HETEROCHRONY IN A FOSSIL REPTILE: JUVENILES OF THE RHYNCHOSAUR *SCAPHONYX FISCHERI* FROM THE LATE TRIASSIC OF BRAZIL

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ABSTRACT. A juvenile (?one year post-hatching) specimen of *Scaphonyx fischeri*, an advanced rhynchosaur from the Late Triassic Santa Maria Formation (Carnian) of Brazil, is described. This is the youngest rhynchosaur ever reported, and it was probably 0·38 m long overall, compared to adult body lengths of 1·3–1·6 m. It is compared with an ontogenetic series of skulls of this species, ranging in length from 55 to 250 mm. An allometric analysis suggests that the posterior portion of the skull roof widens relatively more rapidly than overall size increase (positive allometry), while the length of the posterior region of the skull shows negative allometry. These relative shape changes during ontogeny are compared with ancestral rhynchosaurs whose ontogenies appeared to stop earlier than that of *Scaphonyx*. This peramorphic shift in ontogeny is tentatively identified as an example of hypermorphosis.

THE recent debates about the relationships between development and evolution have led to a number of studies of heterochrony, differences in the timing of developmental processes. The fossil record can contribute a great deal of data to this debate when temporal sequences of ontogenies of closely related taxa are discovered. So far, most such studies have concerned microfossils and invertebrates because of the abundance of well-dated specimens.

In the present study, a juvenile (?near-hatchling size) fossil reptile, *Scaphonyx fischeri*, is described. Its anatomy is compared with older juveniles and adults of the same species and allometric relationships are established. The ontogeny of *S. fischeri* is then compared with earlier, presumably ancestral, taxa, and a heterochronic explanation is proposed for the major evolutionary changes in adult morphology.

THE RHYNCHOSAURS

Rhynchosaurs were an abundant and widespread group in the middle and early late Triassic (240–225 million years ago). Typical forms were 1–2 m in body length, with a heavy body and a massive skull. The front of the head was characterized by a 'beak' formed from the horn-covered premaxillae. There were large eyes, and the back of the skull was very wide in order to accommodate the jaw adductor muscles. The dentition consisted of a heavy maxillary tooth-plate (upper jaw) with numerous rows of teeth, and a V-shaped crest on the lower jaw which fitted perfectly into the V-groove.

The diet of rhynchosaurs has been variously interpreted as either molluscs or plants. The plant interpretation seems more likely (Benton 1983*a*, *b*, 1984) because the teeth are pointed and not at all 'crushers', the bite is precision-shear and not grinding, the body is massive (to accommodate a large gut?), and the rhynchosaurs are nearly always abundant in their faunas (generally about 50% of all animals collected).

Rhynchosaurs are known from all parts of the world, and their anatomy is remarkably uniform. Indeed, the late Triassic forms (*Scaphonyx* from Brazil and Argentina, *Hyperodapedon* from Britain and India, and other less well-known forms) are virtually indistinguishable except on minor points.

These late Triassic forms are distinguished from a middle Triassic group by their dental

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anatomy and other characters. The first rhynchosaurs were rather different small forms from the early Triassic of South Africa (Benton 1983*b*).

MATERIALS AND METHODS

Occurrence and specimens

Scaphonyx fischeri was named in 1907 by Woodward who had received some fragments of bone from the Triassic beds of the Santa Maria Formation of southern Brazil. He interpreted the fossils as those of phytosaurs or dicynodonts, although rhynchosaurs had been described from other parts of the world in the nineteenth century. In 1926, Huene assigned further fragmentary material which he had received to *Scaphonyx* and also erected the genera *Cephalonia*, *Cephalastron*, *Cephalastronius*, and *Scaphonychimus*, together forming six new species, all of which he believed belonged to a specialized archosaur group, which he called the Pelycosimia. By the time this study was published, Huene had received further specimens which showed that his 'pelycosimians' were all rhynchosaurs. Huene (1929) retained all of his new taxa of Brazilian rhynchosaurs, but collections of better material which he made on an expedition to Brazil in 1928–1929 suggested that there were in fact only two valid species, *Scaphonyx fischeri* and *Cephalonia lotziana* (Huene 1942). *Cephalonia* was apparently more lightly built than *Scaphonyx*. Later, Sill (1970) showed that the differences in the relative proportions of the bones in the two forms was diagenetic rather than genetic. Chemical changes during preservation of the bones had caused some ('*Scaphonyx*') to expand, which is shown by the 'exploded' appearance of the bone tissue in cross-section. *Cephalonia* is then identical to *Scaphonyx*, and only one genus of rhynchosaur is known so far from Brazil. A second Brazilian species, *S. sulcognathus*, which differs from *S. fischeri* in proportions and dental features, has been described (Azevedo and Schultz 1988). The present specimen is almost certainly *S. fischeri* since the new species is largely restricted to the Caturrita Formation which overlies the Santa Maria.

S. fischeri is the most abundant element in the Santa Maria fauna, representing nearly 70% of all individual specimens found. Well over 150 partial or complete skeletons are known (Benton 1983*a*). Other Santa Maria animals include the large herbivorous dicynodonts *Dinodontosaurus* and *Stahleckeria*, the small cynodonts *Traversodon*, *Chiniquodon*, and *Belesodon*, and the large meat-eating thecodontians *Prestosuchus* and *Rauisuchus*, as well as ten other less common genera.

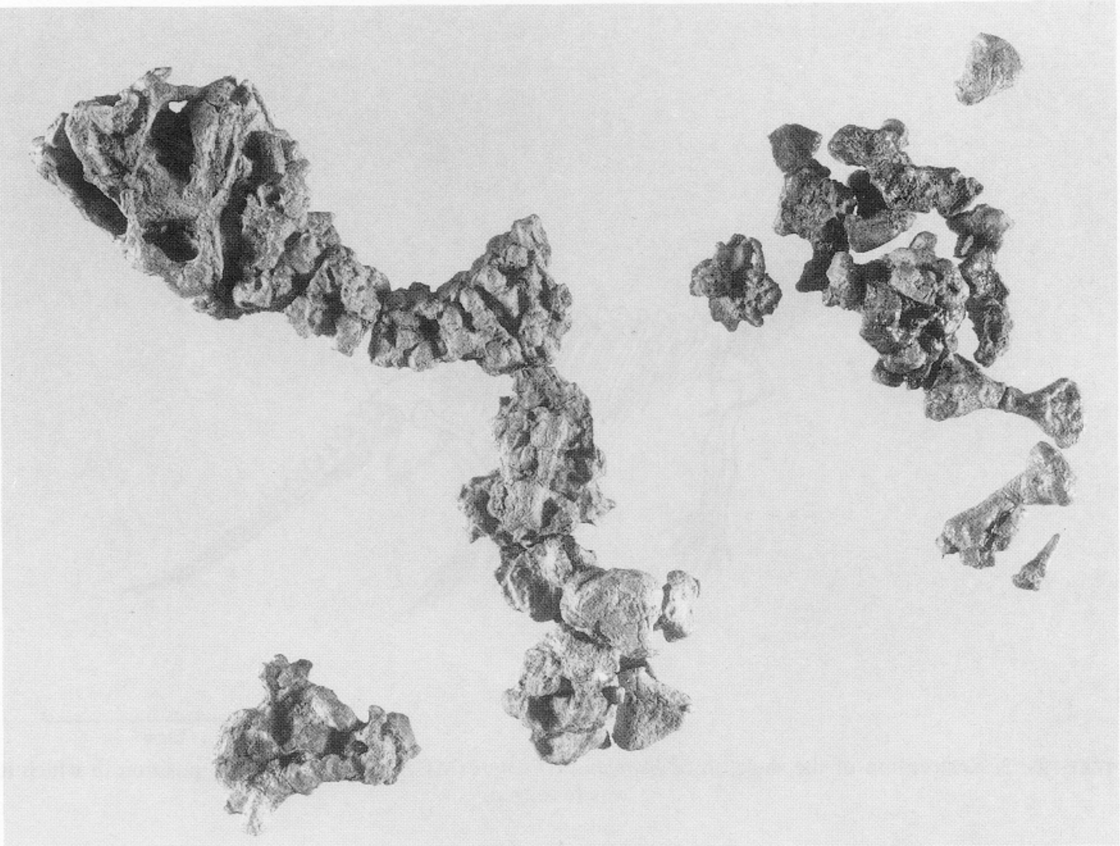
The *S. fischeri* remains have been found in upper portions of the Santa Maria Formation, in Part 'C' of the Upper Santa Maria Member (Bortoluzzi and Barberena 1967). The localities are mainly close together, about 3 km south-east of the town of Santa Maria in Rio Grande do Sul province in southern Brazil. Bortoluzzi and Barberena (1967, pp. 175–177) record the abundance of articulated rhynchosaur skeletons at several horizons over a 15 m thickness of sediments in Sanga Grande (their locality 4). More recently, *S. fischeri* has been found elsewhere in Brazil (C. Schultz, pers. comm., 1988). The upper part of the Santa Maria Formation is dated as Carnian, possibly middle Carnian (Bonaparte 1982; Olsen and Sues 1986).

In the present study, specimens of *S. fischeri* were examined in the following institutions: American Museum of Natural History (AMNH); Bayerische Staatssammlung fur Paläontologie und historische Geologie, München (BSP); Institut und Museum für Geologie und Paläontologie der Universität, Tübingen (GPIT); Museum of Comparative Zoology, Harvard (MCZ).

Juvenile and adult material of *S. fischeri* has already been described (Huene 1929, 1942; Sill 1970, 1971; Barberena 1971). The ontogenetic series of this species can now be extended back to a juvenile stage that was probably just post-hatching, by a hitherto unrecorded specimen, MCZ 1664. This specimen is briefly described and illustrated here before the allometric and heterochronic study.

MCZ 1664 (text-fig. 1) is a skull and partial skeleton. The skull is nearly complete, except for the premaxillae and most of the snout. As a result of crushing, the braincase has been extruded from the right posterior margin of the skull and the palate and occiput cannot be viewed. The skull has been preserved with the first three vertebrae of the vertebral column. Other postcranial remains include cervical vertebrae 4–8, three dorsals, one sacral, two caudals, most of the forelimbs and pectoral girdles, as well as fragments of the pelvic region and hindlimb. The three anterior cervical vertebrae have been twisted 90° clockwise and, when viewed from above, they are in left lateral view. This fact, and the pattern of preservation of the other bones of the skeleton suggests that the animal was fossilized lying on its right side, with its limbs extended (text-fig. 2).

The quality of preservation is poor, with the rock matrix encrusted on the bones in a nodular manner. This makes it impossible to comment on the surface features and textures of the bones. Such poor preservation may be due to the fossilization process. Sill (1970) demonstrated that the voluminous nature of the bones of



TEXT-FIG. 1. *Scaphonyx fischeri* (MCZ 1664), juvenile specimen in dorsal view. The skull is at the top left, with the cervical vertebral column behind. The left shoulder girdle and forelimb (and hand) runs down in the centre and left of the picture. The pelvic remains are shown at the top right, with parts of the left hindlimb below. Half natural size.

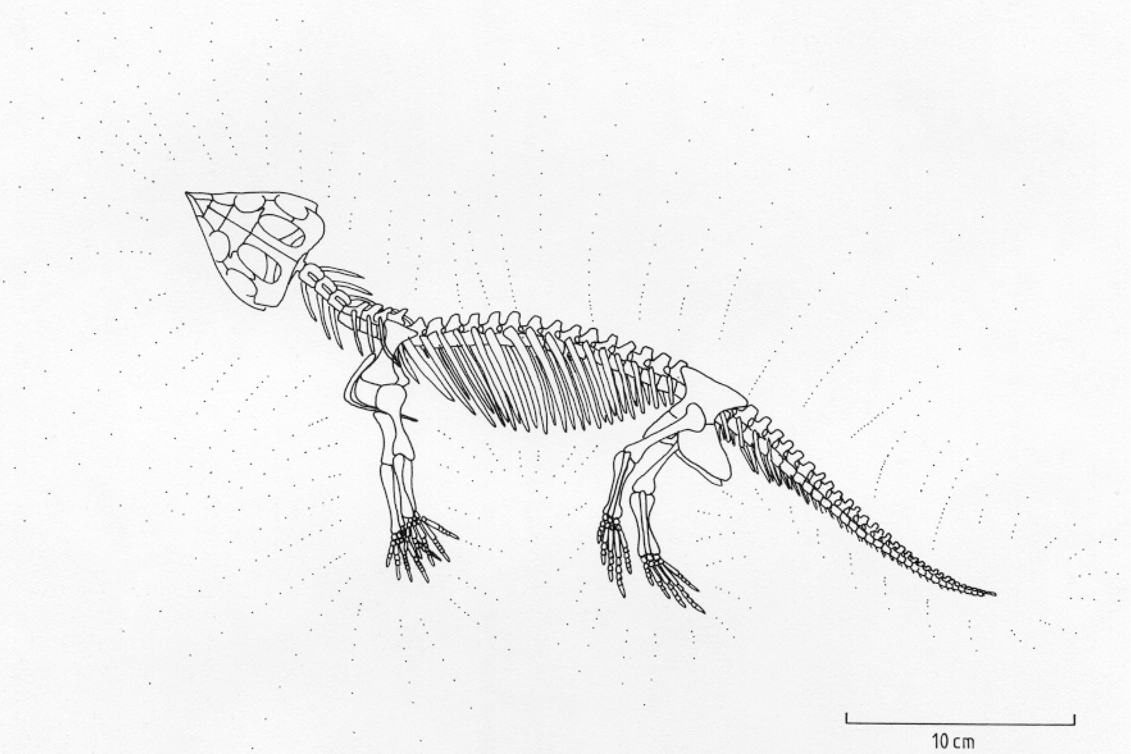
S. fischeri was due to the chemico-mineralogical reactions during fossilization. Petrographic analysis and radiographic diffraction showed that such reactions resulted in the entire replacement of the bone with calcium carbonate, the total destruction of the cellular structure and the expansion of the microstructure which subsequently refilled with microcrystalline mud.

Preparation of MCZ 1664

There were two stages in the preparation of the material—chemical and mechanical. The initial chemical preparation involved soaking of the specimen in 6% acetic acid, and subsequent neutralization in water. This method removed the fine film of surface rock particles, but in no way dislodged the large nodules of rock matrix. A small hand drill was used for the mechanical preparation. This was successful in removing prominent nodules of rock matrix, but much of the encrustation could not be removed because of its chemical and physical similarity to the preserved bone. The exposed bone surfaces were painted with butvar in propan-2-ol (isopropyl alcohol, *c.* 1 : 10) for protection.

Allometric study

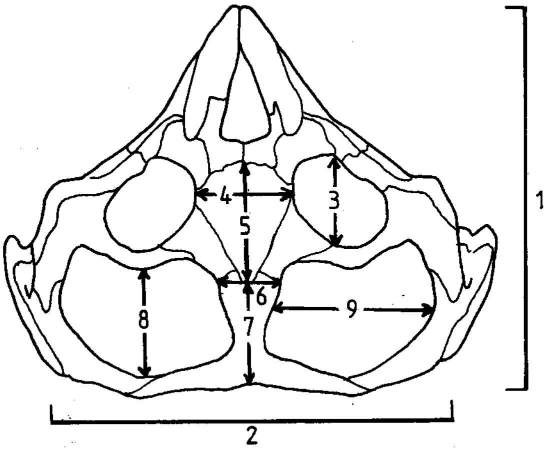
This study was limited to measurements of the skull. Thirteen skulls of *S. fischeri* were measured, ranging in length from 55 to 270 mm. Nine measurements were made on dorsal views of the skull (Table 1; text-fig. 3). Where possible, symmetrical variables were measured on both sides of the skull and averaged. It should be



TEXT-FIG. 2. Restoration of the skeleton of *Scaphonyx fischeri* (MCZ 1664) lying in the position in which it was fossilized.

TABLE 1. Measurement of skulls of *Scaphonyx fischeri* (in mm) used in the allometric study. BARB A–D are the four skulls figured by Barberena (1971). Characters 1–9 are: (1) total mid-line length of skull; (2) posterior width of skull between lateral margins of quadrates (in dorsal view); (3) maximum length of orbit; (4) greatest width of frontal; (5) mid-line length of frontal; (6) greatest width of parietal (excluding the posterial lateral processes); (7) mid-line length of parietal; (8) maximum length of upper temporal fenestra; (9) maximum width of upper temporal fenestra.

Specimen	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
MCZ 1664	55	60	14	15	15	16	19	18	14
BARB A	90	120	34	30	34	18	32	24	23
BSP 18/4	150	190	45	26	53	22	54	65	60
BSP 19/4	155	190	45	30	48	30	53	50	57
BARB B	164	170	40	40	44	40	58	46	50
GPIT	170	200	55	34	38	26	52	50	55
MCZ 3640	180	180	67	43	72	30	43	49	70
BARB C	200	230	66	60	60	40	58	52	68
BARB D	205	270	60	90	70	60	60	42	72
MCZ 1529	205	210	64	42	71	29	60	78	86
AMNH 7805	205	216	53	60	80	42	55	50	89
AMNH 7799	210	290	61	55	73	40	63	52	68
MCZ 1636	250	300	80	57	73	38	72	100	106



TEXT-FIG. 3. The measurements made on skulls of *Scaphonyx fischeri* for the allometric study. Measurements 1–9 are described, and values are listed in Table 1.

noted that some of the specimens measured have been distorted during fossilization (but none as badly as MCZ 1664), so that the measurements of skull length and width, and of skull openings (characters 1–3, 8, 9) may be subject to an error of ±5%.

The measurements were fitted in turn to the logarithmic expansion of the equation of simple allometry, $\log Y + \log b + a \log X$, where a is the allometric coefficient, b is a constant, X is a standard comparative measure (here, total skull length), and Y is the measurement of the part or organ under consideration. The value of the allometric coefficient, a, gives a measure of the rate of relative growth of the part, and in the logarithmic form, a is simply the slope of the straight line; a can be greater than 1 (positive allometry), equal to 1 (isometry), or less than 1 (negative allometry). When compared with phylogenetic changes, the values of a in an ontogenetic series can give information on the kind of heterochrony, if any, that is involved. The relative shape changes with growth were also examined by preparing transformed coordinate diagrams on five skulls of very different sizes.

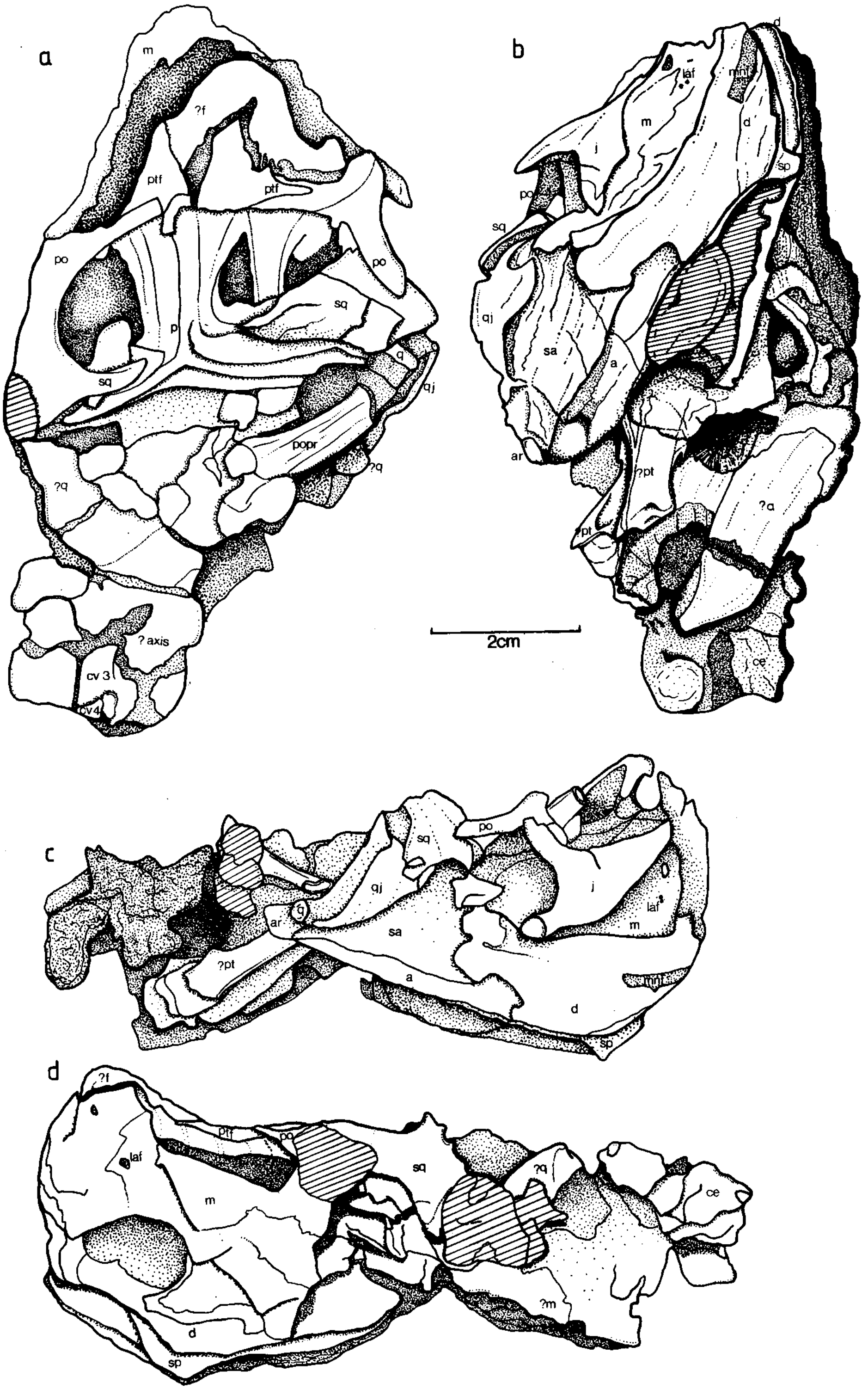
DESCRIPTION OF MCZ 1644

Class REPTILIA
Subclass DIAPSIDA
Order RHYNCHOSAURIA
Family RHYNCHOSAURIDAE Huxley, 1877
Scaphonyx fischeri Woodward, 1907

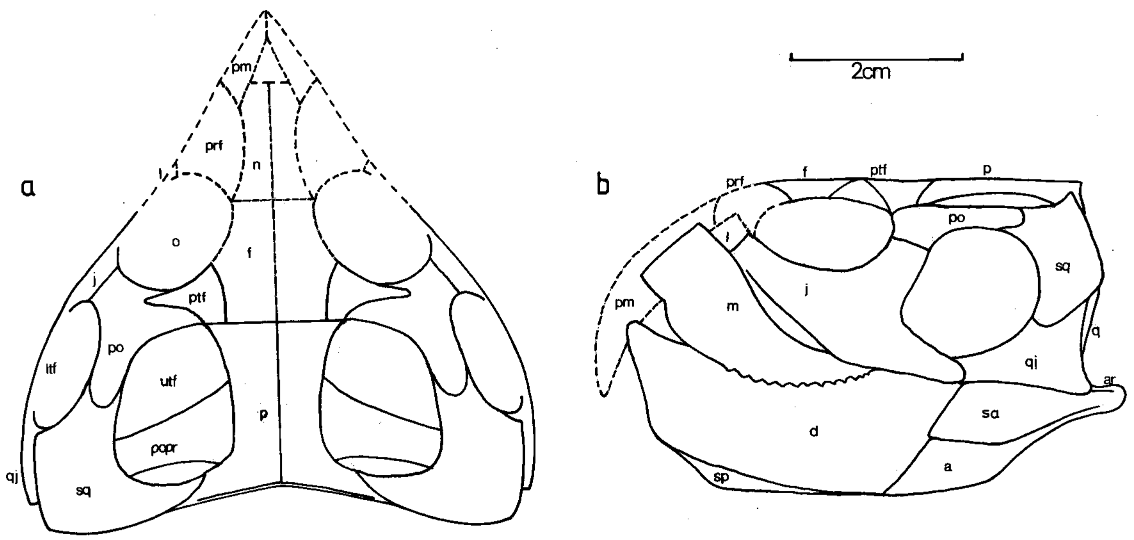
Skull

General appearance. The skull approximates to the shape of a triangle in dorsal view (text-figs. 4*a*, and 5*a*). The height of the skull is difficult to appreciate since it has been subjected to dorso-posterior crushing during fossilization, but a careful reconstruction (text-fig. 5*b*) indicates that it was relatively deep. An accurate determination of the length of the skull cannot be made as the premaxillae, nasals, prefrontals, and lacrimals are all absent, but the reconstruction (text-fig. 5*a*) suggests that the skull length is of the order of 55 mm and approximately equal to the maximum width. The palatal and occipital portions of the skull cannot be viewed clearly because of the distortion in preservation. Crushing has also resulted in the protrusion of the braincase at the right posterior margin of the skull (text-fig. 4*a*). The paroccipital process is clearly visible, which enables a confident estimation of the width of the skull. All preserved features of the skull confirm that this is a typical *Scaphonyx fischeri* specimen, but with juvenile features.

Dermal skull roof. The paired *premaxillae* are absent. They are restored as beak-like elements as in other rhynchosaurs (text-fig. 5). Both *maxillae* are preserved (text-figs. 4*a–d*, and 5*b*), and they bear small markings which could be blood vessel openings (lateral alveolar foramina; laf, text-fig. 4*c*, *d*). The *nasals* are absent in this specimen, and the exact limits of the *frontals* are also not clear (?f, text-fig. 4*a*) but their approximate position and size is illustrated in the skull reconstruction (text-fig. 5*a*), on the basis of other rhynchosaurs.



TEXT-FIG. 4. Skull of juvenile *Scaphonyx fischeri* (MCZ 1664) in dorsal (*a*), ventral (*b*), right lateral (*c*), and left lateral (*d*) views. Abbreviations are listed in the Appendix.



TEXT-FIG. 5. Restoration of the skull of the juvenile *Scaphonyx fischeri*, based on MCZ 1664, with restored areas shown by dashed lines.

The *parietals* are fused to form an inverted T-shaped element in the posterior third of the skull roof between the upper temporal fenestrae (text-figs. 4*a* and 5*a*). There is the typical crest in the mid-line and a dorsal ridge on the posterior crossbar. Longitudinal striations are visible on the surface of the parietals which may reflect the surface texture of the bone.

The *lacrimal* and *prefrontal* are not preserved in this specimen, but their approximate positions and sizes are indicated in the reconstruction (text-fig. 5*a*, *b*), on the basis of other rhynchosaurs. The *postfrontal* is a typical three-pronged bone in the posteromedial border of the orbit (text-figs. 4*a* and 5*a*, *b*). The exact limits of the left *postorbital* are obscured by a nodule of rock matrix (text-fig. 4*a*), but the right postorbital is clearly visible, although anteriorly displaced. The *jugal* is a deep four-pronged bone forming the middle part of the side of the skull (text-figs. 4*b*, *c* and 5*b*) as in adult *Scaphonyx*. Only the right jugal is preserved in this specimen and it lacks the posterior quadratojugal process.

Only a partial right *quadratojugal* is preserved, and it is posteriorly displaced (text-fig. 4*c*). It would have been an L-shaped bone that formed the posterolateral angle of the skull (text-fig. 5*b*). The *squamosal* is a large bone which forms much of the posterior margin of the skull (text-figs. 4*a*–*d* and 5*a*, *b*). Both squamosals are preserved, although they are displaced inwardly towards the parietal, thus reducing the apparent overall width of the skull in this region. The right postorbital has been displaced from its point of overlap on the squamosal and the groove on the squamosal in which the postorbital sits is clearly visible (text-fig. 4*c*).

Palate. The palatal surface of the skull is obscured by the mandibles. However, in the ventral view of the skull (text-fig. 4*b*), there are two overlapping long elements of bone protruding from the posterior margin of the skull, which could be the quadrate wings of the *pterygoids*.

Quadrate and epipterygoid. The *quadrate* is a strong columnar element of bone which lies vertically in a groove on the posterior side of the squamosal and quadratojugal (text-figs. 4*a*, *c*, *d* and 5*b*). The head of the right quadrate is visible, as well as the probable distal end. A displaced left quadrate is also indicated (?q, text-fig. 4*a*, *d*). The *epipterygoid* cannot be identified in this specimen.

Braincase. In the dorsal view of the skull (text-fig. 4*a*), elements of the braincase can be seen protruding from the right posterior margin of the skull. The only identifiable element is the *paroccipital process*, whose distal end is oval in cross-section. The shaft of the paroccipital process diverges as it approaches the braincase, but the midline elements of the braincase are not discernible.

Lower Jaw

Only the right lower jaw is well preserved in the specimen. It is a deep boat-shaped element, which curves to a pointed process at its anterior end. When the jaws were closed the premaxillae would have curved down between the pointed processes of the upwardly curving lower jaws like a pair of tongs (text-fig. 5*b*).

The *dentary* constitutes the anterior two-thirds of the mandible (text-figs. 4*c*, *d* and 5*b*). It is not possible to view the occlusal surface and the teeth of the dentary. In lateral view, near the anterior tip of the dentary, there are small indentations which could be blood vessel openings (mental foramina; mnf, text-fig. 4*c*). The *splenials* are visible in ventral (text-fig. 4*b*) and lateral (text-fig. 4*c*, *d*) views, but the *coronoid*, being a medial element, cannot be seen. The *angular* forms the base of the mandible in its posterior half, and the *surangular* the lateral margin (text-fig. 4*c*). Only the right surangular is preserved in this specimen, and it can be seen to contact the dentary in front. The *prearticular*, a medial element, cannot be viewed in this specimen, and only the right *articular* has been preserved (text-fig. 4*c*).

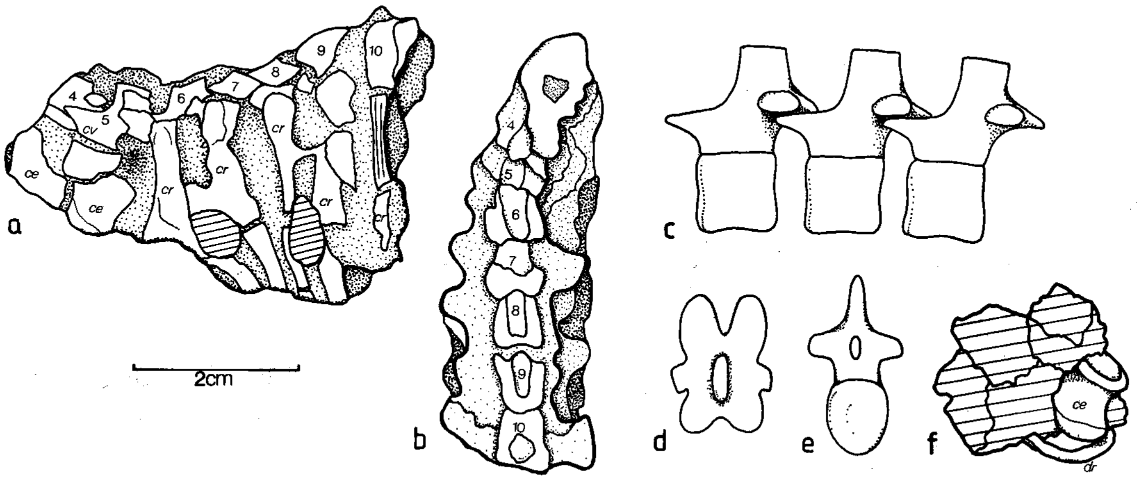
Axial skeleton

Vertebral column. Fourteen vertebrae can be identified; three cervicals in association with the skull (text-fig. 4*a*, *d*), a closely fitting block with a further seven cervical and dorsal vertebrae in association with the shoulder girdle (text-fig. 6), a sacral vertebra and rib in a block with the left femur and part of the ilium (text-fig. 9*a*), and two anterior caudals in association with the right pubis (text-fig. 9*e*, *f*). A possible mid to posterior dorsal is preserved in a separate block (text-fig. 6*f*).

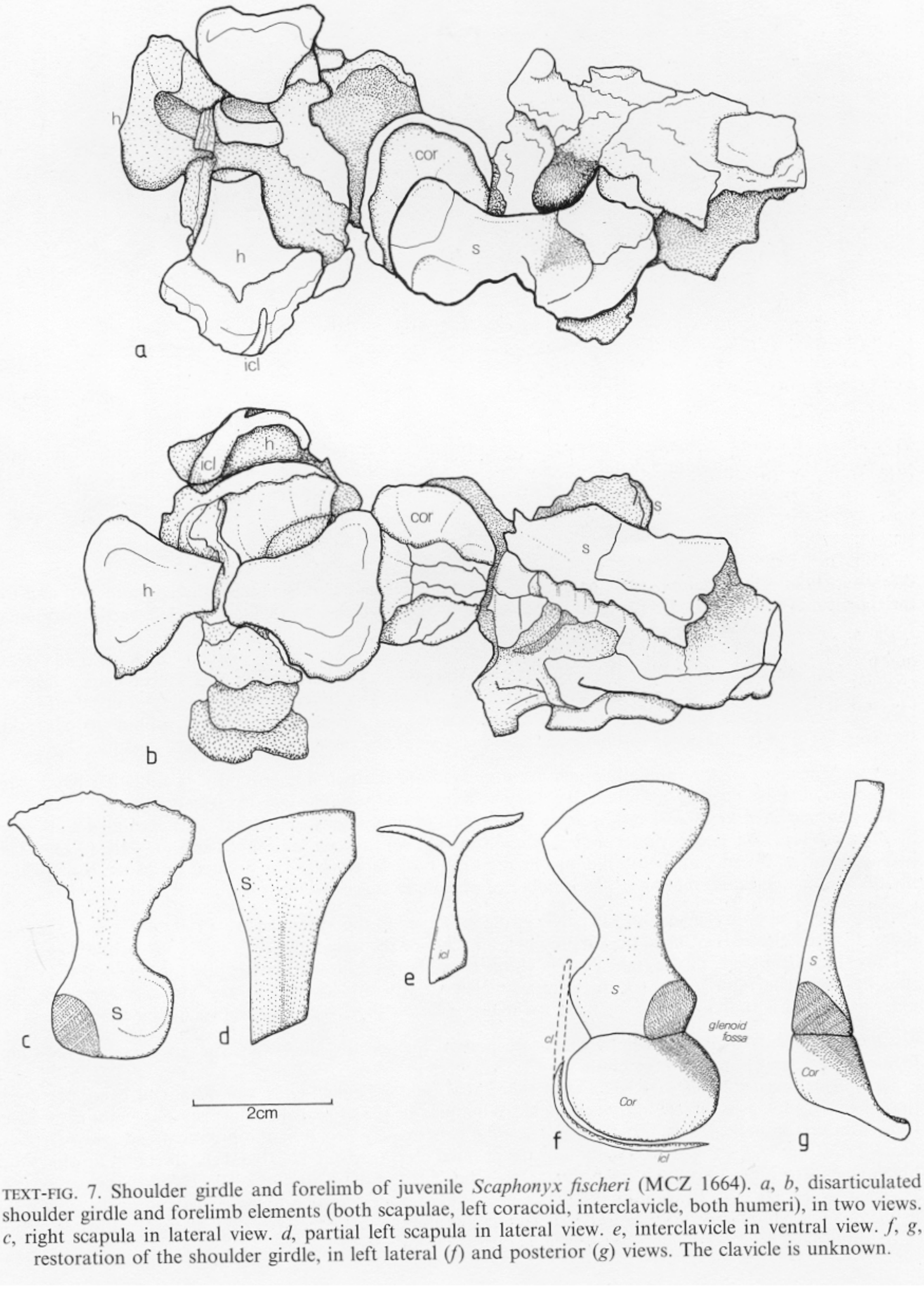
The most anterior preserved vertebra is probably the *axis*, seen only as an ill-defined outline (text-fig. 4*a*). This is followed by a poorly defined third *cervical* and a small part of the fourth. The seven anterior presacrals (text-fig. 6) presumably consist of cervicals 4–8 (on the assumption that *Scaphonyx* had eight cervical vertebrae, as in other rhynchosaurs) and dorsals 9–10. These eight vertebrae are apparently very similar. A possible posterior *dorsal vertebra* is represented by a centrum and a partial rib in an isolated small block (text-fig. 6*f*).

A single centrum and rib from the right side (text-fig. 9*a*) represent one of the two *sacral vertebrae*, and they are preserved in context on the medial face of the ilium. Two probable *caudal* centra are preserved with the right pubis (text-fig. 9*e*, *f*).

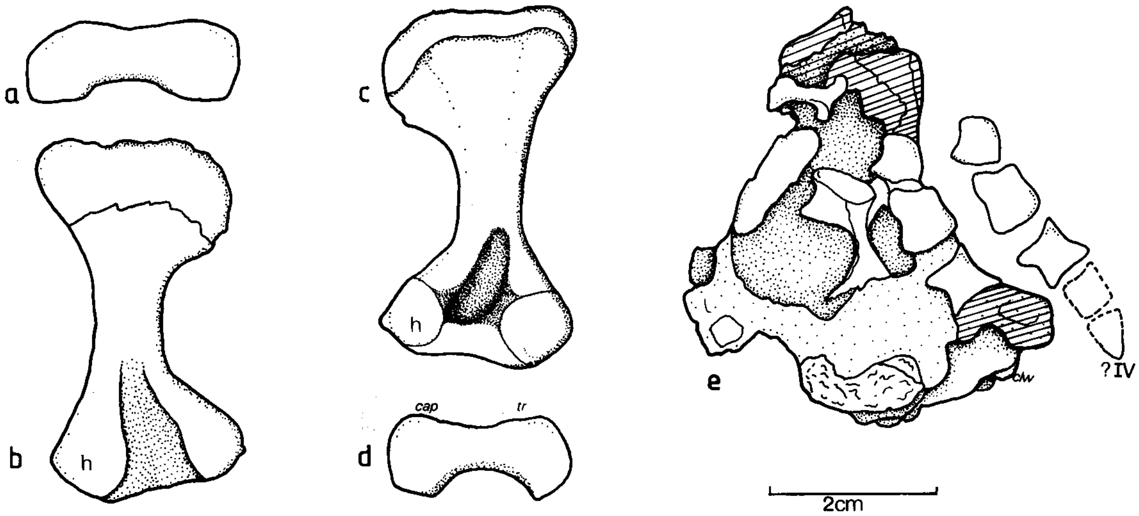
Ribs. The outlines of five cervical ribs can be traced on the block of seven vertebrae (cr, text-fig. 6*a*). A number of fragments of possible dorsal ribs are preserved in isolation, and a proximal end of a rib is associated with the posterior dorsal vertebra (text-fig. 6*f*). No *chevron* bones or *gastralia* are preserved in this specimen.



TEXT-FIG. 6. Vertebrae of juvenile *Scaphonyx fischeri* (MCZ 1664). *a*, *b*, cervical vertebrae 4–10, with associated cervical ribs, in left lateral (*a*) and dorsal (*b*) views. *c*, *d*, *e*, cervical vertebrae from the middle of the neck, restored in left lateral (*c*), dorsal (*d*), and anterior (*e*) views. *f*, Centrum of a dorsal vertebra and a dorsal rib in partial ventral view, embedded in matrix (diagonal shading).



TEXT-FIG. 7. Shoulder girdle and forelimb of juvenile *Scaphonyx fischeri* (MCZ 1664). *a*, *b*, disarticulated shoulder girdle and forelimb elements (both scapulae, left coracoid, interclavicle, both humeri), in two views. *c*, right scapula in lateral view. *d*, partial left scapula in lateral view. *e*, interclavicle in ventral view. *f*, *g*, restoration of the shoulder girdle, in left lateral (*f*) and posterior (*g*) views. The clavicle is unknown.



TEXT-FIG. 8. Forelimb elements of juvenile *Scaphonyx fischeri* (MCZ 1664). *a–d*, left humerus, in proximal (*a*), dorsal (*b*), ventral (*c*), and distal (*d*) views. *e*, left hand in dorsal view, with a reconstruction of digit IV on the right. Matrix is shown with diagonal shading.

Appendicular skeleton

Shoulder girdle. The shoulder girdle is represented by the left and right scapulae, the left coracoid, and the interclavicle. These elements have been preserved in a block which also includes the left and right humeri (text-fig. 7*a*, *b*). There is no trace of the clavicles.

The reconstruction of the left *scapula* (text-fig. 7*f*, *g*) has been based on the blade of the left scapula (text-fig. 7*d*) and the articular end of the right scapula (text-fig. 7*c*). The *coracoid* is a saucer-shaped element approximately half the height of the scapula (text-fig. 7*f*, *g*). The *interclavicle* is a three-pronged structure (text-fig. 7*b*, *e*) with a long dagger-like plate that extends horizontally between and behind the coracoids (text-fig. 7*f*). The lateral prongs would each have met one of the *clavicles*, but these are missing.

Forelimb. Elements of the forelimb which are preserved are the two humeri and a possible left hand. The radius and ulna are missing, although they may be represented by some isolated fragments.

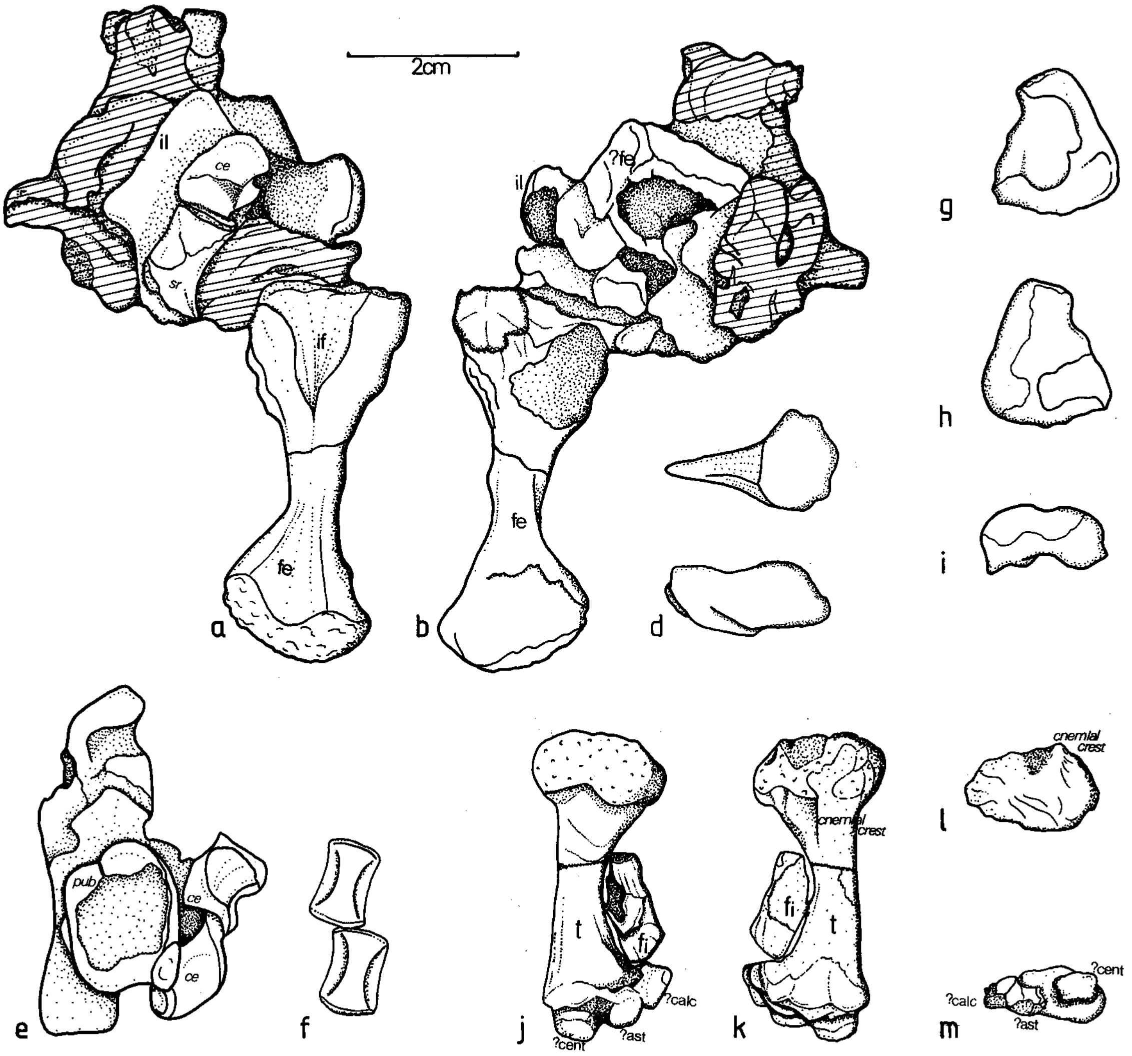
The *humerus* (text-figs. 7*a*, *b* and 8*a–d*) is a sturdy bone with a constricted shaft and expanded ends as in all rhynchosaurs. The poorly preserved left *manus* (text-fig. 8*e*) shows a fan-shaped spread of the fingers. The carpal region is absent and the outline of one digit only can be traced. The pointed tip of the claw of this digit is visible and an estimation of the number of phalanges suggests that it is digit IV.

Pelvic girdle. The only elements of the pelvic girdle preserved in this specimen are a right pubis and a partial ilium. Isolated elements of bone may represent fragments of the ischia and the other ilium or pubis.

Only the dorsal blade of the right *ilium* is visible. It is thin and bowed and slightly thickened at the edges (text-fig. 9*a*). The right *pubis* is a quadrangular element which is seen in ventral view (text-fig. 9*e*). The anterior margin is rounded and runs from the mid-line into a short uncinate process directed laterally.

Hindlimb. Elements of the hindlimbs which are present include the left femur, the distal end of the right femur, a tibia, and a fragment of fibula.

The *femur* (text-fig. 9*a–d*, *g–i*) has a constricted shaft and expanded ends, the distal end being narrower than the proximal, as is typical in rhynchosaurs. What may be the proximal end of the right femur embedded in rock matrix is indicated in text-fig. 9*b*. The *tibia* is extremely broad at the proximal end and narrower distally (text-fig. 9*j*, *k*). From the position of the cnemial crest (text-fig. 9*k*, *l*) and the direction in which the tibia arches, this is most probably a left tibia. Only a fragment of the shaft of the left *fibula* has been preserved attached to the left tibia (text-fig. 9*j*, *k*). Three elements of bone attached to the distal end of the tibia may be the three proximal *tarsals*, the centrale, the astragulus and the calcaneum (text-fig. 9*j*, *k*). No other elements of the foot have been preserved.



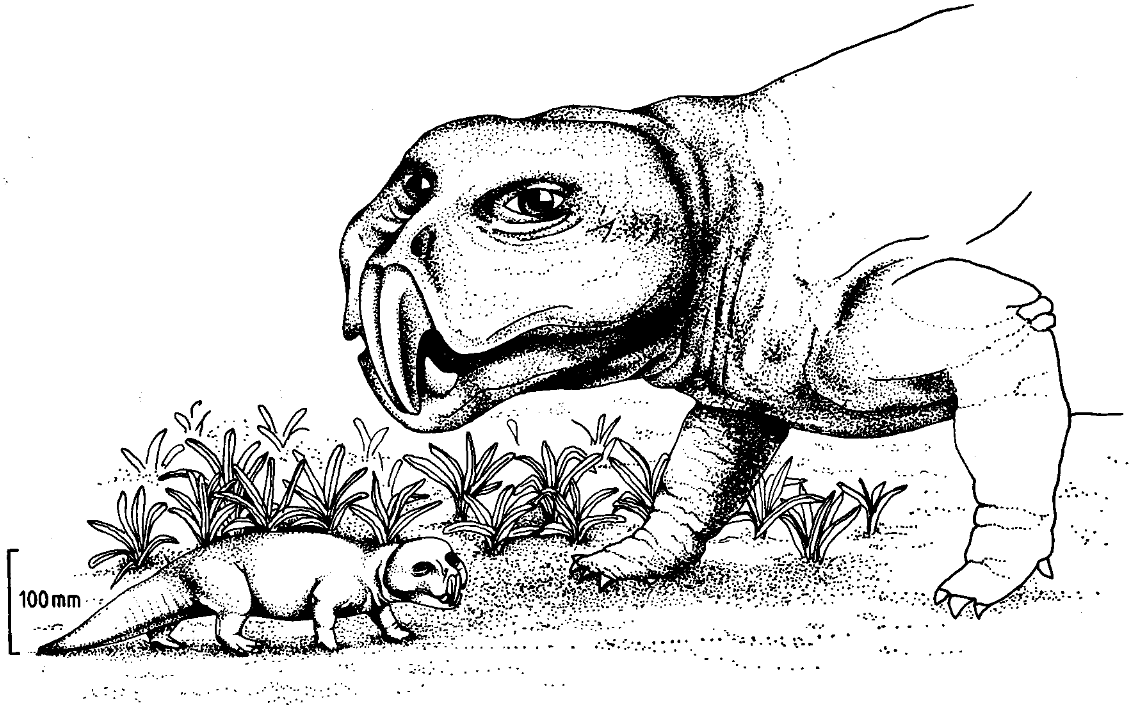
TEXT-FIG. 9. Pelvis and hindlimb elements of juvenile *Scaphonyx fischeri* (MCZ 1664). *a*, *b*, hindlimb and pelvic elements (ilium, sacral vertebra and rib, left femur), in ventral (*a*) and dorsal (*b*) views. *c*, *d*, left femur in proximal (*c*) and distal (*d*) views. *e*, *f*, pelvic region, showing the right pubis and two caudal vertebral centra in ventral (pubis) and lateral (vertebrae) views (*e*), and in ventral (vertebrae) view (*f*). *g–i*, distal end of the fragmentary right femur, in ventral (*g*), dorsal (*h*), and distal (*i*) views. *j–m*, left tibia and fragmentary fibula, in anterior (*j*), posterior (*k*), proximal (*l*), and distal (*m*) views. Some probable tarsal elements are indicated adhering to the distal end of the tibia.

RECONSTRUCTION AND AGE

The reconstruction of the side view of the juvenile *Scaphonyx* (text-fig. 10) is based on the available parts of the specimen, with other portions (dorsal vertebral column and ribs, tail, foot) modified from adult *Scaphonyx* (Huene 1929, 1942; Barberena 1971). Total body length is about 380 mm (skull length, 55 mm; presacral length, *c*. 180 mm; sacral length, *c*. 10 mm; tail length, *c*. 135 mm). The posture and relationships of the limbs and girdles to the axial skeleton are based on other more fully preserved (adult) rhynchosaurs (Chatterjee 1974; Benton 1983*b*).

Adult *S. fischeri* have skull lengths typically of 170–220 mm, and total body lengths of 1·3–2·0 m (Huene 1942, p. 294). Huene (1942, pp. 294, 295, 313) quoted skull lengths ranging up to 400 or 500 mm (body lengths ?2·5–3 m), but these large estimates were based on fragmentary material, and it is unlikely that such huge sizes were attained. The present specimen of *S. fischeri* is clearly very young. Is it a hatchling or a juvenile of a year or two old?

Eggs of *Scaphonyx* have not been reported, but the maximum diameter of a typical egg can be estimated from the internal width of the pelvis which would have accommodated the birth canal. This maximum figure ranges from about 60 mm in a 1·3 m long individual to an estimated 70 mm in a 1·6 m long specimen. These figures represent either the maximum distance between the medial faces of the ilia, or the maximum distance between the ventral face of the sacral vertebrae and the dorsal face of the ischia, whichever is the smaller.



TEXT-FIG. 10. Restoration of the juvenile *Scaphonyx fischeri* based on MCZ 1664 (*left*), with an adult specimen (*right*), drawn to the same scale.

The largest eggs that typical *Scaphonyx* adults could lay would have been smaller than 60–70 mm in diameter, which corresponds to lengths of 60–140 mm, depending upon whether the egg was spherical or ovoid, both of which are known in different reptile groups. A full-term embryo may be as much as twice the length of its egg, assuming that it is curled up, with the head tucked down on the chest, and the tail wrapped up in front and meeting the head. Hatchling *Scaphonyx* could then have ranged in length from 120–280 mm in total body length. The present specimen, at 400 mm, could then have been as much as 6 months to a year old.

Another approach to the calculation of hatchling size in reptiles is to use the formula derived by Currie and Carroll (1984, p. 76) from a study of 120 species of living lizards and crocodilians. They found that the ratio of adult to hatchling length was described by the formula:

$$2{\cdot}7+3{\cdot}3\times(\text{adult length in m})^{-1}$$

(misprinted as 'adult length in mm' in their paper). The adult length of S. fischeri is typically 1.3–2.0 m (see above), which gives ratios of 4·3 to 5·2 (i.e. hatchlings are 19–23% of adult body length). On the assumption then that *Scaphonyx* had the general physiology and growth rates of modern reptiles, its hatchling size is predicted as 247–460 mm, depending on which of the 'adult' body sizes is correct. The present specimen falls in the upper half of that range, which might suggest that it is either a hatchling or aged up to 6 months, on the assumption that rhynchosaurs doubled their body length in the first year of life as do most modern reptiles (Currie and Carroll 1984).

JUVENILE CHARACTERS

The present specimen, although rather incomplete, shows a number of juvenile characters. For example, the skull seems to be relatively large in relation to the rest of the body, but not by a great amount. The ratio cannot be calculated with respect to total body length, since that measurement is not known independently, but the ratio of skull length : estimated trunk length is 29%, compared to 20–26% in adults (Huene 1942, p. 294). The ratio of skull length : humerus length in the present specimen (1·28) is within the range of values for adult late Triassic rhynchosaurs (1·25–1·73 for *Scaphonyx;* 1·24–1·38 for *Hyperodapedon*). The articular ends of the long bones are relatively heavy (the same phenomenon that gives rise to the outsize knees and paws of puppies) in comparison to undistorted adult specimens of *Scaphonyx*.

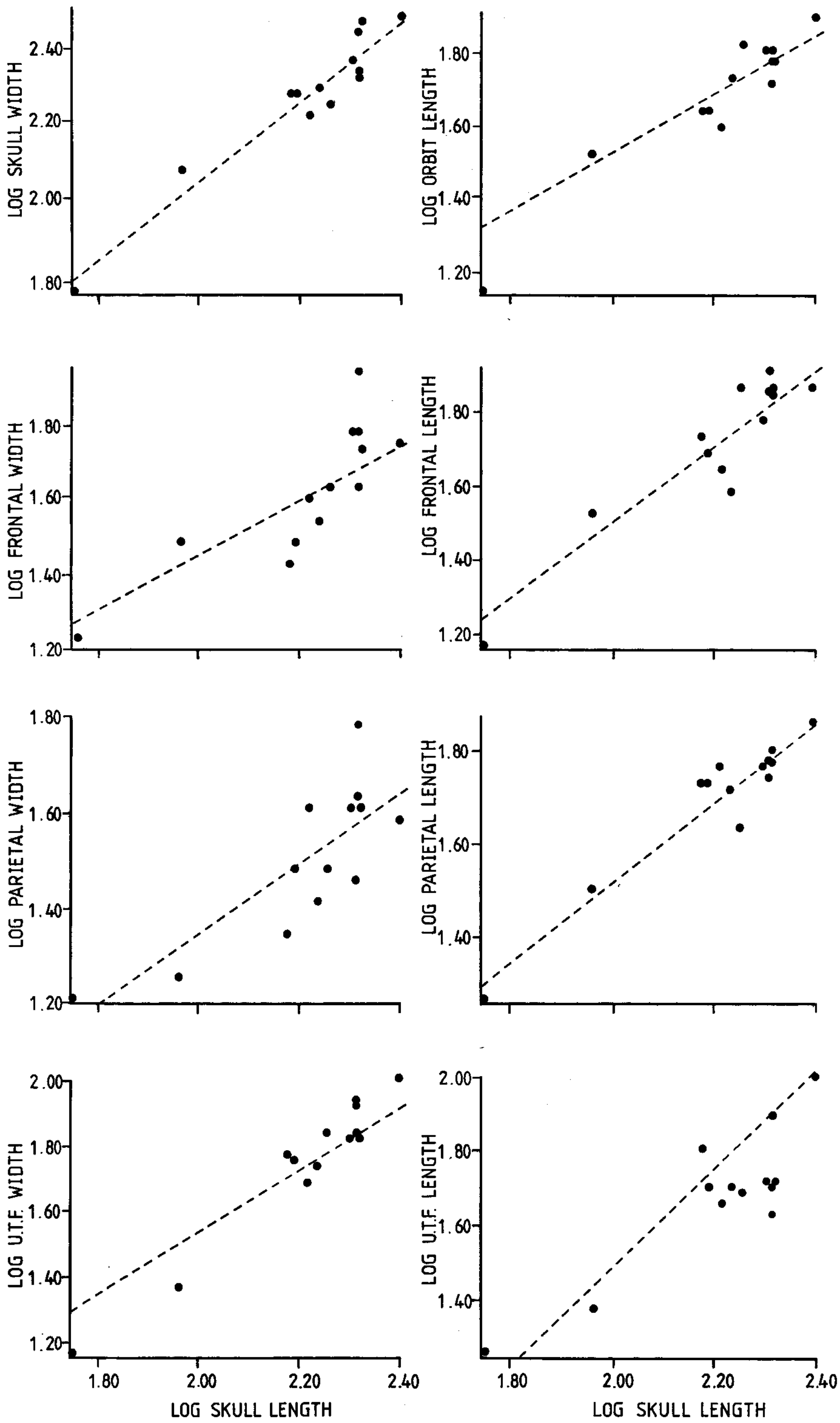
The apparently rather loose association of the skull elements also suggests youth. In adult *Scaphonyx* the cranial sutures rarely separate, but most of the skull elements in the present specimen have shifted apart. Evidently, juvenile rhynchosaurs had rather weakly sutured cranial bones. It is not possible to comment in detail on the osteological state of the articular ends of the limb bones because of their slight diagenetic alteration. The roughness of the articular facets suggests, however, that growth was not complete, and that cartilaginous epiphyses would still have been in place. Of course, since rhynchosaurs are archosauromorphs (see Benton 1983*b*), rather than lepidosaurs as once thought, one would not expect to find bony epiphyses.

ALLOMETRIC STUDIES

Regression analysis. The regression analysis indicated that ontogenetic growth of the skull of *Scaphonyx* was isometric for most characters (slope close to 1·00; Table 2; text-fig. 11). However, the correlation coefficients (*r*) are low in most cases, being greater than 0·95 only for skull width, orbit length, parietal length, and upper temporal fenestra width (characters 2, 3, 7, 9), and between

TABLE 2. Regressions of log skull length against eight other variables in thirteen skulls of *Scaphonyx fischeri*. Values for the slope of the regression lines, the standard deviation, and correlation coefficient are given. One asterisk (*) indicates $r > 0{\cdot}90$, while two (**) indicates $r > 0{\cdot}95$. Utf = upper temporal fenestra.

Variable	Slope	Standard deviation	Log *y* intercept	*r*
(2) Skull width	1·00	0·16	0·073	0·966**
(3) Orbit length	1·04	0·18	−0·603	0·954**
(4) Frontal width	0·95	0·16	−0·481	0·838
(5) Frontal length	1·06	0·19	−0·628	0·933*
(6) Parietal width	0·74	0·13	−0·132	0·810
(7) Parietal length	0·82	0·14	−0·119	0·958**
(8) Utf length	0·95	0·17	−0·411	0·874
(9) Utf width	1·34	0·24	−1·202	0·979**



TEXT-FIG. 11. Regression lines of the eight skull measurements (see Table 1) plotted against skull length, all transformed to logarithms (base 10). Details of the regressions are given in Table 2.

0·90 and 0·95 for frontal length (character 5). Thus, linear regressions may not be the best representations of the points for characters 4, 6, and 8 (frontal width, parietal width, upper temporal fenestra length). The relatively small sample size (n = 13), however, makes it difficult to assess the significance of the allometric equations.

The slopes of the regression lines range from 0·74±0·13 (parietal width) to 1·34±0·24 (upper temporal fenestra width). Of the characters that yielded statistically significant slopes ($r > 0{\cdot}90$), three can be interpreted as isometric (slope = 1·00): skull width, orbit length, frontal length; one as showing negative allometry (slope < 1·00): parietal length; and one as showing positive allometry (slope > 1·00): upper temporal fenestra width. The three characters with non-significant slopes (frontal width, parietal width, upper temporal fenestra length) all show negative allometry.

Transformed coordinates study. The addition of the juvenile specimen described here to the specimens analysed by Barberena (1971) confirms the conclusions from the allometric equations (text-fig. 12). The posterior part of the skull roof expands laterally when compared with the anterior part. The frontal width also appears to increase rapidly in this sequence of skulls, although that is not confirmed from the larger sample of specimens. In early stages of ontogeny the snout region of the skull appears to lengthen markedly, while the temporal region (parietal length) diminishes with respect to overall skull length.

DISCUSSION

The regression analysis indicated that, during ontogeny, the skull of *Scaphonyx* showed constant growth in five of the eight measured variables (linear regression lines). Positive allometric growth occurred in the width of the upper temporal fenestrae, but not in the overall posterior skull width, according to the present study. This was a surprise, since one would expect both variables to be broadly linked. However, the maximum skull width character was measured between the lateral edges of the quadrate condyles which project laterally some way beyond the skull roof proper. It can be said then that growth in overall skull width is essentially isometric, but the dorsal skull roof broadens relatively faster than the increase in mid-line skull length. Further, the quality of preservation of the specimens varies. C. Schultz (pers. comm.) notes that Barberena's skull D (and his A and B to a lesser extent) are 'exploded' diagenetically which affects these width measurements.

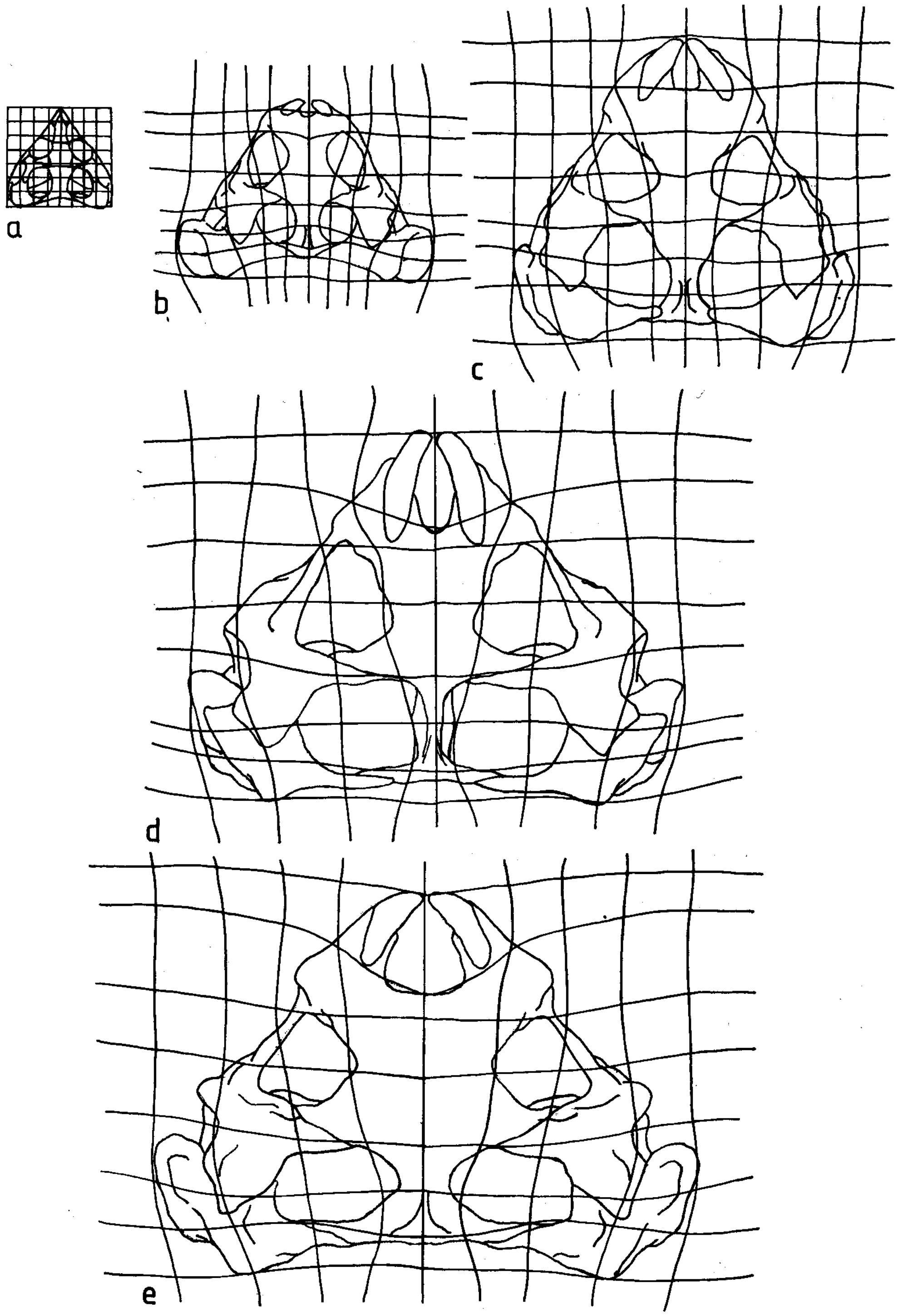
Negative allometric growth occurred in the parietal length (also in upper temporal fenestra length, but slope not significant) which indicates that the posterior region of the skull became shorter relative to the anterior region during growth. The non-significant allometric growth of the width of the frontal and the width of the parietal indicates that these measurements increased relatively more slowly than the skull length. However, both characters are possibly sexually dimorphic in rhynchosaurs (Benton 1983*b*, pp. 612–613) which may have affected the regression analysis.

The isometric growth of orbit length and frontal length suggests that the anterior part of the skull grows at the same relative rate as the overall mid-line skull length, while overall maximum skull width also keeps pace with the skull length. These general results were borne out by the transformed grid study.

In evolutionary terms the ontogeny of *Scaphonyx* appears to show heterochronic change when it is compared with ontogenies of potential ancestors. Regrettably, ontogenetic studies spanning a broad range of sizes of animals, have not been possible for other rhynchosaur taxa owing to the rarity of reasonably complete undistorted skulls. However, some comparisons may be made.

The Late Triassic rhynchosaurs, such as *Scaphonyx*, form a well-defined clade within Rhynchosauria, which is characterized by the following cranial synapomorphies when compared with Early Triassic taxa such as *Mesosuchus*, and Middle Triassic taxa, such as *Rhynchosaurus* and *Stenaulorhynchus* (Benton 1983*b*, 1984, 1987):

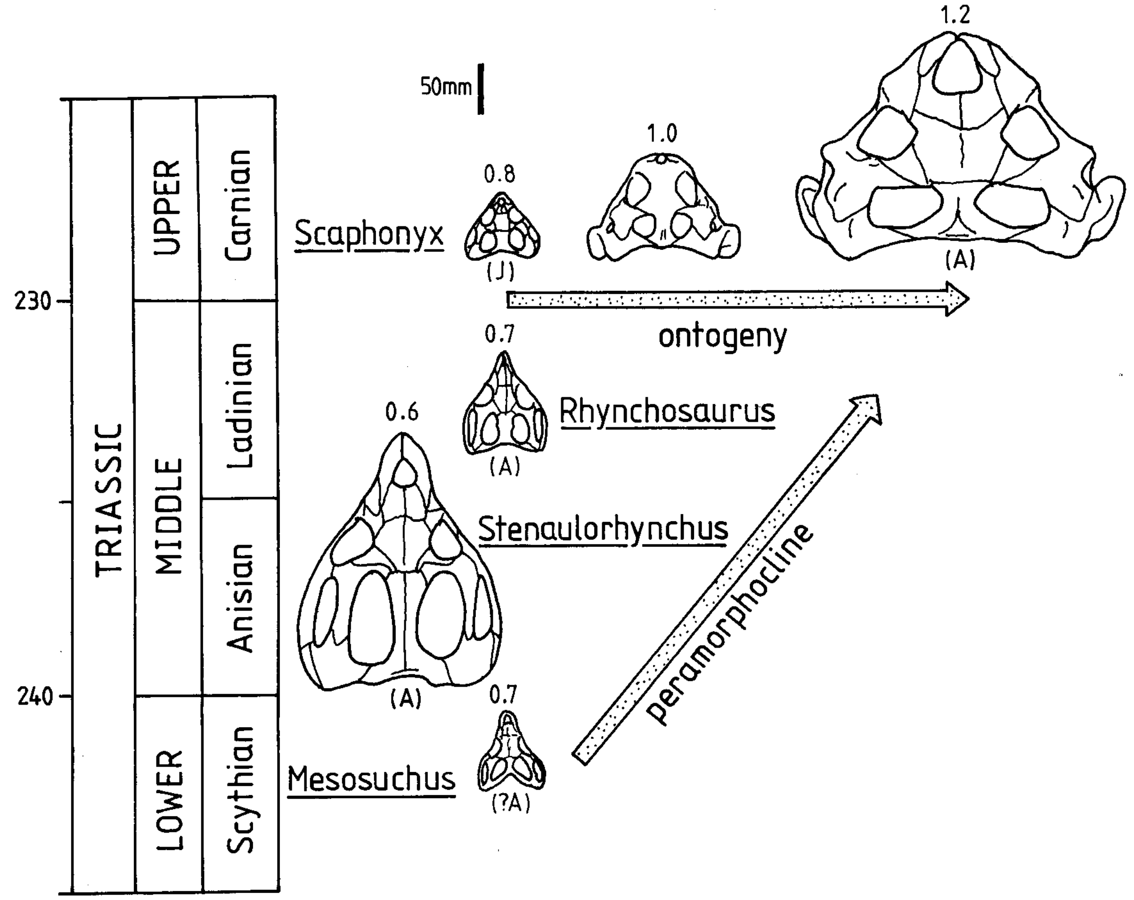
1. Skull is broader than long;
2. Squamosal has broad strap-like ventral process;



TEXT-FIG. 12. An ontogenetic series of five skulls of *Scaphonyx fischeri* from Santa Maria, Brazil. Skull *a* is MCZ 1664 (based on text-fig. 5*a*). Skulls *b*–*e* are traced from skulls figured by Barberena (1971). Modifications in relative shape are shown by transformed coordinates (assumed to be quadratic in skull *a*).

3. Loss of supratemporal;
4. Lower jaw is very deep;
5. Single groove on maxilla;
6. No teeth on lingual side of maxilla;
7. Occipital condyle in line with quadrates.

Three of these characters (1, 2, 4) are major proportional changes that could be heterochronic in nature. The positive allometric growth of the width of the dorsal skull roof, reflected in the width of the upper temporal fenestrae, may represent peramorphosis. The negative allometric growth of parietal length reflects the fact that *Scaphonyx fischeri* has a remarkably short temporal region of the skull when compared to all other rhynchosaurs (length of upper temporal fenestra is one-quarter to one-third of the total mid-line skull length, compared to values of one-third or more). This is not a synapomorphy of the Late Triassic rhynchosaur clade, but it could be an autapomorphy of *S. fischeri*, and it appears to be peramorphic (text-fig. 13).



TEXT-FIG. 13. The postulated peramorphocline (extended ontogeny) seen in the evolution of the rhynchosaur skull. Adult skulls of three Early and Middle Triassic rhynchosaurs are shown (based on Benton 1983*b*, in prep.), and an ontogenetic series of three of the skulls of *Scaphonyx fischeri* (from text-fig. 12). The skulls are positioned vertically according to their occurrence in time (stratigraphic column on the left), and horizontally according to the ratio of posterior skull roof width : mid-line skull roof length (mean values shown at the tip of the snout of each skull). The posterior skull roof width is measured between the lateral edges of the intertemporal bars in dorsal view. Abbreviations: A, adult; J, juvenile.

The particular peramorphic process(es) involved are hard to determine, since the ontogenetic pattern of ancestral rhynchosaurs has not been described, and the timing of the onset of ontogeny is unknown. However, since *Scaphonyx*, and the Late Triassic rhynchosaurs in general, are larger as adults than the more primitive forms, it is likely that this is a case of hypermorphosis ('juvenile development same as ancestor, onset of sexual maturity delayed; adult larger than ancestral adult': McNamara 1986, p. 11).

The three best-known rhynchosaur taxa that predate *Scaphonyx* are *Mesosuchus browni* from the Early Triassic *Cynognathus* Zone of South Africa, *Stenaulorhynchus stockleyi* from the Manda Formation (Middle Triassic, Anisian?) of Tanzania, and *Rhynchosaurus articeps* from the Tarporley Siltstone Formation of England (Middle Triassic, Ladinian?). Very few specimens are known of these taxa, and the majority are assumed to be adults. The most abundantly represented is *R. articeps*, with up to seventeen individual animals, but only five skulls. These range in mid-line length from 60 mm (estimated) to 82 mm (Benton, in prep.), so cannot offer a great deal of ontogenetic information. Nevertheless, the ratio of dorsal skull roof width : mid-line skull length increases from 0·56 to 0·67 from the smallest to the largest specimen, very tentative evidence that this feature shows positive allometric growth in *Rhynchosaurus* as well as in *Scaphonyx*.

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APPENDIX

Key to abbreviations used in the figures

SKULL

a	angular	pm	premaxilla
ar	articular	po	postorbital
d	dentary	popr	paroccipital process
f	frontal	prf	prefrontal
j	jugal	pt	pterygoid
l	lacrimal	ptf	postfrontal
laf	lateral alveolar foramen	q	quadrate
ltf	lower temporal fossa	qj	quadratojugal
m	maxilla	sa	surangular
mnf	mental foramen	sp	splenial
n	nasal	sq	squamosal
o	orbit	utf	upper temporal fossa
p	parietal		

POSTCRANIAL SKELETON

ast	astragalus	fe	femur
calc	calcaneum	fi	fibula
cap	capitellum	h	humerus
ce	centrum	icl	interclavicle
cent	centrale	if	intertrochanteric fossa
cl	clavicle	il	ilium
clw	claw	pub	pubis
cor	coracoid	s	scapula
cr	cervical rib	sr	sacral rib
cv	cervical vertebra	t	tibia
dr	dorsal rib	tr	trochlea