenoids	40 length of 4th digit
11 width between acetabulae	41 length of 5th digit
12 length of posterior cervical vertebrae	42 length of femur
13 width of posterior cervical vertebrae	43 width of femur at proximal end
14 length of anterior dorsal vertebrae	44 width of femur at the middle of shaft
15 width of anterior dorsal vertebrae	45 width of femur at distal end
16 length of posterior dorsal vertebrae	46 length of tibia
17 width of posterior dorsal vertebrae	47 length of fibula
18 length of sacral vertebrae	48 length of calcaneum
19 width of sacral vertebrae	49 length of astragalus
20 length of anterior caudal vertebrae	50 length of 1st metatarsal
21 width of anterior caudal vertebrae	51 length of 2nd metatarsal
22 standard length	52 length of 3rd metatarsal
23 length of humerus	53 length of 4th metatarsal
24 width of humerus at the proximal end	54 length of 5th metatarsal
25 width of humerus at the middle of the shaft	55 length of 1st toe
26 width of humerus at the distal end	56 length of 2nd toe
27 length of ulna	57 length of 3rd toe
28 width of ulna	58 length of 4th toe
29 length of radius	59 length of 5th toe
30 length of ulnare	

featureless, indicating a weak articulation with the epipodials.

The tibia and fibula are short in *Keichousaurus hui*. They are about 30–40% of the length of the femur and about 60–80% of the length of the ulna and radius. Of the two bones, the fibula is a little stronger (Fig. 14). The tibia is quite straight and without significant expansion at either end. The two ends of the fibula, especially the distal end, expand towards the tibia. There is an interosseal space between the two bones, which is comparable to the space between the ulna and radius.

Two elements of the tarsus, the astragalus and calcaneum (Fig. 14), are consistently ossified in *Keichousaurus hui*. The calcaneum is smaller and is situated at the distal end of the fibula. The large astragalus is situated at the distal end of the interosseal space and articulates with both the tibia and the fibula. The astragalus and the calcaneum may also have articulated with each other, though the articulating facets are not well defined. A third element of the tarsus—the fourth distal tarsal—is present in some adult specimens, including GXD7613, GXD7621, and V7919.

The metatarsals of *Keichousaurus hui* follow the pattern of the European pachypleurosaurids. The first metatarsal is the shortest, its length being about 60% the length of the third metatarsal. The length of the second metatarsal is about 80% that of the third. The third and fourth metatarsals are about the same length, and the fifth is only slightly shorter. The phalangeal formula for the pes of *Keichousaurus hui* is 2-3-4-4-4. The last segments are usually broad and pointed. The elements of the pes are more robust than their counterparts in the manus.

Measurements and Proportions

The measurements of *Keichousaurus hui* were made either under the microscope when the part being measured could be enclosed in the field of view of the microscope, using the grid in the ocular lens to calibrate, or else using a caliper for larger elements. A total of 59 different measurements were taken from the specimens (Table 1).

TABLE 2. Metric proportions of *Keichousaurus hui*.

	GXD- 835002	V7917	V7918	GXD- 7602	BPV- 601	V953	GXD- 7603	V7919	GXD- 7601	V952	GXD- 7613	GXD- 7621	GXD- 838028
Trunk/g-a	1.48	—	—	1.26	—	—	1.20	1.30	—	—	1.24	1.27	1.27
Trunk/std	5.35	—	—	4.81	—	—	4.92	4.78	—	—	4.76	4.95	4.71
Skull/trunk	0.65	0.37	—	0.29	0.27	—	0.24	0.29	—	—	—	—	—
Skull/std	3.46	—	—	1.41	—	—	1.17	1.37	—	—	—	—	—
Skull/g-a	0.96	—	—	0.37	—	—	0.28	0.37	—	—	—	—	—
Neck/trunk	0.81	1.03	—	1.07	1.08	—	1.03	0.91	—	—	1.08	—	0.94
Neck/g-a	1.20	—	—	1.35	—	—	1.23	1.19	—	—	1.34	—	1.20
Neck/std	4.35	—	—	5.14	—	—	5.06	4.37	—	—	5.14	—	4.44
Wid/trunk(g)	0.27	—	—	0.25	—	—	0.26	0.28	—	—	0.34	0.33	0.31
Wid/trunk(a)	0.36	—	—	0.33	—	—	0.36	0.35	—	—	0.35	0.38	0.38
Hum/trunk	0.14	0.20	0.21	0.19	0.24	—	0.22	0.30	—	—	0.32	0.31	0.32
Hum/g-a	0.21	—	—	0.24	—	0.31	0.27	0.39	—	—	0.40	0.40	0.40
Hum/std	0.77	—	—	0.92	—	1.14	1.09	1.44	—	—	1.54	1.55	1.50
Wid/len(hum)	0.25	—	—	0.20	—	0.17	0.19	0.14	—	—	0.14	0.12	0.13
Prox/mid(hum)	1.20	—	—	1.40	—	1.21	1.14	1.50	—	—	1.50	1.73	1.46
Prox/dis(hum)	1.00	—	—	1.12	—	0.89	0.82	0.84	—	—	0.80	0.80	0.68
Dis/mid(hum)	1.20	—	—	1.25	—	1.36	1.39	1.79	—	—	1.88	2.17	2.16
Fem/trunk	0.18	0.21	0.22	0.21	0.21	—	0.21	0.25	—	—	0.24	0.26	0.24
Fem/g-a	0.27	—	—	0.27	—	0.29	0.25	0.32	—	—	0.30	0.32	0.30
Fem/std	0.96	—	—	1.03	—	1.08	1.03	1.19	—	—	1.16	1.27	1.13
Prox/mid(fem)	2.50	—	—	2.19	—	2.92	1.95	2.73	—	—	2.04	2.40	2.30
Prox/dis(fem)	0.71	—	—	1.84	—	1.67	1.26	1.86	—	—	1.82	1.71	1.44
Dis/mid(fem)	3.50	—	—	1.19	—	1.75	1.55	1.47	—	—	1.12	1.40	1.60
Hum/fem	0.80	0.97	0.98	0.89	1.12	1.05	1.06	1.21	—	—	1.33	1.22	1.33
Ulna/hum	0.50	—	—	0.50	—	0.46	0.47	0.46	—	—	0.46	0.46	0.45
Len/wid(adv)	0.38	—	—	0.64	—	—	—	—	—	—	—	—	1.29
Len/wid(pdv)	0.54	—	—	—	—	—	—	—	—	—	—	—	1.14
Len/wid(sv)	0.46	—	—	—	—	—	—	—	—	—	—	—	1.07
Len/wid(uln)	1.67	—	—	1.92	—	1.83	2.33	1.74	—	—	2.02	2.15	1.77

When measuring paired elements, such as limb bones, the average of the individual measurements is used. The length is measured along the line parallel to the longitudinal axis, and the longest distance is used. The width is measured along a line perpendicular to the long axis.

Measurements that might be variously interpreted are defined as follows: Skull length is the distance between the tip of the snout and the posterior edge of the parietal; lower jaw length is measured from the symphysis to the posterior end of the retroarticular process; the width of the skull is measured at the widest point across the skull, at about two-thirds the length of the lateral rim of the orbit; the length of the neck is measured from the base of the skull to the anterior margin of the pectoral girdle; the length of the trunk is the distance from the anterior margin of the pectoral girdle to the posterior margin of the pelvic girdle; snout-vent length is the sum of the skull length, neck length, and trunk length; standard length is the length of the last four dorsal vertebrae (Sander, 1989). (This measurement was used as a substitute for the length of the trunk or the glenoid-

acetabular distance to compare the relative size of different individuals, because the other two measurements depend on the position of the pectoral girdle, which is not anchored to the vertebral column.)

The proportions of different parts of the body, which appear in various parts of the discussion, are listed in Table 2.

Sexual Dimorphism

Sexual dimorphism—the morphological and morphometrical differences between the members of the two sexes—is a common phenomenon among modern reptiles. It is manifest in size, shape, ornamentation, and coloration differences between the sexes. There is no reason to believe that the same was not true in the past. However, because of the scarcity of specimens of most fossil species and the fact that only hard parts of animals preserve as fossils, sexual dimorphism is not well documented in extinct taxa. One rare ex-

ception is the Monte San Giorgio pachypleurosaurids, studied by Rieppel (1989) and Sander (1989). Because of the large number of specimens available (over 200 prepared specimens), Sander (1989) was able to perform a statistical analysis of sexual dimorphism.

Sexual dimorphism of Alpine pachypleurosaurids affects mainly the morphology and relative length of the humerus. The morphometric dimorphism is shown in ratios of measurements within the humerus and of the humerus versus other parts of the body. Sander (1989) used the following ratios: distal width/minimal diameter of the humerus, humerus/femur length, humerus/trunk length, and humerus/standard length. Because it is impossible to determine the actual sex of the two morphotypes, they were denoted sex *x* and sex *y*.

In sex *x*, the humerus is about the same length as the femur. In small pachypleurosaurids (i.e., the two species of *Neusticosaurus* and *Serpianosaurus*), the mean of the humerus/femur ratio is about 0.95; the surface of the bone is smooth and featureless. The expansion of both ends of the humerus is not pronounced. By contrast, the humerus of sex *y* is highly developed. The humerus is significantly longer than the femur; the mean of the humerus/femur ratio is 1.11 in small pachypleurosaurids. The muscle scars and crests are obvious. Both ends of the humerus, especially the distal end, expand prominently. *Neusticosaurus edwardsii* is distinct from other species not only because of its larger size, but also because of its body proportions. The mean humerus/femur ratio for sex *x* is 1.54, and for sex *y* it is 1.71. This was attributed to the shortness of the femur by Sander (1989). However, the fact that the humerus is very long is also demonstrated by the humerus/standard length ratio—1.23 for sex *x* and 1.32 for sex *y* (corresponding values are 0.86–1.09 and 1.10–1.28 in small pachypleurosaurids).

Although there are data for only 13 specimens in *Keichousaurus hui*, sexual dimorphism is demonstrable. To facilitate the comparison with the European species, the same set of ratios is calculated for *Keichousaurus hui*. Only mature individuals can be sexed. Growth patterns in *Keichousaurus hui* will be discussed later. At this point, the relative length of the humerus/femur will be used as an indicator of maturity. Among the specimens, GXD835002 (Fig. 15) is obviously an embryo or a hatchling, and its sex could not be determined. Specimens V7917, V7918, and GXD7602 have humeri shorter than the femora and may be considered subadults. The remaining specimens have hu-

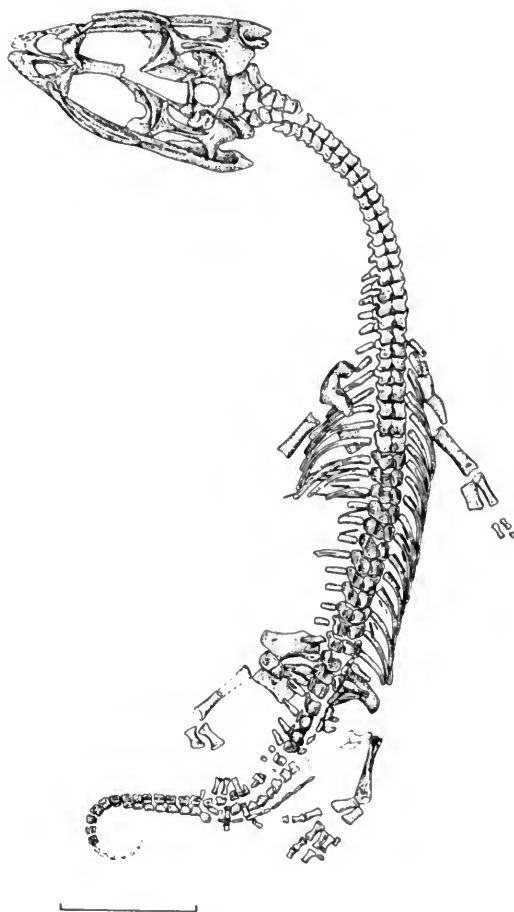


FIG. 15. An embryo of *Keichousaurus hui* (GXD835002). Scale bar = 5 mm.

meri longer than the femora. Specimens V953, GXD7603, and BPV601 have a humerus/femur ratio of 1.05 to 1.16; the humerus/standard length ratios are 1.14 for V953 and 1.09 for GXD7603. While this ratio for BPV601 is not known, the humerus/trunk ratio (0.24) is comparable to that of GXD7603 (0.22). These latter three specimens represent sex *x*. Specimens V7919, GXD7613, GXD7621, and GXD838028 are apparently of sex *y* with humerus/femur ratios between 1.21 and 1.33 (humerus:standard 1.43 to 1.55). The humerus/trunk ratio is 0.30 to 0.32. Sex *y* specimens are all larger than sex *x* specimens, and thus it might be possible that the morphological differences of the humerus are, indeed, age rather than sex related. However, sexual dimorphism has been well documented for other pachypleurosaurids (*Dactylosaurus*: Rieppel & Lin, 1995; *Serpianosaurus*: Riep-

pel, 1989; *Neusticosaurus*: Sander, 1989) and may also be characteristic of *Keichousaurus hui*.

Sex *x* of *Keichousaurus hui* has a slender and smooth humerus, like those of small European species. The expansion of both ends is not pronounced. The ratio of the width at the proximal end versus that at the midpoint of the humerus is 1.21 for V953 and 1.14 for GXD7603. The ratio of the width of the distal end versus the midpoint is 1.36 and 1.39, respectively. In sex *y*, the humerus is highly developed. The ratio of proximal/midpoint is 1.45 to 1.73; that for distal/midpoint is 1.78 to 2.16. The relative length—the ratio of the elements versus the standard length—of other elements of the forelimb also shows dimorphism. The relative length of the ulna is about 0.52 for sex *x* and 0.66 to 0.71 for sex *y*. The relative length of the radius is 0.52 for sex *x* and 0.75 for sex *y*. Apparently, the forelimb as a whole is longer and stronger in sex *y* than in sex *x*.

The femur of *Keichousaurus hui* also shows some sexual dimorphism, though it is not as strongly developed as in the humerus. The same is also true in *Neusticosaurus* (Sander, 1989).

In living reptiles, sexual dimorphism is usually attributed to selection pressure related to reproduction, though sometimes it is diet related. Male land tortoises are often larger than the female, whereas male aquatic turtles are generally smaller than the female. *Sphenodon* has no noticeable size dimorphism between sexes. Male lizards are often larger, but there are many exceptions (Spellerberg, 1982). The actual sex of sex *x* and *y* of *Keichousaurus hui* is therefore difficult to establish. If *Keichousaurus* was highly territorial, then sex *y* probably corresponds to male. The larger overall size and stronger arms are definitely advantageous in conquering and defending territory and impressing potential mates. On the other hand, as argued by Sander (1989), if the female had to go ashore to lay eggs, a pair of strong and more differentiated forelimbs would be necessary, and a larger body could store more energy. The differentiated humerus might also be interpreted as being diet related. It is not unreasonable to assume that sex *y* preyed on more active, faster swimming prey than sex *x*.

Ontogeny

Different ontogenetic stages are present in the sample as demonstrated by the wide range of

overall body size. The standard length of the largest specimen (GXD838028) is more than seven times that of the smallest one (GXD835002).

Description of GXD835002

Specimen GXD835002 is a tiny individual that may be in a late embryonic stage (Fig. 15). The length from the snout to the tip of tail is 48 mm. The only other possible “nothosaur” embryo is that of *Neusticosaurus* (Sander, 1988, 1989), with a body size of 51 mm. Unlike the *Neusticosaurus* embryo, which is preserved in a curled-up posture in lateral view, GXD835002 is exposed in dorsal view similar to the adults.

The skull is relatively large, about 250% longer than the standard length, whereas in adults, the skull is about 50% longer than the standard length. The length of the orbits is two-fifths the length of the skull. The preorbital portion of the skull is short. The frontal is fused even at this stage. The pineal opening is large. Its diameter is about 50% of the length of the temporal openings. A large supraoccipital can be seen in the occipital region, located between the squamosals.

The vertebrae are short. The neural arches are only about 50% of their width. The neural spines are not developed. The neural arches of the two sides are not co-ossified yet, and they are usually separated.

The morphology of the scapula is similar to that of adults. Both ends of the long bones are concave, indicating cartilaginous articular heads. The length of the humerus is only 76% of the standard length and 80% of the length of the femur. The ulna is slightly shorter than the radius and is twice as broad. The carpals are not ossified yet. Only two metacarpals (I and II) are preserved.

Three elements of the left pelvis can be seen. The pubis and the ischium are broad, but the extremities are not ossified, so that the sutural articulation of the three elements seen in the adult stage is not yet developed. The symphysis between the two sides must also have been cartilaginous. The ilium does not differ much from that of the adults. The femur is slender with both ends expanded slightly. Its length is 96% of the standard length. The tibia and fibula are similar to those of the adult. The tarsal bones are not ossified at this stage. The five metatarsals of the right foot are well preserved. As in adults, the first metatarsal is the shortest, only half the length of the second metatarsal and one-third the length of

the fourth, which is the longest. The fourth metatarsal is also the thickest of the five. The pedal digits appear more densely ossified than those of the manus. In the third, fourth, and fifth digits, at least two segments were ossified when the animal died. The ends of the long bones are not fully ossified. This is expected for such an early developmental stage.

The proximal end of the sacral ribs is slightly thicker than that of the dorsal ribs. The distal end is blunt. The first pair of caudal ribs converges toward the ilium, but the distal end is pointed. All the dorsal ribs bear a longitudinal groove on their dorsal side. This is not seen in the adults. The ribs are thinner than those of the *Neusticosaurus* embryo (see Sander, 1989, Fig. 33), and pachyostosis is not apparent. About six caudal ribs are preserved on the left side. The count of caudal vertebrae is 34, including seven impressions. The gastralia are already present in this stage of development.

The tiny specimen of *Neusticosaurus peyeri*, similar in size to GXD835002, was identified as an embryo by Sander (1988, 1989) based on its posture and size. The posture of GXD835002 does not differ much from that of other specimens of *Keichousaurus hui*. In reptiles, the size of the hatchlings is closely related to that of the adults (Andrews, 1982; Currie & Carroll, 1984). If the adult size is known, the hatchling size can be predicted using a power function in the form of:

$$size_{\text{hatchling}} = \alpha \times size_{\text{adult}}^{\beta} \quad [1]$$

Because the total length of most of the specimens of *Keichousaurus hui* is unknown, the formula derived by Currie and Carroll (1984) cannot be used since it relates the total length of hatchlings and adults, whereas Andrews' (1982) formula uses the snout-vent length. Andrews calculated the power and the intercept of the growth line for lizards, snakes, crocodiles, and turtles separately. From his result (Andrews, 1982, p. 281), it is clear that lepidosauromorphs (lizards and snakes) have a very different hatchling-adult size ratio than do turtles and crocodiles. The term β is 0.74 and 0.76 for lizards and snakes, respectively, but 0.20 for turtles and 0.24 for crocodylians. Because among crown-group diapsids with a generalized body plan, sauropterygians are probably more closely related to lepidosauromorphs than to crocodiles (Rieppel, 1994), it is assumed that the formula for lizards would be most appropriate in

determining the hatchling size of *Keichousaurus hui* from its adult size.

Here, the adult size is defined as the mean snout-vent length of sexually mature individuals. Sexual maturity is achieved in modern reptiles when oviducal eggs are found in females or motile spermatozoa are found in the testes or the efferent ducts of males. Since eggs and spermatozoa are never preserved in fossils, only secondary sexual characters can be used to determine the sexual maturity of paleontological material. In the case of Alpine pachypleurosaurids, the first appearance of sex y is used as evidence to indicate the onset of sexual maturity (Sander, 1989). However, as mentioned in the previous section, this is not suitable in the present context. Here, the proportion of the humerus versus femur is used as an indicator of maturity. Should this be incorrect, we are more likely to underestimate rather than overestimate the snout-vent length of mature animals. Another factor that may lead to underestimation is that there are only three adult specimens in which the snout-vent length can be measured, and they are all of sex x , the smaller of the two sexes. As we shall see, however, these factors, even without correction, will not affect our conclusion.

The mean snout-vent length of specimens with a maturity indicator greater than 1 is used to estimate the mean adult size of *Keichousaurus hui*. From this value (147.5 mm), Andrews' formula results in an expected hatchling size of 46.7 mm. Compared with the snout-vent length of GXD835002 (34.2 mm), it is apparent the specimen GXD835002 is too small to be a hatchling.

The fact that specimens of different developmental stages were found at the same locality in the same type of sediments suggests that *Keichousaurus hui* was probably ovoviviparous; otherwise, the egg would have been laid in a terrestrial environment, and in that case, the embryo almost certainly would not have been preserved. However, there is no direct evidence to support ovoviviparity, in contrast to ichthyosaurs, where embryos are found inside the abdominal cavity of the adults.

The Ontogenetic Stage of V7917

The second smallest specimen in this sample is V7917. It has a snout-vent length of 71 mm, a little more than twice the length of GXD835002 and about 152% of expected hatchling size. Most small reptiles in modern biotas double their body

size during the first year of their life (Currie & Carroll, 1984). It is reasonable to assume that V7917 was less than 1 year old when it died.

At this stage of development, most of the bony elements are ossified, but not the ulnare. The proportions of the skull are similar to those of the embryo. The orbits are relatively large. The pre-orbital part of the skull is short. A large fontanelle persists between the parietal and the postfrontal, indicating incomplete ossification of the parietal. Even if this gap were attributed to postmortem damage, it would still indicate a poorly ossified area. The skull table of adult specimens is usually complete.

The skull of V7917 is 10 mm long, only 21% longer than that of the embryo. The other parts of the body, however, grew relatively faster than the skull. The ratio of standard length in V7917 versus the embryo is 277%. That of the neck is 270%. The tail of V7917 is 273% that of GXD835002.

The humerus is shorter than the femur. The whole length of the forelimb is about 70% of the glenoid–acetabular length. The elements of the pes are longer and much stronger than those of the manus.

Subadult Specimens

The skull of specimen V7918 is not preserved; hence, the snout–vent length is not known. However, an estimate can be made. The ratio of the length of the neck versus the length of the trunk is 0.9–1.1 in other specimens with both neck and trunk preserved. Assuming it is 1.0 for V7918, then the length of the trunk plus the neck would be over 87 mm. If skull length is at least the same as in V7917, then the snout–vent length of V7918 would be at least 98 mm, which is more than double the expected hatchling size. This suggests that V7918 was a little more than 1 year old at the time of death. Specimen GXD7602 is slightly larger than V7918. The snout–vent length is about 125 mm. The skull is 15.5 mm long, about 141% of standard length.

In both of these specimens, the ulnare is present. However, the shape of the bone is irregular, which means that its ossification is not yet complete. The distal metacarpals are not ossified at this stage. The forelimbs are still weaker than the hind limbs. Their lengths are 70% of the glenoid–acetabular length, as in V7917.

The Adults

In the adults, the parietal opening tends to close up. In specimen GXD7601, the parietal opening is reduced to a tiny opening, only 0.3 mm in diameter. In the slightly larger specimen, V952, the parietal opening is completely closed. The snout of adult *Keichousaurus hui* is relatively longer than that of the juveniles. The relative size of the orbits does not change. The ratio of the length of the skull/standard length is slightly lower than in the juveniles. The humerus is not only longer but also stronger than the femur, especially in sex *y*. The fourth distal carpal and tarsal are present in all the sex *y* specimens except V7919. In the largest specimens, such as GXD7613 and GXD838028, there are two more distal carpal elements: the second and the third distal carpals. The sequence of carpal ossification is fully in accordance with that of stem-group diapsids (Caldwell, unpubl. data: Carroll, 1985).

Three size landmarks are recognized in growth studies of reptiles: hatching size, size at sexual maturity, and maximum size (Andrews, 1982). The relationship of the first two landmarks was discussed earlier. Data obtained from modern lizards (Andrews, 1982, Appendix II) indicate that the ratio of size at sexual maturity versus maximum size varies between 1.16 and 2.00. The standard length of the adult specimens of *Keichousaurus* ranges from 13 to 19 mm, which means that the largest specimen in the collection under study is 50% larger than the smallest “adult” specimen. This is in accordance with the data derived from modern lizards.

Allometric Growth of *Keichousaurus hui*

The last column in Table 1 lists the ratios of different measurements in GXD838028 and GXD835002. The most striking phenomenon is the extent of the diversity among different parts of the body. During growth, the width of the skull increases 1.7 times. The length of the neck increases 6.5 times during the same period. The length of the humerus of GXD838028 is 14.4 times that of the embryo. It is apparent that the rates of growth of different parts of the body are different. This phenomenon is known as allometric growth.

Allometry describes the phenomenon in which functionally similar structures may have different proportions due to differences in size (Gould,

1971; Blackstone, 1987). Allometric analysis can be performed either in an interspecific context, in which the same part of the body of the same age group (usually adults) of different but related species is studied, or in an intraspecific context, where different age groups of the same species are studied. In the present study, the second approach is pursued.

In studies of allometry, the relationship of different parts of the body x and y is usually expressed using a power function:

$$Y = aX^b \quad [2]$$

where b is called the allometric coefficient. The value of the allometric coefficient illustrates the relationship of proportions to absolute size. If b exceeds 1, the proportion $y:x$ is larger in larger animals and allometry is said to be positive. If b is less than 1, then $y:x$ is smaller in larger animals, which is known as negative allometry. Isometry prevails if b equals 1, and the proportion $y:x$ is the same regardless of size.

Allometry is always relative: when part y shows positive allometry relative to part x , then part x shows negative allometry relative to part y . To identify the growth rate of different parts of the body, a measurement has to be selected to represent the standard body size. Possible candidates could be snout-vent length, trunk length, glenoid-acetabulum length, and standard length (the length of the last four dorsal vertebrae). The shortcoming of the snout-vent length is that skull length, which is negatively allometric to almost every other body measurement, is included. Also, the skull is not preserved in all specimens. Trunk length and glenoid-acetabulum length are problematic in that they depend on the position of the pectoral girdle. Because the pectoral girdle is not anchored to the vertebral column and hence is prone to postmortem dislocation, it is impossible to rely on trunk length or glenoid-acetabulum length as an accurate indicator of body size. Although the standard length was arbitrarily defined as the length of the last four (instead of three or five or any other number) dorsal vertebrae (Sander, 1989), it has the advantage of being an accurate indicator of the body size, and it is relatively easy to measure.

The allometric coefficients of various parts of the body relative to the standard length (Table 3) are calculated using the least squares linear regression method on log-transformed data. Actually, the calculations were carried out twice, once

including and once excluding the data of GXD835002, the embryo. The significance tests were performed on the hypothesis $H_0:b = 1$ (the growth is isometric), and $H_0:b = 1.5$ (the underlying meaning of which will be discussed later). The significance level is set at 95%, double-sided.

The growth of the skull is strongly negatively allometric. The allometric coefficient is about 0.5 if the embryo is included and 0.85 if it is not. The adjusted r^2 is the unbiased coefficient of determination of the sample when the sample is small. Note that the adjusted r^2 is greater when the embryo is excluded than when it is included, indicating that the allometric coefficient may not be constant during development. Initially, growth of the skull must show highly positive allometry, outgrowing all other parts of the body, as a result of size constraints imposed by the nervous system and related organs. Subsequently, growth of other body parts would catch up, rendering the allometric coefficient of the skull highly negative. The immediately postnatal growth rate of the skull is slightly higher than in the last embryonic stage, but it is still negative. The allometric coefficient in the first case (embryo included) can be thought of as an average over the whole life span of the animal, whereas in the latter case it is specific for postnatal growth. In both cases, the allometric coefficients are statistically significantly lower than 1.

When relative growth rate is more nearly constant, the coefficient of determination would be proportional to the sample size, which is the case for the data on neck length. Although the estimates of b are very similar and close to 1, we can reject the hypothesis that the true value of b was 1.5 if the embryo is included in the analysis, but we cannot do so if the embryo is excluded. The same also applies to the trunk length and the snout-vent length.

The allometric coefficients for neck length, trunk length, and glenoid-acetabulum distance are all very close to 1, especially as the data for the embryo are included. The body width at the glenoid and at the acetabulum show the same pattern as the skull: the overall allometric coefficients are very close to 1, but they are much higher if the data of the embryo are excluded from the calculation. The adjusted r^2 values are greater in the latter cases.

The allometric coefficients for the forelimb elements are much higher than those for their counterparts in the hind limb, whether the data for the embryo are included or not. The humerus, the

TABLE 3. Allometric coefficients of various body parts vs. the standard length in *Keichousaurus hui*.

		Number of Obs.	Adjusted r^2	a	b	T for H0: b = 1	T for H1: b = 1.5
Skull length	GXD835002 incl.	5	0.8430	5.468	0.444	5.937 -	
	GXD835002 excl.	4	0.9995	2.028	0.851	14.207 -	
Skull width	GXD835002 incl.	6	0.9296	2.757	0.481	8.823 -	
	GXD835002 excl.	5	0.9855	1.557	0.703	6.958 -	
Orbit length	GXD835002 incl.	5	0.8525	2.104	0.394	7.557 -	
	GXD835002 excl.	4	0.7527	1.191	0.627	1.891 +	
Neck length	GXD835002 incl.	7	0.9818	4.096	1.059	1.000 +	7.513 -
	GXD835002 excl.	6	0.9162	3.995	1.068	0.477 +	3.018 +
Trunk length	GXD835002 incl.	9	0.9762	5.033	0.975	0.469 +	9.766 -
	GXD835002 excl.	8	0.9696	3.004	1.172	2.201 +	4.186 +
Glen.-acet. distance	GXD835002 incl.	10	0.9801	3.248	1.053	1.069 +	8.958 -
	GXD835002 excl.	9	0.9489	2.314	1.183	1.892 +	3.275 -
Snout-vent length	GXD835002 incl.	5	0.9717	13.613	0.911	1.142 +	7.598 -
	GXD835002 excl.	4	0.9542	6.973	1.186	1.249 +	2.110 +
Glenoid width	GXD835002 incl.	10	0.9123	1.057	1.091	0.810 +	3.647 -
	GXD835002 excl.	9	0.9445	0.292	1.582	4.308 -	0.607 +
Acet. width	GXD835002 incl.	10	0.9303	1.613	1.009	0.102 +	5.354 -
	GXD835002 excl.	9	0.9443	0.585	1.397	3.321 -	0.862 +
Humerus length	GXD835002 incl.	10	0.9558	0.448	1.386	3.891 -	1.150 +
	GXD835002 excl.	9	0.9539	0.156	1.788	5.690 -	2.080 +
Ulna length	GXD835002 incl.	10	0.9608	0.240	1.334	3.727 -	1.851 +
	GXD835002 excl.	9	0.9554	0.094	1.691	5.365 -	1.486 +
Radius length	GXD835002 incl.	10	0.9312	0.290	1.280	2.421 +	1.905 +
	GXD835002 excl.	9	0.9328	0.086	1.743	4.513 -	1.475 +
3rd metacarpal		7	0.9804	0.100	1.380	4.776 -	1.509 +
3rd digit		4	0.7829	0.321	1.160	0.474 +	1.008 +
Femur length	GXD835002 incl.	10	0.9775	0.763	1.136	2.369 +	6.346 -
	GXD835002 excl.	9	0.9738	0.414	1.370	4.662 -	1.634 +
Tibia length	GXD835002 incl.	10	0.9770	0.230	1.204	3.322 -	4.814 -
	GXD835002 excl.	9	0.9620	0.129	1.425	4.256 -	0.755 +
Fibula length	GXD835002 incl.	10	0.9655	0.336	1.114	1.632 +	5.503 -
	GXD835002 excl.	9	0.9624	0.159	1.400	4.097 -	1.025 +
3rd metatarsal	GXD835002 incl.	8	0.9872	0.209	1.193	3.773 -	5.986 -
	GXD835002 excl.	7	0.9825	0.120	1.409	5.334 -	1.184 +
3rd toe		5	0.8057	0.634	0.939	0.273 +	

ulna, and the third metacarpal have allometric coefficients significantly higher than 1—closer to 1.5. The allometric coefficient for the third (the longest) digit of the hand (and the foot) is much lower than for the other limb elements. This may reflect the true situation, or it may be due to the loss of the last segment during preservation.

Locomotion

Aquatic locomotion of the more advanced sauropterygians, such as plesiosaurs, has been a topic of investigation since the first published description of a plesiosaur in the 1820s (for historical reviews, see Robinson, 1975, 1977; Godfrey,

1984; Storrs, 1993). From these studies, a general consensus emerged that the primary swimming apparatus of plesiosaurs was the two pairs of limbs used in paraxial propulsion. Judged from the reinforcement of the limb girdles along the midline, they must have used symmetrical strokes to propel the rigid body in water.

Recent years have seen an increased interest in the study of the functional morphology of more generalized groups of sauropterygians (Carroll & Gaskill, 1985: *Neusticosaurus edwardsii*; Rieppel, 1989: *Serpianosaurus*; Sander, 1989: *Neusticosaurus peyeri*, *N. pusillus*; Storrs, 1991: *Corosaurus*). Schmidt (1987) and Storrs (1993) discussed the functional anatomy of stem-group sauropterygians in general.

The pectoral and pelvic girdles of plesiosaurs

and nothosaurs are functionally similar in that they favor symmetrical movement of the limbs. A calcified sternum, present in generalized diapsids, has disappeared (for a different opinion, see Nicholls & Russell, 1991). In modern lizards, the function of the sternum is to facilitate alternative movements of the forelimbs (Jenkins & Goslow, 1983). Presumably, the same structure would have had a similar function in generalized diapsids, and the lack thereof in sauropterygians indicates that the alternate movement of the forelimbs is not structurally facilitated in a similar way. Also, the dorsal "blade" of the scapula and ilium is reduced to a rodlike structure, whereas the ventral portion of the girdles was elaborated.

The degree of specialization of the girdles and limbs is different in the two groups, however. In plesiosaurs, the scapulocoracoids are massive. They meet in the ventral midline of the body and extend posteriorly a great distance. The limbs of plesiosaurs are highly specialized structures, with almost no difference in fore- and hind limbs. The propodials are massive elements. The elements of the epipodials and beyond have all become rounded bony disks. The manus and pes exhibit hyperphalangy, and the digits are tightly packed. The outline is wing-shaped, with a broad base and a tapering end (Robinson, 1975).

In primitive sauropterygians, the ventral expansion of scapula is minimal, and the coracoids are not elongated anteroposteriorly. The ventral view of the pectoral girdle is more or less a circle with a large fenestration in the middle, which may have been at least partially closed by cartilage in some taxa (Schmidt, 1987). Another difference between "nothosaurs" and plesiosaurs is that the scapular "horn" of "nothosaurs" is placed right above the glenoid, whereas in plesiosaurs, the scapular horn is situated well forward relative to the glenoid. Since the latter arrangement may facilitate the upstroke of the forelimb (Robinson, 1975), it follows that the placement of the scapular horn in "nothosaurs" might greatly limit the extent to which the humerus can be elevated. Therefore, underwater flying is impossible for "nothosaurs." (Godfrey, 1984, argued that underwater flying as observed in sea turtles was also not possible for plesiosaurs.) The same argument applies to the pelvic girdle as well. The outline of the "nothosaur" limbs is more fan-shaped than hydrofoil-shaped. The propodials of "nothosaurs" are slim compared to those of plesiosaurs, and the proportions among the limb segments are not much derived from the generalized diapsid con-

dition. The phalanges of the manus and pes are usually spread out in fossils.

The general similarities of the pectoral and pelvic girdles of plesiosaurs and "nothosaurs" indicate a similar distribution of muscles in both groups, i.e., reduced dorsal and elaborated ventral components. The different degrees of elaboration of the ventral components in the two groups may be partly due to different functions of the limbs.

Function of the Shoulder Girdle and Forelimb

Among "nothosaurs," pachypleurosaurids and "nothosaurids" can be differentiated by their body size and degree of specialization. The humeri of "nothosaurids" are stouter than those of pachypleurosaurids, and the epipodials are wider because of a large interosseous space between the ulna and radius. It is apparent that the symmetrical stroke of the forelimbs was an important component in the locomotion of "nothosaurids."

The humerus of pachypleurosaurids is relatively more slender, and the epipodials are not expanded in most species. Pachypleurosaurids usually have a long tail with high neural spines. For these reasons, they are usually considered lateral undulatory swimmers (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989; but see Storrs, 1993). Modern diapsids (iguanas, crocodiles, and snakes) tend to employ lateral undulation when they swim, which is quite natural because of their locomotor pattern on land. The same pattern of locomotion is also assumed for the younginiform *Hovasaurus* (Currie, 1981).

Keichousaurus hui differs from other pachypleurosaurids in having a stronger humerus, a very broad ulna, and slight hyperphalangy in the manus. The profile of the forelimbs is more paddle-shaped than in other genera. These differences may indicate a more important role of the forelimbs in locomotion of *Keichousaurus hui* than in other pachypleurosaurids. Allometric analysis of growth series supports this conjecture. Assuming that the locomotor pattern did not change during the lifetime of *Keichousaurus hui* (or of other pachypleurosaurids), the function of the forelimbs would have remained the same during growth. If the forelimbs were not heavily used in locomotion, their growth should be close to isometric, if not negatively allometric, relative to body length, as exemplified by the *Neusticosaurus edwardsii* (Table 13 in Sander, 1989). If the limbs were

heavily used for propulsion, positive allometric growth would be expected. The expected allometric coefficient can be approximated as explained below.

Since the forelimbs of *Keichousaurus hui* could not be used as hydrofoils in underwater flight because of the structure of the shoulder girdle, it is only reasonable to assume that they were used as paddles. If *Keichousaurus* did use its forelimbs as paddles, the drag force produced by paddling should be equal to the drag force acting on the body surface. The drag force acting on the body surface is proportional to the product of the swimming speed squared and a characteristic length of the body squared; the second term, in this case, is the standard length. This relation can be expressed as:

$$D_{\text{body}} \propto V^2 L_{\text{body}}^2 \quad [3]$$

where D is the drag force, V is the speed, and L is the characteristic length.

Since swimming speed cannot be estimated on the basis of the fossil record, we have to turn to data of modern aquatic vertebrates to estimate the swimming speed of *Keichousaurus*. Even for modern aquatic vertebrates, however, the data on swimming speed are sparse, but they still indicate that the active swimming speed of aquatic vertebrates is proportional to the square root of the body length:

$$D_{\text{body}} \propto L_{\text{body}}^{1/2} \quad [4]$$

This figure encompasses a body size from a few centimeters to over 20 m and from ectothermic fish to endothermic whales. The body size of *Keichousaurus* is well within the range indicated in the figure, and it is reasonable to believe that its metabolic rate is also within this range. Therefore, the speed relationship depicted above also applies to *Keichousaurus*. Substituting [4] into [3], we obtain:

$$D_{\text{body}} \propto L_{\text{body}}^3 \quad [5]$$

i.e., the drag force acting on the body surface is proportional to the body mass.

The propulsion force produced by the paddle is proportional to the product of the characteristic length of the paddle squared and the speed of the paddle relative to the water squared:

$$D_{\text{paddle}} \propto V^2 L_{\text{paddle}}^2 \quad [6]$$

Hydrodynamics dictates that, for the paddle to be efficient, the speed of the paddle relative to the water should be as small as possible (Alexander, 1968). The paddle can be thought of as a lever and the tip of it as the pivot. The less it slips, the more the body is propelled forward. This applies to adults as well as to juveniles. If we assume that swimming speed is close to constant, then the propulsion force produced by the paddle is proportional to a characteristic length of the paddle squared. Since the propulsion force produced by the paddle should balance the drag force acting on the body surface,

$$D_{\text{body}} = D_{\text{paddle}} \quad [7]$$

Substituting both sides, we get:

$$\text{therefore, } L_{\text{paddle}}^3 \propto L_{\text{body}}^3 \quad [8]$$

or

$$\text{therefore, } L_{\text{paddle}} \propto L_{\text{body}}^{1.5} \quad [9]$$

In other words, the allometric coefficient of the functional paddles versus body length is expected to be 1.5. Recall that the allometric coefficients for most of the forelimb elements of our sample of *Keichousaurus* are statistically significantly different from 1, but the hypothesis that they are statistically significantly different from 1.5 could also not be rejected. It should be noted that the small European pachypleurosaurids (*Serpianosaurus*, *Neusticosaurus pusillus*, and *N. peyeri*) also exhibit positive allometry in their forelimbs, though not to the same degree as in *Keichousaurus*. It has been suggested that their forelimbs are used for terrestrial locomotion (Sander, 1989), but this would not explain why the type of pectoral girdle of sauropterygians, which is adapted to resist the symmetrical pressure from the humeri, evolved.

Reconstruction of the Muscular System of the Shoulder Girdle and Forelimb

The structure of the pectoral girdle of sauropterygians differs greatly from that of terrestrial diapsids, and there is no living form with a similar configuration. Any attempt to reconstruct the muscular system of *Keichousaurus* can only be an approximation. Fortunately, the study of living tetrapods shows that the muscular system tends to

be conservative, and rugosities on the bony elements indicate the position of muscle insertions with a reasonable degree of accuracy. Among living terrestrial vertebrates with a generalized body plan, lizards are most closely related to sauropterygians. Therefore, the attempted muscle reconstruction is based on lizards. Major references are Romer (1922) and Jenkins and Goslow (1983).

In terrestrial tetrapods, the thorax is suspended on the supporting structure formed by forelimbs and pectoral girdle via the serratus, trapezium, and levator scapulae. These muscles originate from the scapular blade and occupy the major part of the inner surface and the anterior and posterior edges of the blade. Because of the buoyant medium in an aquatic environment, the supportive function of the girdle and limb is not as great, and the importance of these muscles is diminished. As a result, the size of the scapular blade, as well as that of the three muscles, is greatly reduced. Furthermore, a less solidly attached pectoral girdle increases the effective length of the power stroke.

The muscles of the forelimb proper can be divided into a dorsal (levator) and a ventral (depressor) group, according to their embryological origin (Romer, 1922). The former includes the latissimus dorsi, subcoracoscapularis, deltoideus, scapulohumeralis, triceps, and extensors of the lower limb. The latter includes the pectoralis, supracoracoideus, brachialis, biceps, coracobrachialis longus, c. brevis, and flexors of the lower limb. However, since *Keichousaurus* (and all other "nothosaurs") is dorsoventrally compressed and the muscle attachments on the pectoral girdle are more horizontally distributed, it might be more appropriate to group these muscles into abductors and adductors, depending on the position of their origin and insertion relative to the glenoid fossa.

There is no evidence as to the size of the latissimus dorsi, because this muscle originates from the dorsal fascia. The insertion of the latissimus dorsi is at the convergence of the Y-shaped crest at the dorsal side of the humerus. The latissimus dorsi is the only muscle in the pectoral girdle of pachypleurosaurids that originates well above the level of the glenoid, and it would have some mechanical advantage when acting as a "levator" of the humerus. In lizards, the origin of this muscle is at, and behind, the level of the glenoid, and it functions as an adductor of the humerus. This may also be the case in *Keichousaurus*.

The subcoracoscapularis originates from the medial surface of scapula and coracoid, and it passes behind the scapular blade to insert between

the upper two arms of the Y-shaped crest on the dorsal side of the proximal head of the humerus. In some reptiles, this muscle can be separated into two slips, a subscapularis and a subcoracoideus. Since in *Keichousaurus* and other "nothosaurs" the scapular blade is small and the coracoid is large, the subcoracoideus would be the larger muscle of the two. Because the major part of the scapulocoracoid is horizontal, this muscle would work most effectively when the humerus was in a horizontal or near horizontal plane. Also, since the major part of the scapulocoracoid is behind the glenoid in *Keichousaurus*, the function of the subcoracoscapularis would be to pull the limb back to the side of the body. Therefore, it is part of the adductor group.

Primitively, the deltoideus originates from the upper part of the scapular blade (deltoideus scapularis) and from the clavicle (deltoideus clavicularis). The insertion is at the anterodorsal part of the proximal humerus head. In *Keichousaurus*, the deltoideus scapularis was either very small or was lost, due to the small size of the scapular blade. Because of the peculiar relation between clavicle and scapula, the anterior portion of the ventral part of the scapula may share the origin of the deltoideus clavicularis with the clavicle. Since the deltoids originate anterior to the glenoid, they function as abductors of the humerus.

Inferred from lizards, the scapulohumeralis should originate from the lower part of the scapular blade and insert into the anterior aspect of the proximal end of the humerus, functioning as a levator and abductor. However, its origin and insertion are not apparent in *Keichousaurus*. If present, it must have been quite small and insignificant.

The triceps is the major extensor of the lower arm. In terrestrial tetrapods, the insertion of the triceps is on the olecranon of the ulna. In *Keichousaurus*, the lower arm is always in an extended position and moves in unison with the humerus. The triceps is therefore basically a static muscle of lesser importance than in terrestrial forms. As a consequence, there are no conspicuous muscle scars on the humerus and pectoral girdle where the muscle may have originated and inserted, and the olecranon of the ulna is not ossified.

In living lizards, the pectoralis is a broad sheet of muscle originating from the clavicle and interclavicle along the ventral midline of the pectoral girdle, including sternum and sternocostale, from the ventral midline along the linea alba and from

thoracoabdominal fascia (Jenkins & Goslow, 1983). In *Keichousaurus* and other "nothosaurs," the sternum has disappeared, and the coracoids meet in the ventral midline. The pectoralis probably shifted part of its origin to the coracoids. The densely packed gastralia may have provided reinforced anchorage for the abdominal muscles and the thoracoabdominal fascia, and hence stronger support for the posterior part of the pectoralis. The insertion of the muscle is into the deltopectoral crest, which is a major landmark on the humerus. The direction of the force would be posteromedially, toward the ventral midline of the body. It is basically an adductor, and when contracting in concert with other adductor muscles, it would contribute significantly to the power stroke, although the anterior part of the muscle could act as an abductor.

The supracoracoideus is an important muscle in terrestrial reptiles for maintaining posture by stabilizing the glenohumerus joint. In lizards, the origin of the supracoracoideus is on the anterior part of the coracoid, anterior to the glenoid. The insertion is at the proximal margin of the deltopectoral crest of the humerus. Since the coracoid does not extend anteriorly to the glenoid in *Keichousaurus*, the orientation of this muscle might shift to a lateral one. The supracoracoid foramen can be used as an indication of the position of the supracoracoideus. In *Keichousaurus*, the supracoracoid foramen is situated at the middle of the border between scapula and coracoid, which is where the supracoracoideus should originate. If this is correct, then the supracoracoideus would be much smaller and shorter than that in terrestrial forms. Considering that *Keichousaurus* lived in an aquatic environment, this may indeed be expected.

The coracobrachialis longus and c. brevis are the major muscles that function as adductors of the humerus. The origin of these muscles spreads across the major part of the external (ventral/lateral) surface of the coracoid in lizards and *Sphenodon*. The insertion of these muscles is into the flexor surface of the humerus, with the c. brevis more proximal and covering more surface. In *Keichousaurus*, the scar for the c. brevis is prominent on the ventral-medial surface of the humerus. Judging from the size of the origination and insertion area, c. brevis could be very strong.

The brachialis and biceps brachii are very closely related to coracobrachialis muscles developmentally, though they are basically forearm flexors. In some reptiles, the origination of the

biceps can hardly be separated from the *coracobrachialis* muscle (Holmes, 1977). In lizards, where the sternum is present, the biceps arises along a narrow area adjacent to the coracosternal joint (Jenkins & Goslow, 1983). In *Keichousaurus*, the sternum is absent. Therefore, the origin of the biceps may have moved to the midline of the body. In terrestrial forms, the proximal belly of the biceps is usually tendinous (Holmes, 1977), which might be related to the reduction of the coracoid. Since the coracoid of *Keichousaurus* is enlarged, the biceps may have had a fleshy proximal belly and may have contributed to the power stroke. The distal belly of the biceps and brachialis, in contrast, may not be as important as in terrestrial forms, where the precise control of the forelimb is more critical in locomotion and posture maintenance. The function of the brachialis and of the distal belly of the biceps is to stabilize the elbow joint.

The muscles of the lower arms are not discussed here because there is no evidence of their specific distribution. However, it is logical to assume that *Keichousaurus* was able to spread out its fingers to increase the surface area during the power stroke and pull them together in the recovery phase to reduce drag.

The power stroke starts with the forelimbs forward and outward, horizontal with the main axis of the body, palms facing downward. The contraction of the adductor muscles would bring the arms backward with a shallow down curve. At the same time, the forearms would pronate (rotate inward) so that the palms faced backward. The fingers would spread to maximize the drag surface, with the web between the fingers. In the recovery phase, the levator and the abductor muscles would bring the supinated arms forward, with palms facing down and fingers collected to reduce the drag.

Function of the Pelvic Girdle and Hind Limb

It is common for secondarily aquatic vertebrates to hold their hind limbs close to the tail to reduce drag, rather than utilizing them for propulsion. This arrangement is characteristic of crocodiles and alligators (Manter, 1940), sea lions (English, 1976; Godfrey, 1985), and penguins (Clark & Bemis, 1979) among living animals, as it might also be in some pachypleurosaurids (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989). Therefore, the pelvic girdle and hind limbs of secondarily aquatic vertebrates are usually not

very well developed, and the articulation between the pelvis and the vertebral column tends to loosen. If the hind limbs are not used for other purposes, selective pressure might eventually eliminate them, as is the case in cetaceans. In plesiosaurs and sea turtles, however, the hind limbs are strong and are as highly developed as the forelimbs.

As in other pachypleurosaurids, the pelvic girdle and the hind limbs of *Keichousaurus hui* are not as well developed as the pectoral girdle and forelimbs. The femur is slim, but the lower limb is expanded anteroposteriorly. The epipodial is only about 50% the length of the femur. The growth of the hind limbs shows a lesser degree of allometry than the forelimbs, indicating a less important role in propulsion.

The iliac blade is reduced to a small dorsal process, comparable to the reduction of the scapular blade. However, two lines of evidence indicate that the suspension of the pelvis from the vertebral column is still quite strong. First, the sacral ribs are pachyostotic, and second, there is a recess at the end of one of the sacral ribs (the middle, or principal sacral rib), which receives a projection from the midshaft of the ilium. The advantage of this unusual arrangement may be the achievement of some mobility while maintaining the stability of the pelvis. It may have been possible for the pelvis to rotate around the functional sacral rib to a small degree when needed, such as when the animal used the hind limb for propulsion. However, it may also have been easy to "lock" the pelvis into place using axial muscles when maneuvering required stability of the pelvis, for example, during a sharp turn, when the hind limbs were used as the steering devices, or during a sudden stop. The auxiliary "sacral ribs" in front of and behind the principal rib may have provided support or reinforcement and transmitted the bracing force along a larger part of the vertebral column. If this hypothesis is accepted, the conclusion is that those genera with a larger number of sacral ribs may have been more agile.

Reconstruction of the Muscular System of the Pelvic Girdle and Hind Limb

As noted earlier, the most intimate connection between the pelvic girdle and the sacrum in *Keichousaurus* is at the middle of the iliac blade. The lateral portions of the dorsal musculature seem to have been divided by the ilium, as in all verte-

brates with a well-developed pelvic girdle. The pelvic muscles include the longissimus dorsi and iliocostalis in the trunk and the extensor caudae lateralis and/or abductor caudae externus in the tail (Romer, 1922). The iliopubic, puboischadic, and ilioischadic ligaments of terrestrial forms must also have been present in *Keichousaurus*, although the precise position of their attachment to the girdle remains uncertain. The ventral muscles include the obliquus, transversalis, and rectus abdominis in the front and the ischiocaudalis in the tail. Since the pelvic girdle may have been capable of some mobility in *Keichousaurus*, these muscles may have controlled motion of the girdle.

The muscles that originate from the ilium and insert on the femur or the lower limb are the iliiofemoralis, iliofibularis, and iliiotibialis. Since the ilium is very small, the muscles that originate from it may also have been small and weak, and their contribution to the movement of the hind limb may not have been significant.

The major muscles acting on the femur originate from the two surfaces of the ventral plate of the pelvic girdle and associated ligaments. They include the puboischiofemoralis internus and p. externus, ambiens, adductor, and ischiotrochantericus. Although the caudifemoralis longus and c. brevis originate from the vertebral column instead of from the pelvic girdle, developmentally they belong to the same ventral limb muscle mass (Romer, 1942).

The puboischiofemoralis internus originates from the broad inner (dorsal) surface of the puboischium plate. It runs outward in front of the ilium-pubis margin and inserts on the proximal dorsal surface of the femur. The function of this muscle is to pull the femur upward and draw it close to the side of the body. When acting with the triceps, it would cause the hind limb to form a large fan-shaped area facing the direction of the current, thus either braking the forward thrust of the animal or changing its direction.

The ambiens together with the iliiotibialis and femorotibialis form the pelvic triceps. It originates from the anterolateral edge of the pubis and merges with the other two heads to insert on the proximal end of the tibia. Judging from the preservational posture of the *Keichousaurus* specimens, where the hind limbs are always in a flexed position, these muscles were not very strong.

The puboischiofemoralis externus occupies the entire ventral (external) surface of the puboischadic plate. The insertion of this muscle is into the intertrochanteric fossa at the ventral proximal

end of the femur. This muscle is the major depressor of the femur when working with the adductor, and it also contributes to keeping the hind limb close to the side of the tail when acting together with the caudifemoralis muscles.

The caudifemoralis longus and c. brevis originate from the underside of the anterior caudal vertebrae and their associated ribs. In lizards, the muscle fibers converge into a strong tendon that passes under the femur and inserts into the anterior side of the proximal end of it. A thinner tendon branches out from the stronger one and runs along the femur, attaching to the ligaments on the knee joint. The situation would not be much different for *Keichousaurus*, except that these muscles might be stronger, thus stabilizing the limb.

The ischiotrochantericus is a small muscle originating from the rear corner of the ischium and inserting via a tendon on the proximal head of the femur. Its function is to stabilize the acetabular joint.

Function of the Neck

The intervertebral articulations of *Keichousaurus hui* constitute a complex functional unit. The prezygapophyses face inward and rearward, as well as upward, whereas the postzygapophyses face outward and forward, as well as downward, so that the successive vertebrae are interlocked with each other. In the dorsal region, the postzygapophyses are swollen and interlock tightly with the prezygapophyses of the following vertebrae, so that there can be very little intervertebral movement, and the body is kept very stiff. In the neck region, however, the zygapophyses are not as swollen, so that the neck can move more freely. As shown by Holmes (1989), when zygapophyseal surfaces of the two sides of the vertebrae are not in the same plane and form an angle with the longitudinal axis of the vertebral column, coupling of movements tends to occur. In the case of *Keichousaurus hui*, when the neck flexes sideways as the animal is turning, the cervical vertebrae tend to bend upwards relative to the succeeding vertebrae and rotate in such a manner that the neural spines lean toward the center of the curve. The body then rotates such that the broad area of the abdomen faces the outside of the curve. The effect is that the centrifugal force, which tends to keep the animal moving in a straight line, is now better balanced by the increased drag force due to the increased surface

area that faces the outside of the curve. When birds make a turn, they do exactly the same thing: they rotate so that the belly and the large area of the wings face outward. The difference is that, for *Keichousaurus*, the mechanism was built into the skeleton, whereas in birds it is a locomotor behavior.

Function of the Tail

The European pachypleurosaurids are generally considered lateral undulatory swimmers, the tail providing the major propulsive force (Carroll & Gaskill, 1985; Sues, 1987; Rieppel, 1989; Sander, 1989; but see Storrs, 1993). However, there are several factors that would preclude *Keichousaurus* from being an effective lateral undulatory swimmer. The first few caudal vertebrae of *Keichousaurus* bear long caudal ribs; their neural spines are low. Therefore, the cross-section at the base of the tail would show a dorsoventrally compressed outline. It is evident that such a tail could not produce much thrust if undulated laterally. If *Keichousaurus* used its limbs during locomotion in a symmetrical fashion as is implied by the structure of the pectoral girdle, its tail could not be used in a laterally undulating fashion as proposed for other pachypleurosaurids, because the two patterns of locomotion are incompatible. In lateral undulatory swimming, undulatory waves travel from the head backward to the tail, producing the propulsive force. For each cycle of body wave, there are two phases. The force produced by the two phases is directed alternatively to the rear left and rear right. The posterior component drives the animal forward. The lateral component is compensated for by the force that points to the opposite direction, which is the lateral component of the force produced by the other half-phase of the undulation. Therefore, the pressure field along the body alternates constantly (Manter, 1940). In contrast, the symmetrical strokes of the limbs produce a symmetrical pressure field along the two sides of the body. For the symmetrical strokes to be effective, there should exist a symmetrical pressure field along the two sides of the body. If the pressure at the two sides of the body were different, the limbs would have to exert different amounts of force, thus destroying the symmetry. In lateral undulatory swimming, the direction of the body is constantly changing, and the force produced by symmetrical strokes is not directed just posteriorly, but posteriorly as well as to one

side. This, in turn, destroys the regularly alternating pressure field produced by the undulatory movement and requires compensation of the body. There are two alternatives: the tail was either trailed behind passively or was actively propelling, but moved dorsoventrally. However, there is no modern reptile that can undulate its tail dorsoventrally.

The Swimming Pattern of *Keichousaurus*

Subaqueous locomotion of secondary aquatic vertebrates falls into two broad categories: axial undulatory and appendage oscillatory. Members of the first class, such as ichthyosaurs and whales, employ the tail and/or part of the body as the main source of propulsion. Members of the second class use the paired fins or limbs. In reality, however, the situation is not as simple or clear-cut. Some swimmers may mix locomotor patterns. Examples of the mixture of drag-based and lift-based swimming patterns are the sea lion and possibly the plesiosaur (Godfrey, 1984). Axial and appendage propellers can also be used simultaneously. One example is human swimmers using the butterfly stroke. In this style of swimming, the arms are used in a symmetrical rowing pattern, while the whole body and legs undulate dorsoventrally.

The locomotion of *Keichousaurus hui* may also be a mixture of different patterns. The power stroke of the forelimbs was probably drag based. The recovery stroke may have elements of lift-based propulsion.

The function of the hind limbs of *Keichousaurus* may be similar to that of sea lions (Godfrey, 1985). When swimming in a straight line, sea lions hold their hind limbs in an inverted V position. In this position, the hind limbs act as stabilizers. During turns, the body of sea lions rotates so that the abdomen faces the outside of the curve, and the hind limbs fan out posteriorly so that the plantar surface of the hind limbs also face the outside of the curve, preventing the skidding of the posterior portion of the body. As in sea lions, the hind limbs of *Keichousaurus* are fan-shaped. When swimming in a straight line, the hind limbs of *Keichousaurus* would have trailed passively along the side of the tail. In this position, they would have increased the ventral surface at the base of the tail. When *Keichousaurus* turned, the bending of the neck would have caused the body to rotate so that the abdomen and the broad area of the base of the tail faced the

outside. At the same time, the hind limbs would have spread out posterolaterally, adding more surface to prevent skidding. The hind limbs of *Keichousaurus* could also be used as paddles in concert with the forelimbs when precise maneuvering was called for, such as for backing up from a tight place where turning was difficult.

Conclusions

The primitive quadrupedal tetrapods are (or were) sprawlers. The feet are placed laterally to the body, as opposed to beneath the body as in dinosaurs and mammals. The vertebral column is usually flexed laterally to increase the length of steps. It is natural for these animals to use lateral undulation when they swim. Many semiaquatic and aquatic reptiles are (or were) lateral undulatory swimmers. Alpine pachypleurosaurids are also believed to have employed a lateral undulating swimming pattern. However, the more advanced sauropterygians, the plesiosaurs, were definitely not lateral undulatory swimmers. Both fore- and hind limbs of plesiosaurs are equally highly developed as flippers and are believed to have been used for propulsion, either as wings or paddles. Judging from their stout forelimbs, "nothosaurids" were probably not undulatory swimmers either. However, probably only the forelimbs were used in locomotion. The elaboration and inclusion of hind limbs into the swimming apparatus may have occurred after the paraxial stroke pattern had been established. *Keichousaurus* was the only known pachypleurosaurid that employed a swimming pattern similar to that of the "nothosaurids." The cause or causes of this pattern switch in primitive "nothosaurids" and *Keichousaurus* is not clear.

The mode of reproduction of *Keichousaurus hui* is tentatively hypothesized to be ovoviviparous. The limb structure of *Keichousaurus hui* is adapted to aquatic locomotion. The elbow joint was greatly simplified, and the olecranon process of the ulna did not ossify. Crawling up the beach to lay eggs would be a very awkward business. The fact that an embryo was discovered in the same sedimentary environment also favors an ovoviviparity hypothesis.

At birth, the forelimbs of *Keichousaurus hui* were shorter than the hind limbs. However, since the growth of the forelimbs relative to the body was highly positively allometric, while the growth

of the hind limbs was isometric or slightly allometric, the adult *Keichousaurus hui* had longer and stronger arms than legs. It is believed that the forelimbs were the primary locomotion apparatus of *Keichousaurus hui*. Sexual dimorphism is apparent in *Keichousaurus hui* and is manifested primarily in the configuration and length of the humerus.

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