A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa

A. D. WALKER†

Department of Geology, Bedson Building, University of Newcastle upon Tyne, NE1 7RU, U.K.

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SUMMARY

A detailed description is given of the osteology of the holotype of *Sphenosuchus*. The skull, particularly the braincase, is excellently preserved and shows a wealth of anatomical detail. *Sphenosuchus* was one of the largest of the early crocodylomorphs, with a skull length of 192 mm and an estimated total length of 1.4 m.

The primary head of the quadrate meets the prootic and squamosal but not the opisthotic (or laterosphenoid); quadrate and pterygoid are not fused to the braincase and the basipterygoid articulation is free. The braincase and some other skull bones are pneumatized. The otic capsule is crocodilian but the subcapsular buttress (ossified subcapsular process) does not enclose the vagus nerve or the internal carotid artery.

The scapula blade is triangular; the coracoid has a long posteroventral extension which is thought to have articulated firmly with a large interclavicle. Clavicles were absent. Metatarsal I is reduced; metatarsals II and IV are symmetrical about III, which is longest. A paired series of dorsal scutes was present.

Sphenosuchus is considered to have been cursorial and carnivorous.

Comparison is made between the pneumatic spaces in the *Sphenosuchus* skull and those of modern crocodiles and birds, and homologies are discussed. Representatives of the main cavities found in the crocodilian skull are present in the skull of *Sphenosuchus*, in some cases in a less clearly defined state. On the other hand, certain pneumatic spaces in the *Sphenosuchus* skull are not found in the modern crocodile but resemble cavities in the bird skull.

The courses of the internal carotid and stapedial arteries are reconstructed; the latter is considered to have passed through the postquadrate foramen, temporal canal and anterior temporal foramen as it does in modern forms. The problem of the position of the stapedial artery in the crocodile is discussed. It is believed that enclosure of the artery took place as a result of the forward migration of the quadrate head, leading to the formation of a temporal canal.

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† Permanent address: 17 Kingsley Avenue, Melton Park, Newcastle upon Tyne NE3 5QN, U.K.

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Detailed comparisons are made between the otic capsule of *Sphenosuchus* and those of modern crocodiles and birds, which it closely resembles. Changes in otic capsule structure in archosaurs to give the crocodilian or bird condition, starting from a primitive form like *Euparkeria*, are outlined.

The skull is believed to have been kinetic, and the quadrate streptostylic, in the juvenile *Sphenosuchus*.

The parts of the proximal end of the crocodilian quadrate are differentiated; in particular, the 'true' head is distinguished from the anterodorsal process. Although very reduced in the modern crocodile, the 'true' head is in the same morphological position as in *Sphenosuchus*; contact with the laterosphenoid has been brought about, not by further forward movement of the head, but by geniculation of the upper portion of the bone. The anterodorsal process is considered to have arisen as a result of the dorsal migration of an anterolateral projection somewhat similar to that of the thecodontian *Stagonolepis*. This change was also responsible for the elongation of the quadratojugal in crocodylomorphs.

The validity of the order Crocodylomorpha is discussed. It is concluded that the most important steps in crocodylomorph evolution, particularly in the skull, had taken place in sphenosuchians, hence they should be included in the same taxon as protosuchians and more advanced crocodilians, rather than with thecodontians.

1. INTRODUCTION

The holotype of *Sphenosuchus acutus* was first described by Haughton in 1915. The specimen comes from the uppermost part of the Elliot Formation (Kitching & Raath 1984) of South Africa of late Triassic or early Jurassic age. Haughton gave a brief description of the skull and what was preserved of the postcranial skeleton. He mentions both clavicles, a probable radius and ulna, and three metacarpals. The specimen was simply described as a thecodont. In 1924 Haughton gave a somewhat longer description, in which the identification of the clavicles was changed to coracoids. He considered that *Sphenosuchus* was unarmoured, although some scutes are in fact present. The resemblance of the coracoids to those of modern crocodiles, the slightly younger *Notochampsa*, and birds, is noted. On the other hand Haughton thought that the humerus and tibia of *Sphenosuchus* were more like those of 'the Saurischia and *Massospondylus*' (a prosauropod dinosaur). He considered it sufficiently unusual to merit the foundation of a new family for it, the Sphenosuchidae. (In this, however, he had been forestalled by von Huene (1922).) A later remark in the same paper (p. 365) shows that he regarded the animal as 'undoubtedly a Pseudosuchian'.

Von Huene refigured the material in 1925, including the 'radius' and 'ulna' (which in fact are metatarsals). His *Sphenosuchus*-Group' comprises *Sphenosuchus* and *Erythrochampsa* from the upper Elliot Formation, and *Notochampsa* and *Pedeticosaurus* from the overlying Clarens Formation, of South Africa. He considered that typical crocodiles have developed via the '*Sphenosuchus*-Group' from the Pseudosuchia, and stressed the terrestrial origin of the Crocodylia. He preferred, however, to let the '*Sphenosuchus*-Group' remain as 'very plastic Pseudosuchia'.

In 1927 Broom described the skull again, with new restorations; he also gave a restoration of the shoulder girdle. He noted many features that he considered that one would expect to find in an ancestral crocodile, and concluded that '*Sphenosuchus* is a Pseudosuchian which is well advanced along the line which leads to the true Crocodiles'.

For many years *Sphenosuchus* was usually classed as the sole representative of its family in the suborder Pseudosuchia of the order Thecodontia (Zittel 1932; Romer 1945, 1956), with a rider to the effect that it represented a stage transitional to crocodiles. In 1966, however, Romer placed the family, with doubt, in the suborder Protosuchia of the order Crocodilia.

In 1970 I made some preliminary observations on *Sphenosuchus* and attempted to show that it, and certain other forms previously classified as thecodontians, were more closely related to crocodiles than had hitherto been thought. These forms included *Pedeticosaurus* (van Hoepen 1915) from the Clarens Formation of South Africa, *Saltoposuchus* (von Huene 1921) from the Stubensandstein of Germany, and *Hesperosuchus* (Colbert 1952) from the Chinle Formation of Arizona. The concept of an order Crocodylomorpha of wider compass than the traditional order Crocodylia was put forward (Walker 1968, 1970) to accommodate these rather poorly known late Triassic or early Jurassic forms, which seemed difficult to regard as crocodiles in the generally accepted sense of that term.

At that time the braincase of *Sphenosuchus* had not been fully prepared, so that critical points such as the nature of the upper quadrate articulation and the structure of the otic capsule remained unknown and were not included in the diagnosis of the order. The upper portion of the quadratojugal also remained unexposed so that the typically crocodilian nature of this bone was also unknown. These features, however, were briefly described or figured in a paper published shortly afterwards (Walker 1972).

The suggestion as regards the Crocodylomorpha did not at first meet with general acceptance, and some authors (e.g. Bonaparte 1982; Kitching & Raath 1984; Busbey & Gow 1984) continue to regard sphenosuchids as thecodontians. The utility of the Crocodylomorpha as a taxonomic grouping appears, however, to have been increasingly recognized in recent years (e.g. Gauthier (1986); Parrish (1987); Benton & Clark (1988) and Gow & Kitching (1988)). Whether a simple division of the early crocodylomorphs into two infraorders, Protosuchia and Pedeticosauria, as originally proposed is feasible is doubtful, however (Walker 1972, p. 261), although Gow & Kitching have recently (1988) endorsed this viewpoint. These authors ascribe to me the view (erroneously citing Walker (1968)) that the Protosuchia were aquatic, a position that I have never held; indeed, I have always been of the opinion that the Protosuchia were predominantly terrestrial and that some probably had cursorial tendencies (Walker 1970, p. 365).

In the earlier papers (Walker 1968, 1970) *Sphenosuchus* and allied forms were placed in the family Pedeticosauridae (van Hoepen 1915), which has priority over Sphenosuchidae (von Huene 1922). However, the holotype of *Pedeticosaurus leviseuri* (of which I have casts) is an unsatisfactory specimen as has been pointed out by other workers, and is unsuitable as the type of a family. Gow & Kitching (1988) claim to have identified another specimen as *Pedeticosaurus* sp., but the preservation is so different from that of the holotype that this identification seems doubtful; in addition the proportions of the two specimens differ, as the authors point out, and there are also other differences, notably in the scapula. It seems desirable, therefore, as others have done, to use Sphenosuchidae for the family and 'sphenosuchid' in informal usage. The following genera may now be added to the Sphenosuchidae: *Pseudhesperosuchus* (Bonaparte 1969, 1971) from the Los Colorados Formation of Argentina; *Terrestrisuchus* (Crush 1984) from a fissure-filling in the Carboniferous Limestone of Glamorgan, South Wales; and *Dibothrosuchus* (Simmons 1965; Wu 1986) from the Dark Red Beds of the Lower Lufeng Formation, China. The family is interpreted rather broadly in this paper. Bonaparte (1971) has based an infraorder upon it; in his opinion this lies within the order Thecodontia. Whether *Pedeticosaurus* s.s. should be included in the family is a moot point. Bonaparte (1972) has attempted to show that it is a protosuchian, although none of the criteria that he uses are diagnostic. It is very difficult in fact to decide whether it is a sphenosuchian or a protosuchian.

Although little reference will be made to these forms, for the sake of clarity it should be stated that the Protosuchia, usually regarded as a suborder of the order Crocodylia, is considered here to include the following genera: *Dyoplax* Fraas 1867; *Notochampsa* Broom 1904; *Stegomosuchus* von Huene 1922; *Erythrochampsa* Haughton 1924; *Protosuchus* Brown 1934; *Platyognathus* Young 1944; ?*Microchampsa* Young 1951; *Clarencea* Brink 1959; *Hemiprotosuchus* Bonaparte 1969; *Orthosuchus* Nash 1968; *Eopneumatosuchus* Crompton & Smith 1980; *Lesothosuchus* Whetstone & Whybrow 1983; *Baroqueosuchus* Busbey & Gow 1984. No account is taken of possible synonymy between these forms.

The skull of *Sphenosuchus* is the best preserved and the most complete of the sphenosuchids so far known. The braincase, in addition, is extremely well preserved and shows the otic capsule and other anatomical structures in a detail very rarely found in fossil reptile skulls, particularly from such as early period. The detailed description that follows of the otic capsule of *Sphenosuchus*, indeed, would very nearly serve for that of an extant crocodilian, for which such a description is still lacking. In addition to its critical position in relation to the phylogeny of crocodiles, *Sphenosuchus* has also been used in an attempt to develop a hypothesis of a particularly close relationship between crocodiles and birds (Walker 1972, 1974, 1977) which has been the subject of some controversy. For these reasons it seemed desirable to describe and illustrate the holotype, particularly the skull, in the detail that is warranted by the excellent preservation.

This paper is not intended to be a review of the various theories concerning the origin of birds, but aims to offer some basic data which, it is hoped, will help towards the elucidation of this problem, together with consideration of certain theoretical questions such as the homologies of the pneumatic cavities in the bird and crocodilian skulls, the stapedial artery problem and the evolution of the otic capsule. Neither does it include a phylogenetic analysis of inter-relationships within the Crocodylomorpha. Dr James M. Clark has been working for some years on these problems (Clark 1986) and has been able to examine at first hand a great deal of the relevant material. A preliminary account of his results has already been published (Clark, in Benton & Clark (1988)), and the reader is referred to this for further information. However, I hope to show that the concept of the Crocodylomorpha as a taxonomic unit is a valid one, largely from a comparison between the skull of *Sphenosuchus* and the modern crocodilian skull.

It has been found necessary in this study to propose several new anatomical terms, partly for structures in the crocodilian skull that seem to lack them, and partly for structures, especially pneumatic cavities, in the skull of *Sphenosuchus*. It is considered to be preferable to give these cavities independent names and then to attempt to homologize them with cavities in the modern crocodilian and bird skulls, rather than to assume homologies at the outset and to apply crocodilian or avian terminology to them.

I have attempted to restrict the term 'fenestra' to an actual aperture in the skull, and to use 'fossa' where a peripheral sunken area is involved. It is difficult, however, to be entirely consistent in such usage.

2. MATERIAL AND METHODS

The unique specimen (South African Museum no. 3014) was collected by Dr A. L. du Toit from the Upper Triassic or Lower Jurassic Red Beds (now the Elliot Formation) at 'Paballon, Mount Fletcher, Cape Colony' (Haughton 1915). It is preserved in a maroon matrix that varies from a rather hard sandstone with thin shale partings to a sandy mudstone that can be removed with a mounted needle. Fortunately, the matrix associated with the skull is almost entirely of the latter type. A thin calcite layer covered most of the skull bones and was of great help in obtaining a clean separation of the matrix from the interior of the cranium. In some areas of the skull a thin film of red clay intervened between the calcite layer and the bone surface.

The specimen consists of three main units: the skull and associated anterior cervical vertebrae, mostly cleared of matrix; a large slab with several pieces which fit on to it, containing postcranial remains (figure 1); and a right tibia and distal third of the

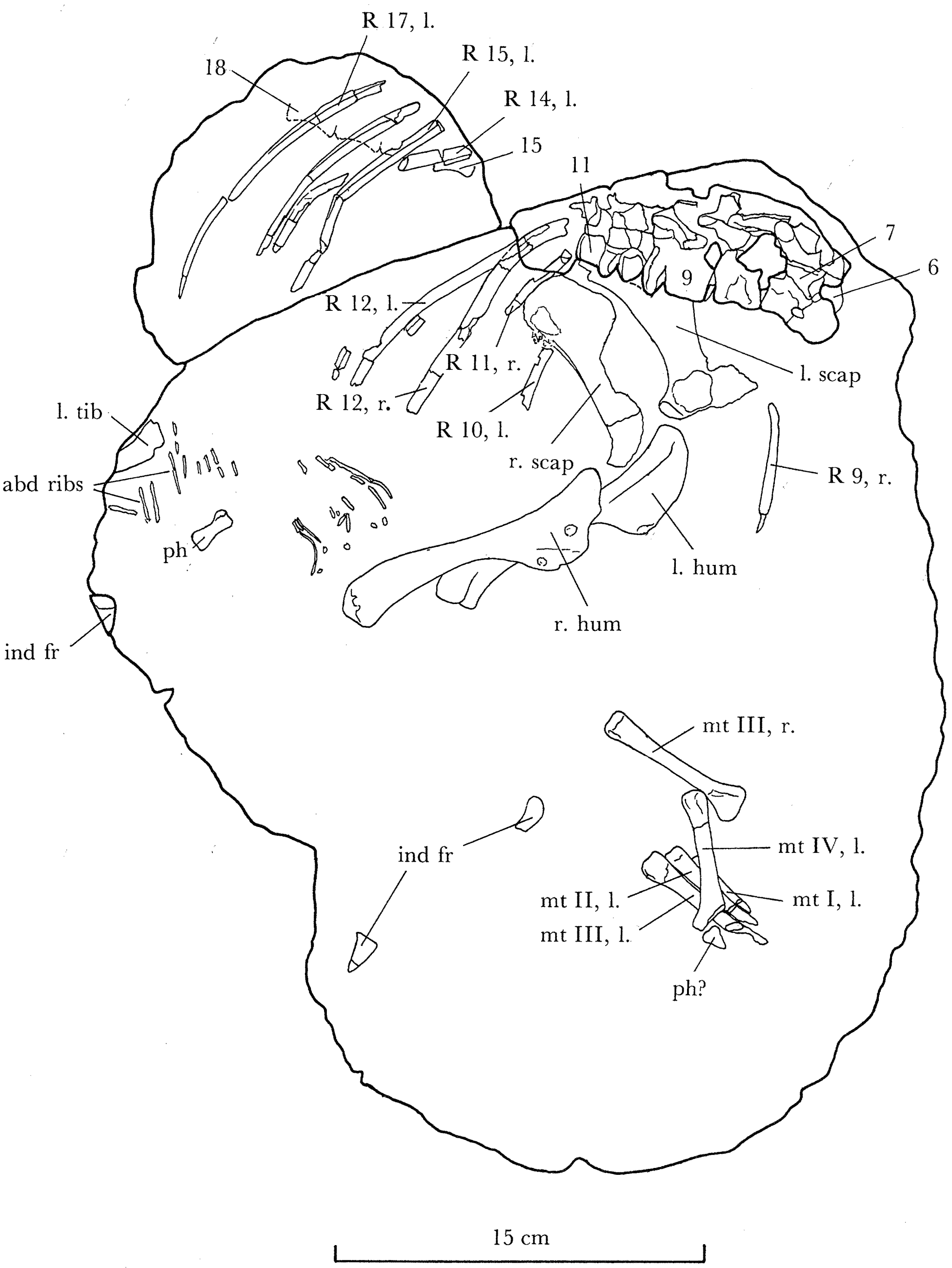

Figure 1. *Sphenosuchus acutus* Haughton (Htn). Layout of bones on main slab and additional pieces, magn. × 0.33. For explanation of abbreviations used in figures, see p. 119.

fibula, clear of matrix. Haughton (1915, p. 98) implies that the skull fits on to the main slab, but this is not possible as the slab is now, and it seems unlikely that the slab has been reduced in size since 1915. His account of the anterior cervical vertebrae also suggests that the state of the specimen was then very similar to what it is now. This point is discussed further in the taphonomic section.

As no details of the arrangement of the skull and skeleton have previously been given, it is desirable to do so here. When I first received the skull, it was in continuity with several pieces containing the anterior neck as far as the neural spine of the fifth cervical vertebra, as stated by Haughton (1915, p. 104; 1924, p. 352). There appears to be no contact between these vertebrae and those of the main slab. This latter block is roughly triangular in shape and measures 39 cm in maximum length. Parts of a series of six posterior cervical and anterior dorsal vertebrae, with their ribs, have been broken through and are partly preserved running across the corner of the slab and partly in three small pieces which fit on medial to the left scapula blade. The first of these vertebrae is identified as the posterior part of the sixth cervical. The vertebral column, with associated ribs, is continued after a gap on another piece. Between this piece and its counterpart (not figured) are traces of centra, the last of these being presumed to be the eighteenth presacral or ninth dorsal. There is no record of the original position of the single caudal vertebra figured by Haughton (1924). No other vertebrae are preserved.

The shoulder girdle is preserved in approximately a natural position in relation to the ribs and vertebrae, except that it has been compressed from side to side, and the left side is a little in advance of and dorsal to the right. The girdle is considered to consist of scapulae, coracoids and interclavicle, the sternum being cartilaginous and thus unrepresented, and it is believed that the clavicles had been lost. The slender bone lying just in front of the girdle and regarded as a possible clavicle (Haughton 1924; Walker 1972) has proved upon further preparation to be almost certainly the distal portion of a rib. The humeri were almost in contact with the glenoids, but have since been cleared of matrix. Although Haughton (1915) and von Huene (1925) identified a radius and ulna, preparation has proved that these are metatarsals, so that nothing more is known of the fore-limb.

The pelvis and femora are not preserved. The right tibia and distal end of the fibula were separated when I received them. Fortunately, von Huene (1925, fig. 16) showed them joined together by a thin layer of matrix, otherwise it would have been difficult to confirm Haughton's identification of the rather featureless fibula fragment. There was some initial doubt (Haughton 1915, p. 98) as to the correctness of the association of these bones with the rest of the skeleton. However, the damaged proximal end of the left tibia, and a fragment of the proximal end of the fibula, are present at the posterior corner of the main slab. The very similar, but opposite, curvatures of the proximal ends of the tibiae provide valuable confirmation of the correctness of the association of the detached elements, and this is further supported by comparisons with related forms, such as *Saltoposuchus* (von Huene 1921), *Hesperosuchus* (Colbert 1952) and *Pseudhesperosuchus* (Bonaparte 1971).

A group of metatarsals is preserved in an isolated position on the main slab. Four are of the left foot and one of the right. Several scattered, slender bones occur in the area between the right humerus, the left tibia and the distal ends of the ribs. These are probably abdominal ribs. An isolated phalanx also lay in this region. Three other fragments on the main slab have proved indeterminable.

Although *Sphenosuchus* has been stated by previous authors to be without armour, a single dorsal scute was discovered lying between the neural spines and zygapophyses of the seventh and eighth cervical vertebrae. This is sufficient to establish the existence of a paired series of dorsal scutes. When the skull came into my hands there was also a very conspicuous thin triangular bone lying in the right lateral temporal fossa. Curiously, this bone was unmentioned by previous authors. It is identified as a first cervical scute, probably the left-hand member of the pair. Behind the shoulder girdle and just dorsal to the right humerus was found a fragment of sculptured bone, which may be a ventral scute or possibly two scutes joined together.

Radiography carried out for Dr J. Attridge at Birkbeck College, London, revealed nothing further within the slabs.

The skull was made up of several pieces stuck together, and some other pieces that do not appear to have been used by previous workers. This may have been because the contact and bone surfaces were obscured by a mixture of old adhesive and red muddy matrix. Four of these pieces contain the right quadrate, pterygoid, basipterygoid process and the articular region of the right lower jaw. The 'snout piece' (the names of the pieces of the skull are listed on p. 11) has only a touch-contact with the 'prefrontals piece', but their relative positions can be fixed by the general continuity of surfaces and by details of the dentition. The anterior ends of the lower jaws, in symphysis, were separate from the skull and could be fitted to their impression on the matrix which blocked the anterior end of the palate. As most of the teeth were broken and the jaws had been distorted and were clearly not in correct occlusion, there seemed no point in retaining this impression, so that it was removed to expose the anterior part of the palate. The skull was prepared in several stages, culminating in the removal of the matrix from the interior of the braincase to as far forward as was feasible, i.e. the rear ends of the laterosphenoids. Limitations on the removal of matrix were set by the lack of certain pieces, the distortion, and the preservation of certain areas only in the form of impressions. The braincase proved to be much better preserved than the description and figure by Haughton (1924) might suggest, revealing details of the otic capsule that are to be seen on few fossil reptile skulls, and enabling all the cranial nerve foramina to be identified. It is also penetrated by a complex series of pneumatic cavities. As a consequence, preparation of the braincase occupied a great deal of time, likewise the illustration of its complexities.

Sufficient areas of contact have been left between the pieces so that they can be fitted together in their original relationships for study. Some of the drawings were made during the earlier stages, so that differences of detail will be noticeable from those made more recently.

Preparation has been entirely mechanical, using needles mounted in a pin tong, and a vibrotool. Cleaning of the interior of the cranium was greatly facilitated by the use of a half-reflecting mirror attachment to the binocular microscope, enabling the examination of deep cavities without interference by shadows.

Preparatory work on the postcranial skeleton need not be described in detail except for the shoulder girdle and humeri. When received, the scapulae and left humerus were embedded in the main slab, but the rest of the girdle and the right humerus were detachable. Sufficient matrix had been left between the bones so that all could be re-assembled in their original positions of occurrence. However, this matrix was a hindrance to proper study. A series of photographs was taken (of which a set has been deposited in the South African Museum) showing the progressive assembly of the girdle and humeri (figures 1 and 39), and the coracoids, interclavicle and right humerus were then cleared of matrix. Finally, the left humerus was removed from the slab and cleaned.

It is possible that the median ossification in the shoulder girdle is the sternum rather than the interclavicle. Hence a considerable amount of matrix was chiselled away in the region ventral to the girdle in a search for a possible second median element.

However, no such bone was discovered, although the shoulder girdle is preserved in a very natural attitude. Against this must be set the presence of what appear to be tooth marks on some of the bones, so that a thin superficial bone might have been gnawed away.

The following crocodilian skulls have been the main basis of comparison during this study:

	mm
Crocodylus niloticus, hatchling, skull length (snout–quadrate)	41
C. niloticus juvenile	86
C. acutus	550
C. porosus	675
Osteolaemus tetraspis	130
O. tetraspis	*ca.* 220
Alligator mississipiensis	203
Caiman latirostris juvenile	78
Gavialis gangeticus	815
G. gangeticus	780

The skull of the larger *Osteolaemus* was a disarticulated and wired specimen, parts of which have been completely disarticulated. One of the gavial skulls, and the skull of *Crocodylus acutus*, have been sectioned longitudinally in the sagittal plane. Several of the skulls have been partly sectioned or disarticulated to show various features, in particular the otic capsule. Other crocodilian skulls have been examined in the collections of the Natural History Museum and other institutions.

The systematic position of the genera of living birds referred to in the text and figures is as follows:

	order
Pygoscelis, *Eudyptes*	Sphenisciformes
Struthio	Struthioniformes
Rhea	Rheiformes
Casuarius, *Dromaius*	Casuariiformes
Gavia	Gaviiformes
Fulmarus, *Daption*	Procellariiformes
Ardea	Ciconiiformes
Anas, *Somateria*	Anseriformes
Falco	Falconiformes
Gallus, *Meleagris*, *Perdix*, *Phasianus*	Galliformes
Vanellus, *Larus*, *Alca*, *Uria*	Charadriiformes
Columba	Columbiformes
Strix	Strigiformes

3. TAPHONOMY

As exposed on the main slab, the skeleton lies on its left side. That this is the right way up is shown by the fining-up of the sediment from the base of the slab, and the more abundant mudclasts associated with the coarser sediment at the base (Dr B. R. Turner, personal communication). Confirmation is provided by the single dorsal scute that is lodged between the seventh and eighth cervical vertebrae. This scute is standing on edge with its originally dorsal surface facing ventrally (with respect to the vertebrae) and its lower edge rests on the medial side of the left postzygapophysis of the seventh cervical and the right side of the base of the neural spine of the eighth cervical (the right prezygapophysis of the eighth vertebra was removed to render the scute more clearly visible). Although the scute is partly supported by sediment in its present attitude, it would surely have fallen out had the skeleton been lying on its right side.

The skull and anterior cervicals, on the other hand, evidently lay on their right sides, or tilted in that direction. When first received, the two halves of the proatlas were lying on the right paroccipital process (figure 35*a*) and the succeeding vertebrae followed in series, passing close to the right quadrate. Clearly, these vertebrae had collapsed over to the right. Furthermore, the left articular is missing, although the rear end of the left jaw was otherwise complete and in place, and this bone could only have dropped out towards the right side, presumably as the skull lay drying out on the ground. It may, however, have been removed by a predator or scavenger.

This difference in attitude, taken with the lack of continuity between the fifth and sixth cervicals, suggests that there was an actual break in the neck at this point; the skull with its associated vertebrae may even have been at some distance from the remainder of the skeleton. Also, a vertebra may be missing, because the numbering of the posterior cervicals cannot be regarded as certain. The signs of damage done by a predator or scavenger to these vertebrae make it not improbable that continuity of the neck had been broken.

The left side of the skull has been pulled down with respect to the right, and this side has also been moved relatively forward. In the shoulder girdle, on the other hand, it is the right half that has moved ventrally with respect to the left. However, the distortion is presumably due simply to compaction of a muddy fine-grained sandstone which initially held rather a large volume of water. The differences in the sense of the distortion would thus be caused by slight variations in original attitude and are not of great significance.

Although interpretation is hampered by the lack of many counterpart pieces and the numerous breakages presumably caused by compaction of the sediment, there is clear evidence that a predator or scavenger had been at work on the carcase. The posterior cervical vertebrae in particular were found upon preparation to be considerably damaged (figure 37*a*, *b*). Large areas of the side walls of the neural canals are missing, this being particularly marked in the case of the eighth cervical, which appears to have been bitten through so that the anterior end is deeply notched on both sides. The eleventh vertebra is similarly affected. A deep pit behind the left prezygapophysis of cervical 8 appears to be a tooth mark; so also may be a pit on the left side of the ninth centrum. Other damage to the centra, and to the left side of the axis centrum, could be due to later decay. However, the twelfth centrum has nearly all disappeared, together with most of the neural arch. The right diapophysis of cervical 7 was certainly missing, likewise the right parapophysis and diapophysis of cervical 8. The left diapophysis of cervical 9 is represented by a matrix-filled hole. Other damage to these vertebrae was caused by the breakage of the pieces at the time of collection. Preparation of the left scapula has removed much of the evidence, but there is no sign of the anterior dorsal ribs of the right side passing below the right scapula blade, that is, in front of the fragments identified as the eleventh right rib. The slender bone in front of the left coracoid is probably the distal end of the ninth right rib, turned round. A displaced cervical rib, probably the seventh right, lies just within the rear end of the right lower jaw, and has itself apparently been gnawed. Thus there is evidence that the anterior ribs of the right side had been disarranged, but little can be said about the left side. Further back, there is a gap with rib 13 of the left side apparently missing. The right ribs behind the twelfth could have been present originally but lying a little higher up in the matrix, so that they were not collected, hence no conclusion can be drawn from their absence.

The incompleteness of the rear ends of the coracoids may also be attributed to predator action, because two grooves, apparently tooth marks, on the outer surface of the right coracoid (figure 41 *e*) occur just in front of the damaged area which itself has a suspiciously straight edge, as if the bone had split away. Other probable tooth marks include a circular hole on the right side of the interclavicle (figure 40*c*, *d*), which was found upon preparation to pass right through the bone, and two circular pits on the proximal end of the right humerus (figure 43*h*). A curious deep notch in the internal tuberosity, and damage to the deltopectoral crest of this bone may have a similar origin. The loss of the internal tuberosity on both humeri could have occurred at the time of collection or during initial preparation, which was rather careless in some places.

There is a strong possibility that the death of the animal was caused by the bites to the neck region, and that the same predator was responsible for the removal of the lower portions of the fore-limbs and the displacement of the hind feet, and probably for the removal of the posterior dorsal vertebrae and their ribs, although this is less certain. The disturbance to the skeleton could, however, equally well have been caused by a scavenger or scavengers. A curious feature is the survival of the single dorsal scute in the neck region. This scute must surely have attained its present position after the damage was done to the vertebrae, but it is surprising that so few dorsal scutes are to be seen (one other was lying near the skull), because in animals that possessed them they usually occur in articulation or scattered about the slabs (e.g. *Saltoposuchus*). They may have lain to the dorsal side of the vertebrae as in *Pedeticosaurus*, in which the skeleton also lies on its side (van Hoepen 1915), or may have been stripped off *en masse* in the thick skin in which they were embedded. In either case the survival of this scute is hard to explain.

Injury to the skull by the same agency or agencies is less easy to define, because there has been much breakage caused by the distortion. However, the considerable damage to the right articular was all exposed during preparation. The right medial pterygoid flange, and the lower edge of the quadrate wing of the right pterygoid were also found to be incomplete. The anterior wall of the cavity within the right ectopterygoid had been broken away. The lack of the missing pieces in the adjacent matrix, and the nature of the damage to the articular, shows that these effects cannot all be ascribed to distortion. It is possible that the left articular was removed at the same time. It is difficult to visualize this bone dropping out, although the other elements of the jaw were somewhat splayed apart at their rear ends. Du Toit (quoted in Haughton (1915, p. 100)) stated that virtually no bone was lost from the front of the snout when he prepared it, so that its incompleteness (which is unlikely to be an original feature of the skull, as Haughton thought) was probably also caused by the same agency.

Table 1. *Main measurements of Sphenosuchus*

(All measurements are in millimetres; e, estimated length.)

skull length (snout–quadrate)	192 (e)
lower jaw length	195 (e)
presacral column length	473 (e)
left scapula height	82
left coracoid length	76
right coracoid length	77
interclavicle preserved length	52
left humerus length	114
right humerus length	113
right tibia length	128
metatarsal I, left, length	48 (e)
metatarsal II, left, length	57 (e)
metatarsal III, left, length	63 (e)
metatarsal IV, left, length	55
metatarsal III, right	63
anterior cervical scute (?first), length	16
breadth of same scute	14
posterior cervical scute (?eighth), length	25

After the action of the predator or scavenger, there may have been a period of decay *in situ*, which could account for the larger areas missing from certain vertebrae, such as the left side of the axis centrum and the right sides of the centra of the sixth and ninth cervicals, and for the corroded area on the medial side of the anterior end of the left coracoid. However, this is very difficult to distinguish from effects due to 'gnawing'. It may be significant that the axis lay on its right side, whereas the more posterior vertebrae lay on their left sides.

There are numerous small fragments of bone in the matrix adjacent to vertebrae 6–13. Presumably, these fragments came from the vertebrae, were lying on the same surface, and were redistributed within the matrix by the influx of sediment-laden water. However, final deposition must have been relatively quiet, because of the preservation on the right side of the skull of the fragile sheet of poorly ossified bone that forms the floor of the hollow basipterygoid process. The sediment would have gained access to the interior of this by the various pneumatic apertures leading into it.

4. DESCRIPTION OF *SPHENOSUCHUS*

Family Sphenosuchidae von Huene 1922

Diagnosis: Slender-limbed crocodylomorphs of small to moderate size (0.76–1.4 m in total length). Skull long and low but not flattened. Half or more of maxilla lies in front of antorbital fenestra. Supratemporal fenestrae large, usually elongated, with a median crest or narrow flat zone between them. Transverse or oblique parietal–squamosal crests usually present (apparently not in *Terrestrisuchus*). Frontal usually enters anterior border of supratemporal fenestra. Infratemporal fenestra large, subrectangular, quadratojugal forms all of posterior margin, not meeting postorbital. Quadrate as a whole not greatly inclined. Squamosal with long posterior overhang and moderate to large lateral overhang. Prefrontals meet interorbital septum but do not meet palate. Maxillae form short secondary palate.

Proximal end of quadrate meets prootic but not laterosphenoid. Quadrate and pterygoid usually free of braincase (quadrate head fused in *Dibothrosuchus*). Prootic unreduced. Braincase pneumatized. Basipterygoid joint free. Basipterygoid processes large and pneumatized, extending posteriorly. Otic capsule of crocodilian type with fenestra pseudorotunda, but 'exoccipital' does not enter cochlear recess and lagenar region is mainly in basioccipital. Nerves of the vagus group usually not enclosed in subcapsular buttress (may be enclosed in *Terrestrisuchus*).

Lower jaw slender; usually an enlarged anterior dentary tooth bites into a cavity in the palate between premaxilla and maxilla. Prearticular present. Teeth compressed, recurved and serrated, or with lanceolate crowns.

Vertebrae relatively primitive, parapophysis does not rise on to transverse process. A tendency towards procoely in the vertebrae. Ribs of last cervical and most dorsal vertebrae with anterior, and in some cases also posterior, flanges.

Coracoid with posteroventral extension, articulating with large, elongated interclavicle; clavicles lost. Radiale and ulnare elongated, manus small. Ilium with long anterior process; pubis entering acetabulum; symphysis long; acetabulum open. Femur with inturned head. Distal half of tibia usually curves forwards and inwards; distal end has flat, posteroventrally facing facet to meet dorsolateral process of astragalus. Tarsus crocodilian. Usually a double row of dorsal scutes long the mid-line.

Genus Sphenosuchus Haughton 1915

Type species by monotypy *Sphenosuchus acutus* Haughton 1915.

Diagnosis: A relatively large sphenosuchid; skull length 192 mm, total length estimated at 1.4 m. Antorbital fenestra of moderate size. Supratemporal fenestrae large and elongated, frontal just enters anterior margin. Maxilla and jugal strong. Some skull bones weakly ornamented. Postorbital bar inclined forwards at top. Frontals with cruciform pattern of ridges on dorsal surface; four or five marginal notches or foramina pierce rim on each side. Canal runs through crista cranii frontalis in upper part of orbit. Squamosal with moderate lateral overhang. Lateral temporal fenestra tall and narrow. No foramen between quadrate and quadratojugal. Anterior temporal foramen large, between squamosal and prootic only. Post-temporal fenestra small, rather medially placed. Supraoccipital inverted shield-shaped. Occipital plate crescentic.

Deep cavities in anterior part of palate between premaxillae and maxillae. Palatine with ridge system that supports a spout-like ventral prolongation of the choana. Pterygoid with medial as well as lateral flange.

Laterosphenoid elongated. Articulation for quadrate head borne on both squamosal and prootic. Large post-quadrate foramen present.

Enlarged third and fourth dentary teeth alternate in biting into cavity between premaxilla and maxilla. Mandibular fenestra of moderate size. Retroarticular region of jaw short and hoof-like. Articular with internal ascending process and anteroventral pneumatic foramen in addition to large foramen aërum. Symphysis weak. At least 4 rather small premaxillary teeth; 13 maxillary teeth; 15 dentary teeth.

The following skull bones or spaces are pneumatized: basioccipital, basisphenoid (highly), prootic, opisthotic (incipiently), temporal canal, quadrate (pit in posterior surface), articular. Probably pneumatized: ectopterygoid, pterygoid. Possibly pneumatized: preorbital fossa, dorsal channel in maxilla-jugal.

Posterior cervical vertebrae have hypapophyses. Dorsal ribs slender, with anterior and posterior flanges.

Scapula blade triangular, moderately expanded dorsally. Coracoid with projection presumed to be for biceps origin, and long, broad, posteroventral expansion. Interclavicle with median dorsal ridge. Deltopectoral crest of humerus continuously convex in profile. Metatarsal I reduced, metatarsals II and IV symmetrical about III which is longest. A paired series of dorsal scutes present.

Sphenosuchus acutus Haughton 1915

Haughton, S. H. 1915, pp. 98–105, figs 15–17.
Haughton, S. H. 1924, pp. 344–358, figs. 9–16.
Huene, F. von 1925, pp. 307–320, figs 1–17.
Broom, R. 1927, pp. 359–369, figs 11–13.

Diagnosis: as for the genus.

Holotype: South African Museum no. 3014. Skull and partial skeleton.

Locality: Paballong, Mount Fletcher District, Cape Province, South Africa.

Horizon: near top of Red Beds (Elliot Formation), late Triassic or early Jurassic.

(*a*) *Skull*

Distortion and preservation (*figures* 56–58)

The skull as a whole has been deformed in two main ways: (*a*) the left side has been pushed forwards and compressed, and the right side pulled backwards and stretched, the difference at the quadrates being about 20 mm; (*b*) the skull has been pushed over to the right so that the heights of the right orbit and lateral temporal fenestra have been reduced. The bones of the left side thus lie at an obtuse angle to the skull-roof, those of the right side at an acute angle. In addition, the occiput, quadrates and squamosals have been tilted down on the left and up on the right; on the right side the upward arch of the squamosal–postorbital bar has been exaggerated. The upper end of the left quadrate and the squamosal and postorbital have been moved forwards relatively further than the remainder of the left side of the skull, so that the upper part of the left orbit has been strongly squeezed. The quadrate has, in effect, been rotated about a transverse axis so that its lower end, together with the quadratojugal and the rear end of the jugal, have been lifted up. The tip of the left paroccipital process and the underlying flange of the squamosal have also been bent upwards. The whole occiput has, in fact, been swung round so that the rear end of the sagittal crest has been bent over to the left. Nevertheless, the high degree of symmetry of the occipital surface, with minor undulations mirrored on each side, shows that as a whole it has remained practically intact.

The 'snout unit' – premaxillae, maxillae, nasals, palatines and vomers – has been pushed back relative to the rest of the skull, so that the premaxillae have been bent inwards and downwards, and the left preorbital fossa has been reduced in length by some 7 mm. The upper part of the right maxilla has been bent medially at right angles; the central parts of the nasals are missing except for some broken pieces of the right nasal.

The distortion of the left lateral temporal fenestra has broken the upper part of the quadratojugal. A distinctive fragment of the upper end of this bone was recovered from the left orbit, and a piece from the middle region was found lying just in front of the left jaw articulation. Some thin pieces at the anteroventral corner of the temporal fenestra probably also belong to this bone. All these pieces seem to have 'drifted' within the soft sediment during the compaction process, indicating that breakage took place at an early stage. Fortunately the upper half of the quadratojugal was found to be *in situ* on the right side.

The interior of the skull shows similar effects to those visible externally. The forward drive of the left quadrate has brought the anterior end of the pterygoid ramus close to the mid-line. The irregularities on its lower edge have caught against the posterior edge of the medial pterygoid flange, pushing forward in turn the quadrate wing of the pterygoid. The medial pterygoid flange has buckled laterally, and this line of sharp bending is continued upwards and forwards as a geniculation of the lower part of the quadrate ramus of the pterygoid. The latter has parted along a horizontal fracture from the main part above it. This upper portion largely retains its natural curvature, but its nearly vertical anterior edge has been pushed forwards, cutting into the side of the rostrum of the basisphenoid. The curving ridge leading from this edge to the parabasal process of the pterygoid has been fractured and intruded into the anteroventral corner of the hollow basipterygoid process.

A further consequence of the accidental locking between quadrate and pterygoid is that a narrow strip has apparently been split off the lower part of the pterygoid ramus of the quadrate and partly bent down, partly telescoped, giving the appearance of an elongated separate process.

On the right side of the skull the quadrate–pterygoid relationships are less disturbed, although the quadrate is considerably fractured and the two bones are some 6 mm farther apart than in life. The effects of distortion on the braincase are similar to those on the skull as a whole.

The lower jaws have been deformed in the same manner as the skull. The outer wall of the left dentary has been pushed forward and bent sharply at the anterior end, whereas the rear end of the right jaw has been slewed round medially. It is clear that the left jaw had been broken in half, but as there is some scope for variation in the alignment of the anterior and posterior portions of the right dentary it is not certain whether the right jaw had also been broken.

As noted in the taphonomic section, incompleteness caused by original damage is difficult to distinguish from that due to collection failure. Fortunately, the portions missing from one side of the skull can in most cases be supplied by the opposite side. Exceptions are the tip of the snout, the anterior ends of the vomers, and the lower surfaces of the pterygoid flanges.

Restoration of the skull and lower jaw (figures 2, 3 and 31)

The effects of the distortion described above have been corrected in the restorations. There is no reason to doubt that the external nares were surrounded by bone (*pace* Haughton 1915, 1924). There were at least four premaxillary teeth, and restoration of the snout tip suggests that there may have been as many as six in all. There does not seem to have been a lateral notch between premaxilla and maxilla as shown previously (Walker 1972, fig. 2*b*). Telescoping of 5 mm at the naso-frontal overlap, and 7 mm at the left preorbital fossa, has been allowed for. The actual bony aperture of the fenestra is thus not as short as shown in previous restorations (e.g. Romer 1956). The palatal processes of the premaxillae are restored, likewise the anterior half of the vomers. Correction has also been made for lateral squeezing of the choanae.

It is believed that the ectopterygoid just failed to meet the maxilla: on the left side the maxilla was later found to have been impacted into the ectopterygoid. This junction was the basis for the contact shown in a previous restoration (Walker 1972, fig. 3*a*). The restoration of the large basipterygoid process is uncertain in detail, especially at the anterior end.

On the skull roof the postorbitals are shown as swinging out abruptly behind the orbits. It should be borne in mind, however, that this region is fragmented on the left side and strongly squeezed on the right. The transverse flanges of the parietals and squamosals appear originally to have lain at right angles to the mid-line.

As restored, the skull measures 192 mm from snout to quadrate, 86 mm across the jugals and 60 mm in height from quadrates to parietal crest.

There is a gap of some 30 mm in the middle of the jaw that is not represented on either side. The left surangular, and a small area of impression of the right surangular, show that this bone curved down again anteriorly from its summit. It is unlikely that the lower edge of the jaw was straight because, after allowance for distortion, the foot of the quadrate is not sufficiently

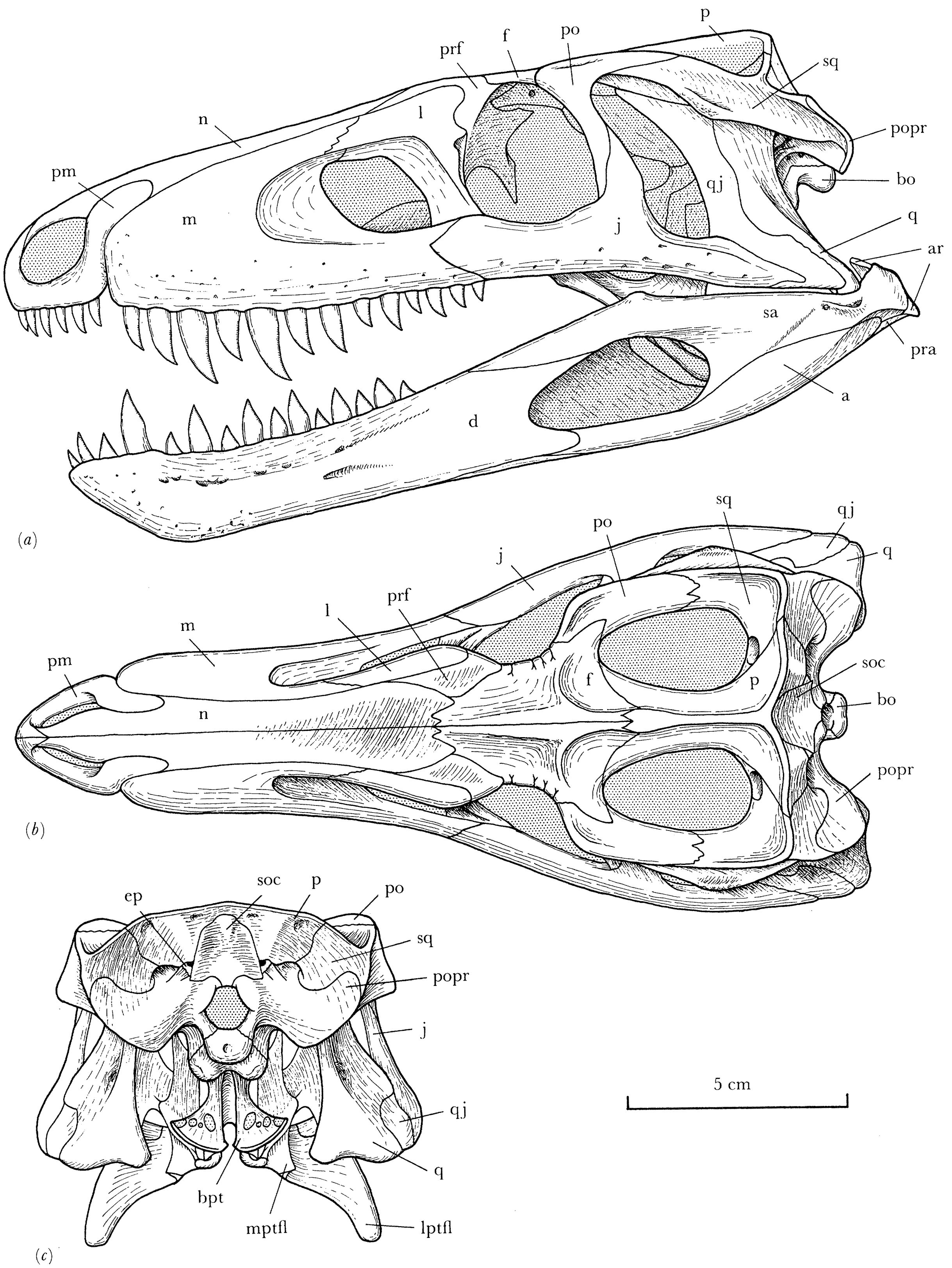

Figure 2. *Sphenosuchus acutus* Htn. Restoration of the skull and jaw in (*a*) lateral, (*b*) dorsal and (*c*) occipital views, magn. × 0.75. Tip of snout and central part of jaw restored.

depressed. Thus it seems that the jaw expanded upwards and downwards in an approximately symmetrical fashion at the mandibular fenestra. The latter was evidently of moderate size and set well back.

The internal ascending process of the articular has been moved back in order to correct for the slewing-round of the rear end of the right lower jaw. In fact, sufficient correction may not have been applied here.

As restored, the lower jaw is 195 mm long.

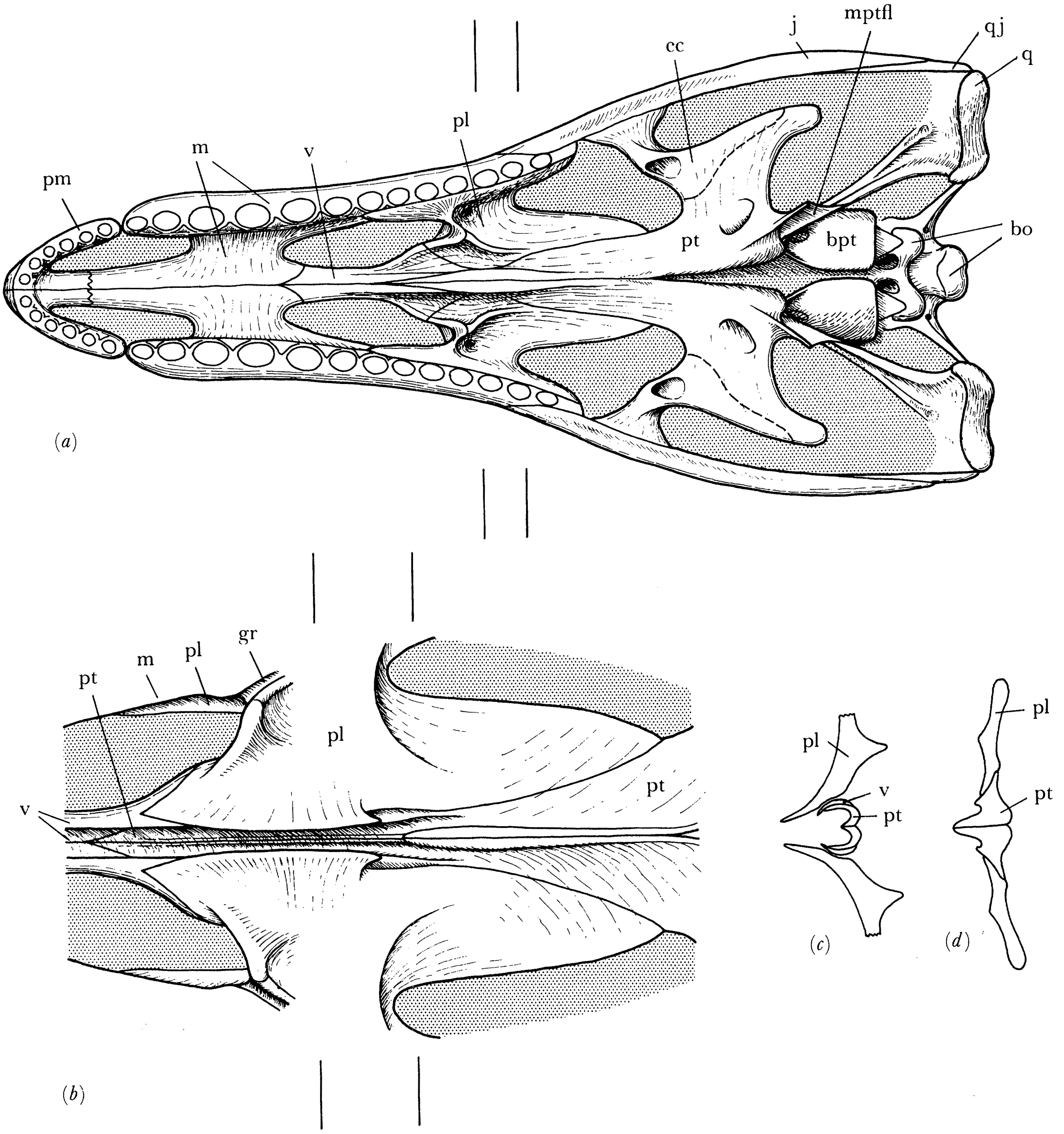

Figure 3. *Sphenosuchus acutus* Htn. (*a*) Restoration of the skull in palatal view, magn. × 0.75; (*b*) upper view of part of palate, magn. × 1.5; (*c*), (*d*) cross sections of the palate along the lines indicated, magn. × 1.5.

The pieces of the skull

It is convenient for description to refer to the pieces by names, and a list follows of the main pieces and the parts of the skull they represent.

1. 'Snout piece'. Premaxillae, most of right maxilla, anterior half of left maxilla, anterior ends of nasals. Shows secondary palate and anterior ends of choanae.

2. 'Prefrontals piece'. Rear ends of nasals, anterior halves of frontals, prefrontals, lachrymals, rear half of left maxilla and anterior end of jugal, palatines, rear ends of vomers, anterior rami of pterygoids. Shows rear half of left choana and left postpalatine vacuity. A small detachable piece has part of left jugal and ectopterygoid.

3. 'Left frontal piece'. A small piece with part of left frontal and postorbital and tip of laterosphenoid.

4. 'Laterosphenoids piece'. Rear ends of frontals and anterior ends of parietals, with anterior portions of laterosphenoids below. Right postorbital, squamosal, part of right jugal and ectopterygoid, upper end of right quadratojugal and anterodorsal process of right quadrate. Rear surface of block shows impression of lateral surface of pterygoid ramus of right quadrate and anterior end of quadrate ramus of pterygoid. Anterior part of rostrum of basisphenoid also present.

5. 'Right pterygoid piece'. Basal region of right pterygoid with medial pterygoid flange; impression of anterior surface of lower end of right quadrate, also lower part of its pterygoid ramus; lower surface of right basipterygoid process; impression of part of right surangular; a cervical rib.

6. 'Right basipterygoid piece'. Right basipterygoid process and impressions of inner surfaces of pterygoid ramus of right quadrate and quadrate ramus of pterygoid.

7. 'Right quadrate piece'. Most of right quadrate, a small area of right prootic, and rear end of right squamosal.

8. 'Braincase piece'. The greater part of the braincase and occiput and the head of the right quadrate.

9. 'Right paroccipital piece'. A small piece which fits on to the right occipital surface and has the distal end of the right paroccipital process and, on a thin layer of matrix overlying this, the impression of the distal end of the squamosal.

10. 'Supraoccipital piece'. Most of supraoccipital, parts of left parietal and squamosal with transverse crest, left paroccipital process and head of left quadrate.

11. 'Left quadrate piece'. Left quadrate with anterodorsal process, left postorbital, squamosal, jugal and lower part of quadratojugal; most of left pterygoid, the transverse flange as an impression of its upper surface; left basipterygoid process.

12. 'Left dentary piece'. Anterior end of left dentary and splenial.

13. 'Left surangular and angular'. In two parts, one of which includes anterior end of prearticular.

14. 'Left prearticular'.

15. 'Left jaw counterpart piece'. Impressions of outer side of rear end of lower jaw and edges of jugal and quadratojugal.

16. 'Right dentary piece'. Right dentary, splenial, coronoid and anterior ends of surangular and angular.

17. 'Right articular piece'. Right articular and rear ends of surangular and prearticular.

Dermal bones of the skull roof

The *premaxilla* (figure 4) appears to have been but weakly attached to the maxilla. Its posterodorsal end forms a tapering or spatulate process of uncertain length running back in a shallow recess formed by the nasal and maxilla, concealing the junction of these two bones. The posterior border is smoothly rounded, apparently just touching the maxilla; posteroventrally the border curves round towards the alveolar portion. Its rugose nature indicates that it projected freely. A group of small foramina emerge on the posterior surface just above the beginning of the rugosities. About two thirds of the laterally crushed palatal part of the right premaxilla and about a quarter of the left are preserved. On the right side a small chip detached during preparation shows longitudinal sections through the posterior three teeth, the last of which appears to be noticeably larger than the preceding two. However, the left premaxilla shows the alveoli and broken stumps of the last two teeth, which are of equal diameter, so that the appearance on the other side is no doubt due to random sectioning (the size of these teeth has been a point of disagreement between previous authors). The small chip fits on to the lower border of the premaxilla, and in front of it from the medial side can be seen a displaced interdental plate and then a very crushed and incomplete tooth. Thus there seem to have been four slender teeth of approximately uniform size, a little over 2 mm in diameter, in a distance of 15 mm.

There is no indication of any internal shelf on the premaxillae which might have extended back to make contact with the anterior palatal processes of the maxillae, apart from a slight medial thickening above the alveoli. Any such connection must have originated well forward, in front of the fourth tooth position from the rear, and must thus have been narrow, lying between extensions of the large anterior palatal vacuities. If the dentition extended to the front of the snout, as seems likely, there would have been five or six teeth on each premaxilla.

The *maxilla* (figures 4, 5 and 10) is a strong bone which probably bore 13 teeth. Anterodorsally the edge forms a shelf, 2–3 mm wide, with a striated surface for the reception of the premaxilla and the anterior end of the nasal. A small fragment of the nasal adhering to this shelf (figure 4*b*) shows a very small striated area for the premaxilla, indicating that the thin posterior tip of that bone lay only against the nasal. The rear end of the premaxilla may therefore have been thinner and more spatulate than I and previous authors have restored it (Haughton 1924; Broom 1927; Walker 1972, 1974). Passing backwards the rear end of the maxilla comes to lie against a vertical flange sent down by the nasal and ends dorsally against a small cornice on the latter. The maxilla thins posteriorly above the antorbital fossa, lateral to the lachrymal, and its rear end is preserved as two projections, one of which has been intruded between lachrymal and prefrontal. The left antorbital fenestra is some 7 mm longer when the effects of telescoping above and below it are allowed for, so that it was not as small an aperture as has previously been thought. It continues forwards as a shallow recess in the side of the maxilla.

There is only a touch-contact, or perhaps even a slight gap, between the 'snout piece', which has the anterior end of the left maxilla, and the 'prefrontals piece', which has the posterior end. The right maxilla on the 'snout piece' is slightly less complete at the rear end than is the left. However, there is evidently only a single tooth-position (the sixth) missing between the two parts of the left maxilla, the rear wall of its alveolus being preserved, and the extent of the gap can be accurately estimated.

The anterior part of the bone is thickened laterally to accommodate the bases of the large anterior teeth. The junction with the jugal has been strongly telescoped. Externally the maxilla overlaps the anterior end of the jugal (figure 5*a*), dividing to give a 'fish-tail' termination, the upper limb of which is inferred from a shallow recess on the jugal. The lower limb had overridden the ledge which received it, and part of the broken bone was removed to expose the nature of the contact. The maxilla runs back medial to this ledge, decreasing in depth and, after a gap equivalent to one alveolus, its apparently blunt posterior tip is seen in contact with the anterior process of the ectopterygoid which it has penetrated and partly disrupted. A broken cross-section at the rear end of the lachrymal pillar shows the maxilla to have been deeply channelled dorsally. It is virtually certain that the lachrymal did not originally contact the maxilla in this region, since the left lachrymal has been pushed downwards.

The secondary palate is formed by the stout

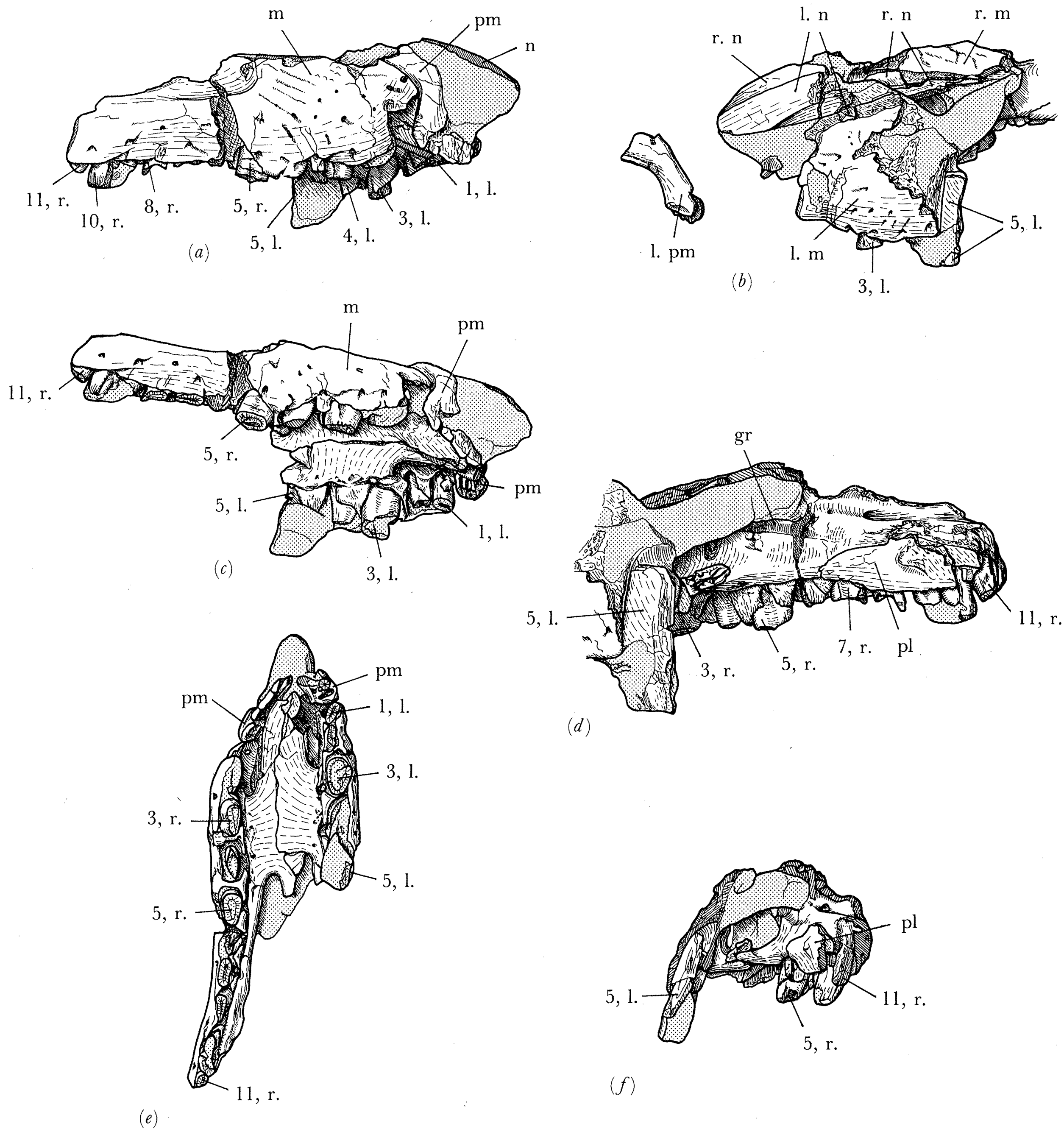

Figure 4. *Sphenosuchus acutus* Htn. The 'snout piece'. (*a*), (*c*) Lateral and ventrolateral views of right side; (*b*) oblique dorsolateral view of left side with premaxilla detached and turned round; (*d*) medial view of rear part of right maxilla showing palatine contact; (*e*) palatal view; (*f*) posterior view. Maxillary teeth numbered. All magn. × 0.75 except (*d*) which is magn. × 1.

maxillary shelves, each 10 mm wide, which met at a strong, interlocking contact. Their lower surfaces are minutely rugose. Anteriorly they are notched as far as to the third maxillary tooth by deep channels walled in by bone. Posteriorly the chambers tunnel back a short distance above the secondary palate. The medial wall on the left side is the better preserved and its anterior edge is deeply embayed by a large semicircular notch, allowing communication with the median space above the anterior processes. Although somewhat broken and distorted there is no indication of any suture within these processes, which thus must have extended forwards well in front of the marginal premaxilla–maxilla contacts. Their anterior ends are apparently still incomplete. The interdental plates are well preserved on the 'snout piece', those along the maxillary shelves being exceptionally well developed, no doubt because of the occurrence of the three largest teeth in this region. A narrow groove runs along the bases of the plates.

The upper surface of the secondary palate has been largely cleared of matrix. Like the modern crocodilian palate, the lower surfaces of the shelves were flush-fitting, but there was a median ridge dorsally, rather wide (3 mm) and flat-topped in the posterior part, but dying out forwards towards the region between the chambers. In the modern crocodilian skull the vomers run forwards as slender processes above this flat-topped ridge. It is probable that they did likewise in *Sphenosuchus*; if so, they extended at least 7 mm in front of their anterior termination on the lower surface. The medial edges of the maxillary shelves curve outwards posteriorly, and it is assumed that the vomers inserted into the median notch thus formed. The contact surface is very irregular, indicating a firm union.

A broad longitudinal groove, presumably vascular, makes its first appearance on the inner side of the maxilla above the anterior end of the palatine contact (figure 4*d*). It runs forward, rising gradually, until it lies along the crest of a ridge some 7 mm above the secondary palate. It dies out about 4 mm behind the broad notch by which the maxillary chamber communicates with the nasal cavity. The upper surface of the secondary palate shows prominent dendritic grooving, running away roughly at right angles from the mid-line, at a point opposite the rear ends of the chambers.

The palatine contact is visible on both maxillae (figures 4*d* and 10), which complement each other. The contact is noteworthy for the very low position attained by its ventral border, which descends to conceal completely the interdental plates from the eighth tooth backwards, lying 3 mm below the inner border of the maxilla. The anterior half of the contact area is seen to have been longitudinally striated. Within the lower rim of the antorbital fenestra and the anterior end of the lachrymal pillar the narrow upper surface of the maxilla is exposed lying alongside the palatine. Further back relationships are partly obscured by the bending up of the outer corner of the palatine by lateral compression, but it is probable that the palatine overlapped the maxilla. At a break near the rear end of the left maxilla a short section of an inwardly projecting shelf is seen, not far above the lower border of the bone. This shelf fits into a corresponding recess in the lateral surface of the palatine. There seems no doubt that the maxilla ended abruptly medial to the jugal, without touching the ectopterygoid.

The *nasals* (figures 4 and 5) are long and narrow, but thick, bones which form the upper, and probably also the anterior, borders of the external nares. The anterior ends are incomplete but the left nasal still has an entire margin above the naris showing that it tapered rapidly forwards to a breadth of 3 mm at the broken end. Doubtless the median processes of the premaxillae would have reached almost to this point. The central parts are mostly missing except for some fragments of the right side. The superior surface is strongly convex from side to side at the anterior end, becoming flat in the middle and developing a shallow central concavity towards the rear end, over the middle of the preorbital fenestra. Behind the naris and beneath the premaxilla, the nasal meets the maxilla at an edge-to-edge contact, a curious feature being the lack of a descending process here.

The relationships between nasal, prefrontal and lachrymal were difficult to discern because of telescoping and the development of shear cracks. Fortunately, however, the 'prefrontals piece' separated into three parts during preparation, making clear the relationships between the bones. Essentially, the posterior ends of the nasals rest in a shallow depression formed by the frontals, prefrontals and lachrymals, which rises gently posteriorly. The posterior ends of the nasals have a long overlap (17 mm) on the frontals and the posterior tips of the interdigitating contact rested in smooth sockets in the latter bones. The vertical flange from the nasal already mentioned has a smooth lower border which rests on the smooth upper edge of the anterior ramus of the lachrymal. The latter also curves round the flange laterally and thins out about halfway up it. Both nasal and lachrymal are in turn overlapped by the maxilla, which was firmly joined on to the nasal anteriorly. The nasal flange declines posteriorly and the cornice expands sideways to overlie the prefrontal.

The rear part of the nasals thus falls into two well-defined regions, an anterior section with marginal ventral flanges, which rests in a smooth, vertically walled trough formed by the lachrymals, and a posterior, flangeless section overlying the latter bones plus the prefrontals and frontals, also with smooth contacts.

On the undersurface the posterior parts of the nasals are thickened along the mid-line to form a strong ridge which is convex downwards in profile. On either side a weaker ridge runs obliquely inwards and backwards, bordering a shallow depression medial to the nasal flange. Telescoping has hidden the rear ends of these structures.

The *lachrymal* (figures 5 and 6) is essentially an inverted L-shaped bone bordering the upper and posterior sides of the antorbital fenestra, the upper limb being quite hollow. A narrow tongue of bone below the overhanging rim of the fossa begins to turn down again just before preservation ceases at the anterior end of the 'prefrontals piece' (figure 5*a*). It appears likely that the posterior process of the maxilla below the rim should be moved forward again to this position to allow for shortening. The situation in *Pseudhesperosuchus* (Bonaparte (1971, pl. III), and photograph kindly supplied by the author) is closely similar as regards the shape of the lachrymal. In this specimen, however, the equivalent part of the bone is exposed laterally, not concealed by the maxilla. Posterodorsally the lachrymal extends beneath the prefrontal as a thin, squamous layer, which did not meet the edge of the frontal. There is a firm junction with the prefrontal posteriorly with only a small amount of overlap. A slightly roughened posterodorsal protuberance is skirted by the suture. Above and behind the antorbital fenestra the overhanging rim has been strongly compressed on the left side.

The lachrymal canal enters about halfway up the orbit, close to the prefrontal suture. It evidently arches upwards and forwards over the antorbital fossa and can be followed as a low ridge on the inner surface. It probably emerged at a deep anterior notch in the inner wall (figure 5*c*) where the lachrymal dies out within the maxilla.

The strong ridge bordering the fossa posteriorly dies out below and the lachrymal terminates as a thin, anteroposteriorly expanded smooth sheet of bone, overlain laterally by the jugal. Its lower end is perhaps

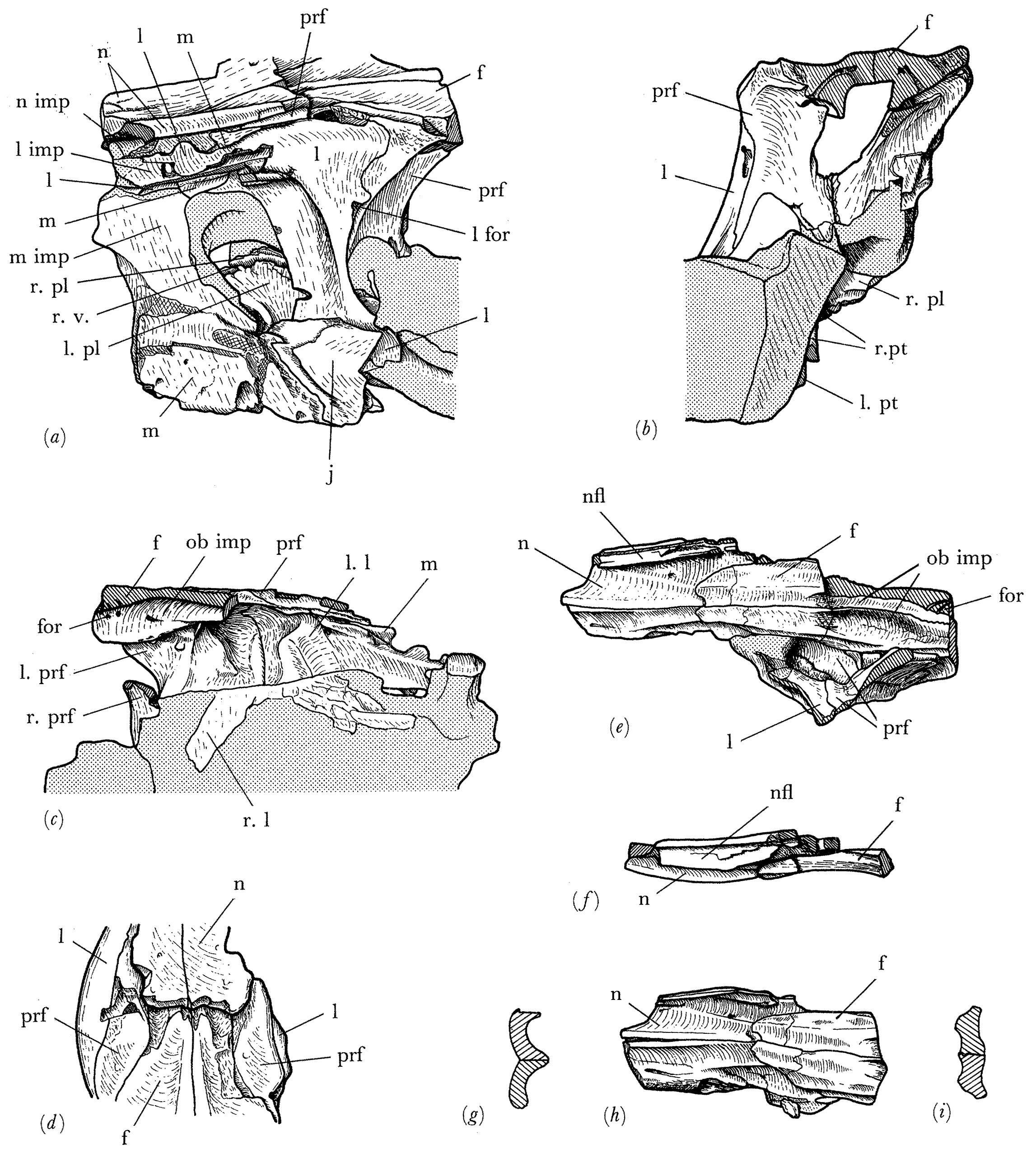

Figure 5. *Sphenosuchus acutus* Htn. The 'prefrontals piece'. (*a*) Left side; (*b*) posterior view; (*c*) medial view of left side with pieces removed; (*d*) upper view of central region; (*e*) left ventrolateral view of portion of skull roof detached in (*c*); (*f*), (*h*) left lateral and ventral views of parts of nasals and frontals; (*g*), (*i*) cross sections at anterior and posterior ends of same fragment. Magn. ×1.

as much as 5 mm below its original position. On the inner side a thickening along the suture with the prefrontal forms an inner buttress which dies out ventrally.

The *prefrontal* (figures 5 and 6) is of complex form. The main body of the bone is a thick mass forming the overhanging upper anterior rim of the orbit and is slightly roughened externally. Here it is firmly sutured to the frontal which it partly underlies. Passing forwards on the skull roof the medial part of the prefrontal emerges from below the frontal (which has been pushed over it on the right side) and develops an edge-to-edge contact with the latter; this part of the suture is mostly concealed by the nasal. The prefrontal and frontal then gradually part company, apparently coming to lie on either side of the declining posterior end of the ventral flange of the nasal.

The prefrontal expands to form a smooth sheet within the anterodorsal part of the orbit and gives off three processes, one of which runs down the inner buttress of the lachrymal and tapers out well above the palate. The second process extends inwards, backwards and downwards and evidently met the cartilaginous interorbital septum. In the fossil the two opposing processes are slightly crushed against each other (figure 5*b*). Their medial edges were originally about 10 mm long and approximately vertical, ending some 8 mm above the median dorsal ridge of the pterygoids, well behind the palatine 'fans'. The third process, complete on the left side, extends upwards, inwards and

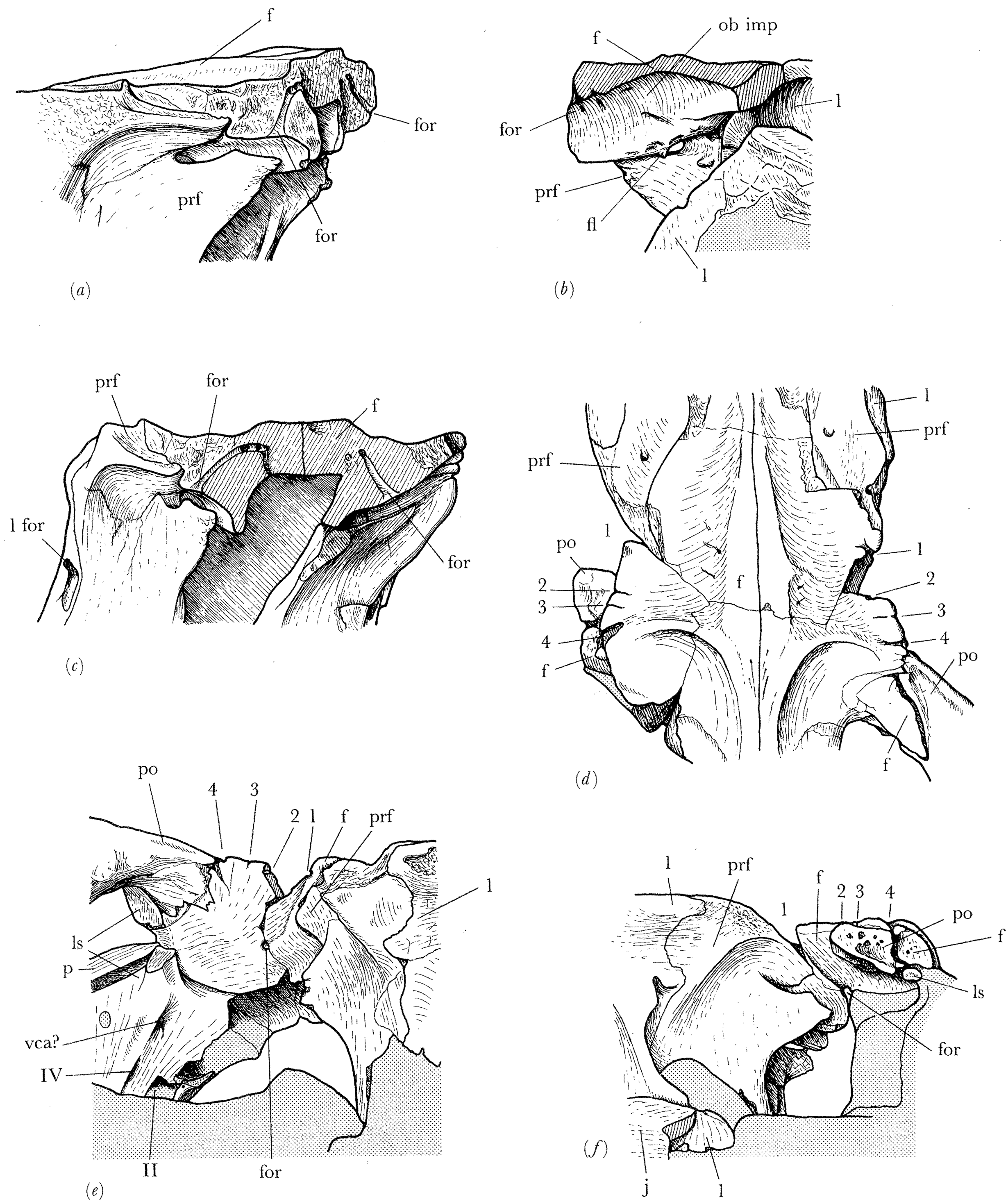

Figure 6. *Sphenosuchus acutus* Htn. (*a*) Rear part of 'prefrontals piece' in left posterolateral view; (*b*) medial view of same with pieces removed; (*c*) posterior view of same; (*d*) upper view of central part of skull roof; (*e*) ventrolateral view of right orbit; (*f*) same of left orbit. (*a*), (*b*), (*c*): Magn. ×2; (*d*), (*e*), (*f*): magn. ×1.5.

backwards. At present its pointed distal end lies *ca.* 1 mm lateral to and alongside the crista cranii frontalis, but it has evidently been affected by the sideways tilt of the skull and its probable original position was immediately below and perhaps slightly lateral to, but not touching, the crista. The upper edge of this process is slightly thickened and gently grooved longitudinally. A small flange arising from the outer border of the groove divides the process into two unequal sections. The larger anterior one forms the lower border of a deep elliptical notch in the prefrontal (figure 6*a*, *b*).

On the inner surface of the skull, that is at the posterior end of the nasal cavity, the lachrymal and prefrontal form a deep dorsolateral cavity whose external expression is the preorbital bulging of these bones. The suture between them follows fairly closely the line seen externally but is a little more anterior. The lachrymal takes up slightly less than half of this cavity, the deeper part being bounded in front by the curving ridge made by the lachrymal canal. A broad, shallow depression flanked by low ridges runs downwards from the front of the cavity into the posterodorsal corner of the antorbital fenestra. The posterior wall of the cavity is marked off from the flattish triangular inner surface of the prefrontal by a sharp angulation running downwards and backwards.

The *frontals* (figures 5, 6 and 9) are thick bones. On their upper surfaces a cruciform pattern of ridges is made up of a strong median ridge which tapers and dies out forwards and is continued backwards into the sagittal crest between the supratemporal fossae, and a pair of narrow ridges which are given off from the median ridge and curve round laterally, separating the recessed areas of the fossae from a pair of shallow, longitudinal depressions lying between the orbits. Posteriorly the frontals meet the parietals at a strongly interdigitating suture on the median crest, and run back beneath them on its flanks. The parietal extends forwards below the frontal in the roof of the cranial cavity, so that the frontal in effect sends a tongue deeply into the parietal on either side of the mid-line. The bone enters the anterior border of the supratemporal fenestra, lying here above the laterosphenoid. The latter sends a very long and narrow tongue laterally in a shallow recess below the posterior border of the frontal (figure 6*e*), ending in a shallow socket in the medial side of the postorbital. The left postorbital has been pushed strongly forwards, bent at right angles and broken and part was not collected, whereas the right postorbital has been pulled backwards, deflecting the posterolateral process of the frontal. The anterior part of the suture between them is indented by shear-fractures. The posterolateral process rests in a socket in the upper surface of the postorbital. On the lower surface the contact is not easy to follow because of compression and shearing (figure 6*e*), but there was evidently deep interlocking of the bones.

The lower surface of the frontal is deeply channelled for the olfactory tracts. Between the orbits the sides of the channel are bounded by deep crista cranii frontales. The outer surfaces of these are concave, sweeping upwards and outwards to the rims of the frontals and forming the upper walls of the orbits. Posteromedially the cristae meet the laterosphenoids at sutures trending inwards, forwards and downwards and, with the lateral expansions of the frontals, form broad areas of bone at the posterodorsal corners of the orbits.

A moderate-sized foramen enters the upper part of the orbit, a little below halfway up the crista, and above the posterodorsal process of the prefrontal. These foramina continue as arching canals within the bone (figure 6*a–c*), each dividing at the highest point into several smaller canals which emerge as a group of small foramina (five on the less-distorted left side) in the dorsolateral angles of the olfactory tract channel, directly behind the cavities which housed the olfactory bulbs. The external foramen lies at the base of an ill-defined fan-shaped impression which converges downwards towards it from the orbital rim. The clearest part of this system takes the form of a shallow groove which runs down and back within the upper wall of the orbit, immediately behind the prefrontal suture, starting from a canal which pierces the orbital rim ('1' in figure 6*e*) and ending at the foramen. The groove is present on both frontals. The canal running through the orbital rim is seen on the right side to be the first of a series of such foramina or notches, four or five in number (figure 6*d*). Unfortunately a fragment of the orbital rim is missing but on each of the broken surfaces a canal is exposed passing outwards and downwards through the orbital rim, from the outer part of the depression on the upper surface. The more anterior of these two canals is very clearly marked. Further back are two narrow clefts, one of which is certainly a foramen; the more posterior appears to have been an open notch. Both have been squeezed by the distortion. The spacing of the three posterior members suggests that there was a fifth canal in the missing section of the rim, but the situation on the left side implies that there may only have been four. The left frontal has suffered even more severely and the upper wall of the orbit is partly obscured by the postorbital (figure 6*d,f*). A small piece is missing at the critical region just behind the prefrontal and there is no certain indication of the most anterior canal on this side, although the groove within the orbit testifies to its former existence. However, two of the more posterior canals or notches are present, but have been squeezed tightly shut. The most posterior canal was probably located at the point where there is a nick in the frontal margin; on both frontals a very shallow groove leads out and back to this point. A slight notch just behind the missing section may indicate a fifth canal, but seems rather close to the position of the first canal. However, the number and spacing of the canals may not have been symmetrical.

The olfactory tract channel broadens out between the posterior parts of the prefrontals and the position of the olfactory bulbs is indicated by a pair of elongated depressions in the undersurfaces of the frontals, separated by a well-marked median ridge (figure 5*e*). These concavities die out below the posterior ends of the nasals, merging into a pair of shallow longitudinal depressions which in turn run forwards on the undersides of the nasals. The lower edge of the crista is marked by a shallow groove which passes obliquely forwards and inwards opposite the posterodorsal process of the prefrontal. Some 3 mm in front of the small ascending flange from the upper edge of the latter, a rather similar small flange (now bent laterally) is given off ventrolaterally from the outer side of the lower edge of the crista (figure 6*b*). This is preserved only on the left side; at the same point on the opposite side there is a small additional ventral projection, this time from the inner side of the lower edge of the crista, a region which is imperfect on the left side. Thus there were originally a pair of these small processes on each side. In front of them the crista declines rapidly and is replaced by a sharp ridge which borders the anterior half of the olfactory bulb impression. Outside this ridge the frontal is bevelled off to form the inner part of the deep cavity in the prefrontal (figure 5*e,h*).

There is no indication of a mid-line suture between the *parietals* (figures 17, 19, 21 and 30), doubtless because they have a well-formed sagittal crest. The combined bones form a T-shaped unit, with pronounced transverse crests separating the supratemporal fossae from the occipital surface. The bone overlies the laterosphenoid in front and the prootic farther back at a broad, straight horizontal contact which is irregular in detail. The lower leaf of the parietal suture, below the frontal, overlaps the base of the lateral process of the laterosphenoid. The sides of the central part are concave on either side of the sagittal crest, becoming convex lower down, swelling out to a maximum breadth along the lower suture. Posterolaterally the parietal meets and partly overlies the squamosal on the lateral arm of the 'T', contributing more than half to the undulating transverse crest and including the culmination on this crest. On the occipital surface the suture with the squamosal enters the upper border of the post-temporal fenestra. A shallow concave area lateral to this fenestra also extends on to the parietal. Medial to this the surface is convex, forming a broad ridge running ventromedially to die out at the epiotic and including the dorsolateral border of the supraoccipital. Lateral to the upper end of the ridge there is a deep tendon-pit below the transverse crest. The summit of the supraoccipital fits into a smooth median recess in the parietal. Lower down the occipital surface the inner corner of the parietal rests on the epiotic; a small venous foramen enters between the two bones, adjacent to the supraoccipital, and passes upwards and forwards, grooving the upper surface of the epiotic. The parietal approaches the opisthotic closely at the inner angle of the post-temporal fenestra, but probably did not touch it in the undistorted skull, resting instead on the intervening cartilage.

The parietal is exposed posteromedially in the roof and inner wall of the large passage (here called the *temporal canal*) which connects the supra-temporal fossa with the post-temporal fenestra. Here its strongly convex lower surface rests in the crescentic area (referred to below) which is probably part of the epiotic, and wedges out forwards between squamosal and prootic halfway along the canal. A small foramen passes inwards and forwards at the contact with the crescentic area. This foramen is paralleled by a larger one, apparently undescribed, in the modern crocodilian skull which enters between parietal and anterior end of supraoccipital (or epiotic) at the anterior end of the temporal canal. It probably permits the entry of the vena capitis dorsalis into the cranial cavity, as does a similar foramen in lizards (Bruner 1907) and *Sphenodon* (O'Donoghue 1920).

The *postorbital* (figures 6, 7 and 9) arches dorsally, overlying the squamosal. The upper surface is concave in the anterior half, adjoining the thickened lateral rim. The bone is deeply excavated posteriorly at the junction with the squamosal, forming a pocket at the anterodorsal end of the lateral temporal fossa, a continuation of the deep channel below the overhang of the squamosal. On the medial side the anterior end of the squamosal bifurcates in the vertical plane. The postorbital evidently sent back a short process between the two points, now broken off, and thus came very close to the anterior point of the quadratojugal, but probably just failed to touch it. I have previously indicated a suture across the posterior ramus of the bone (Walker 1972), because of the virtually symmetrical lines of division on each side. However, I am now convinced that these are merely fractures; their positions would also be very unusual for postfrontal/postorbital sutures.

The contact surfaces between the descending process of the postorbital and the ascending process of the jugal are well exposed on both sides of the skull, and the bones on the right side are removable (figures 8 and 9). Tension cracks indicate that both jugals have been pushed over to the right and bent forwards slightly, but the identity of the outlines and the articular surfaces of the two bones indicates that this distortion has been quite small. The main articular surface on the jugal is a narrow, smooth strip, slightly concave longitudinally, which faces anteriorly and a little laterally. The surface on the postorbital conforms to that on the jugal. Movement between the two bones in a shallow, subvertical arc is possible as they are preserved, and may have taken place in the juvenile. There is also a lateral overlap area for the postorbital at the upper point of the jugal, which curves round medially above and merges into the anterior area. The small flange from the postorbital which fits into this recess continues upwards as the rather sharp posterior edge of the bone, bounding the pocket described above. The descending process is somewhat rugose externally at its upper end. Internally, below the posterolateral process of the frontal, lies a shallow depression (figure 7*h*) which received the tip of the laterosphenoid. Below this the medial edge is strongly rugose, the individual ridges projecting downwards and backwards, and proceeding from the lower end of a smooth recess in the upper posterior corner of the orbit (figure 9*c*), evidently for muscular or ligmentous origin. The rugosities extend round on to the inner surface of the postorbital and up to the tip of the laterosphenoid.

The *squamosal* (figures 7, 13, 15, 19 and 21) is almost excluded from the lateral temporal fenestra by the quadratojugal. On the upper surface it continues the transverse crest of the parietal, which curves round the corner of the fossa and dies out forwards on reaching the postorbital. There is a deep muscle recess in front of this ridge, below which the inner surface curves convexly down into the fenestra proper, forming a short, vertical inner wall adjacent to the quadrate and quadratojugal. Laterally the squamosal overhangs strongly forming, with the postorbital, the roof of a spacious cavity at the upper end of the infratemporal fossa, which is continuous round behind the quadrate. There is a rugose ledge on the lateral border of this overhang. Passing backwards the squamosal twists so that the surface which faced dorsolaterally changes to face ventrolaterally. The rounded posteroventral tip thins out to a feather-edge and is closely applied to the radially striated anterior face of the distal end of the paroccipital process, covering its upper two thirds. The details are well seen on the 'right paroccipital piece' which preserves the impression of the squamosal (figure 15). These pieces of the right side of the skull give a rather different idea of the appearance of this region from that previously available from the left side alone.

On the occipital surface the squamosal enters the outer corner of the post-temporal fenestra and contributes the major share to the shallow depression

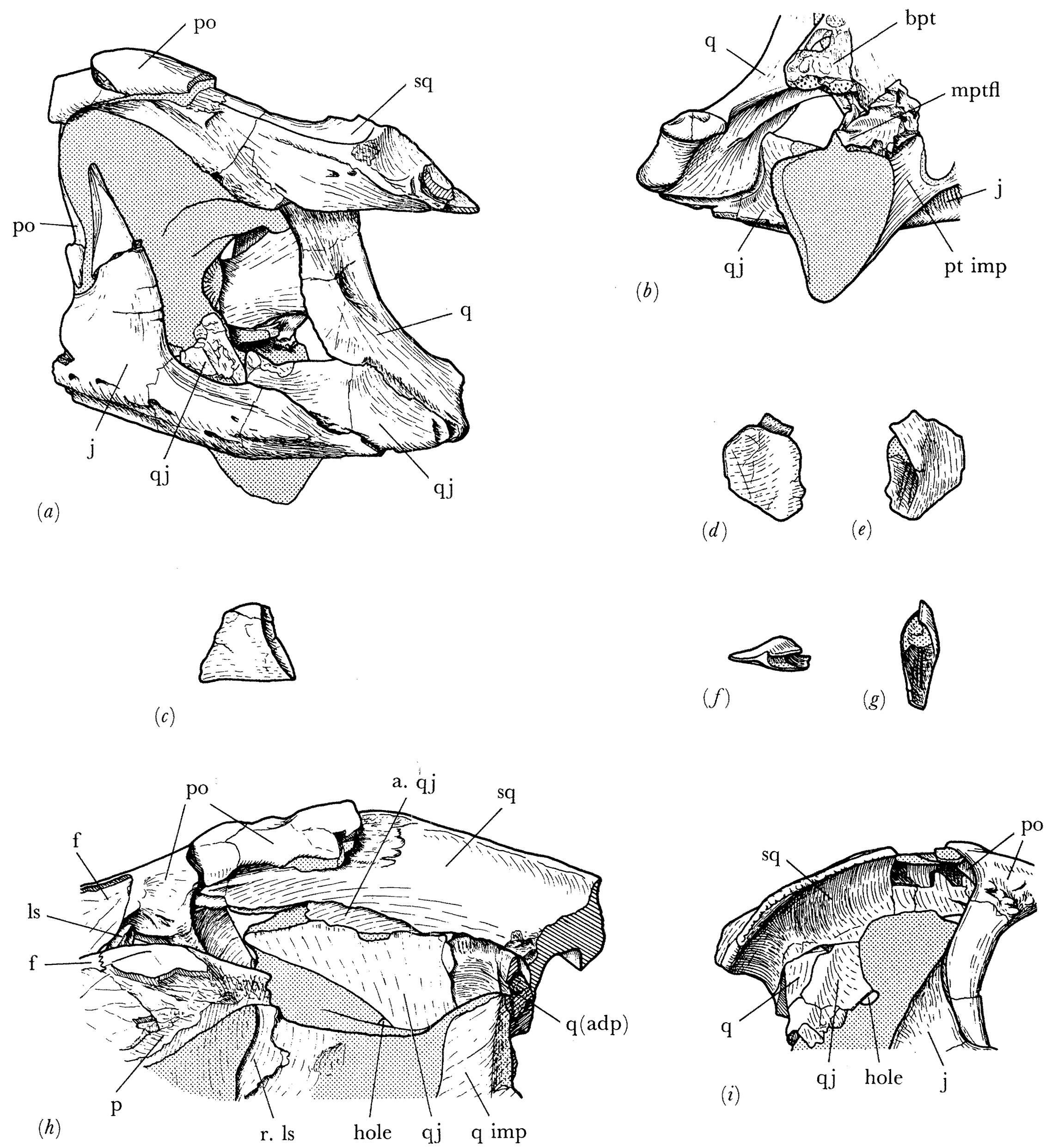

Figure 7. *Sphenosuchus acutus* Htn. (*a*) The left infratemporal fenestra and structures seen through it; (*b*) ventromedial view of left quadrate/quadratojugal joint; (*c*) lateral view of piece from middle of left quadratojugal; (*d*)–(*g*) lateral, medial, upper and posterior views of fragment of top end of same bone. The inner margin of the socket for the anterodorsal process of the quadrate has been bent laterally. (*h*) medial view of upper end of right infratemporal fenestra and surrounding bones; (*i*) lateral and slightly ventral view of same. (*a*), (*b*), (*i*): Magn. × 1; (*c*)–(*g*): magn. × 2; (*h*): magn. × 1.5.

already mentioned. Lateral to the fenestra the bone overlies the paroccipital process, which is thus clasped between a process behind and the one in front already described, and its dorsally expanded outer end rests in a shallow depression in the occipital surface of the squamosal. Both bones are notched to form an interlocking joint at the middle of the **S**-bend in the occipital suture between them, and articulate with each other at a pair of small projections. The whole arrangement is typically crocodilian.

At the posterior end of the supratemporal fenestra the squamosal forms the upper and lateral borders of the entrance to the temporal canal, the medial and lower borders being formed by the prootic. This aperture, which it is convenient to call the *anterior temporal foramen* (figure 61) reduced in size on both sides of the skull, was originally elliptical, measuring *ca.* 7 mm wide × 5 mm high. The squamosal extends forwards on its medial side as a tapering process with a blunt tip, wedged between parietal and prootic, and also forms the greater part of the roof of the temporal canal itself. In the medial wall of the canal it rests on the prootic anteriorly and farther back on the parietal, the suture with the latter running posterolaterally across the roof to emerge in the middle of the upper border of the post-temporal fenestra. The ventrolateral wall of the canal is pierced by a large elliptical foramen (figure 21), originally *ca.* 5 mm wide × 3 mm high, leading outwards and downwards behind the head of the quadrate into the tympanic cavity. This foramen, which is more deeply notched into the prootic below than into the squamosal above, is here called the *postquadrate foramen* (Walker 1972, fig. 1b: 'postquadrate canal'). At the rear of this foramen on the left side the squamosal briefly contacts the prootic. It is doubtful, however, whether this contact would have existed prior to the distortion, and there was probably a slight gap in the original skull.

In front of the postquadrate foramen the squamosal meets the prootic at a firm interlocking joint with only a small amount of overlap (figures 15*c* and 21). On the outer side of this region, and separated from the temporal canal only by the short squamosal/prootic contact, lies the articular area for the head of the quadrate. This consists largely of a laterally compressed cup in the undersurface of the squamosal, the prootic coming in lower down on the medial side, towards the anterior end. The lateral surface is more or less vertical, whereas the medial side curves at first inwards and then downwards. Both surfaces are strongly grooved, the grooves on the medial side curving backwards towards the summit of the cavity. They appear to have been supplied from a vessel within a canal which crosses the posterodorsal corner of the articular cup, and their presence suggests a well-vascularized cartilaginous lining to the articular socket.

At the anterior end of the socket the left squamosal sends an apophysis downwards which, on the 'supraoccipital piece', slightly penetrates the anterior surface of the quadrate head (figures 12 and 13). The existence of this contact led to the statement (Walker 1972) that 'over a small area (the quadrate head) is fused to the squamosal'. However, the top of the quadrate has been pushed forwards relative to the squamosal, and elsewhere the head of the bone is about 1 mm clear of the articular cup. Also, later preparation revealed the existence of a slot running transversely across the top of the quadrate immediately in front of the head. There is little doubt that the apophysis of the squamosal originally fitted into this slot, and that the pushing-over of the quadrate to the right has lifted it out of its socket; subsequently (or almost simultaneously) strong pressure forced the apophysis into the cartilage-covered head of the quadrate. On the right side a piece of the squamosal is missing at the critical region; however, the bottom of the slot on the quadrate head (figure 15*c*) and a tiny fragment of the lateral extremity of the apophysis are preserved. On this side a different part of the squamosal (the outer corner of the anterior temporal foramen) has been forced into the prootic articular area on the quadrate head.

The outer side of the anterodorsal process of the quadrate is slightly recessed along an irregular line to take a short (2 or 3 mm deep) descending flange from the squamosal (figure 12*a*); the slot in the top of the quadrate is in fact a medial extension of this recessed area at a higher level, and the apophysis is a medial extension of the descending flange. The articular surfaces are vertically fluted and evidently prohibited movement of the quadrate relative to the squamosal.

The descending flange of the squamosal does not correspond to the usual descending process which meets the quadratojugal in archosaurian skulls, but rather to a flange of the squamosal in the modern crocodilian skull which sutures to the outside of the anterodorsal process of the quadrate in similar fashion to that of *Sphenosuchus*. The descending process has been lost in *Sphenosuchus* owing to the long upward extension of the quadratojugal.

The recess for the head of the quadrate is open behind and in fact the lateral (squamosal) wall encloses only its anterior half (figure 13*a*, *b*). The lower edge of the squamosal is grooved ventrally in front of the quadrate head and divided into two sections which receive the quadrate and quadratojugal, respectively. The shorter posterior section is relatively wide, with a low medial wall at its posterior end, but broadens and deepens at its anterior end to produce an elongated socket (6 mm × 2.5 mm) to take the anterodorsal process of the quadrate. The surface is smooth but irregular and is supplied with numerous small foramina (figure 13*c*); it was doubtless cartilage-lined. The anterior section of the groove is a narrow slot with thin walls. The outer of these is the deeper and its lower edge is slightly convex downwards. The slot deepens at its middle, conforming to the gently arched top of the quadratojugal (figure 7*h*). The outer wall is a direct continuation of the descending flange mentioned above (figure 7*i*).

The *jugal* (figures 5, 7–9 and 11) is a strong bone, concavo-convex over most of its length, lying at its anterior end mainly lateral to the maxilla ventrally and against the base of the lachrymal dorsally. There is an anterior extension into the base of the antorbital fenestra which tapers to a point, medial to the maxilla, lying in the angle at the base of the low wall formed by the latter bone. Behind this process the margin runs downwards and backwards at about 45° and has a narrow ledge which receives the lower limb of the maxillary 'fish-tail'. Behind it the jugal rises in a 'step' which runs down and back in a gentle curve. The articular area for the postorbital has already been described. The posterior edge of the ascending process is roughened and striated for ligamentous attachment (figures 8*c* and 9*a*, *e*); these markings extend round on to the lateral surface (some superficial bone has been lost from the left jugal).

The posterior end is preserved only on the left side, where it has been bent upwards by the forward movement of the top of the quadrate. Curiously, in spite of this, and the apparently weak joint with the quadratojugal, very little displacement between the two bones has taken place. The close similarity of the jugal–quadratojugal relations to those seen in modern crocodiles, particularly the fact that the anterior edge of the quadratojugal rises vertically medial to a short upward process of the jugal, leaves little room to doubt this. The external angulation of the bone is more marked posteriorly and there is a long, tapering overlap on the quadratojugal, part of which is preserved as an impression on the 'left jaw counterpart piece'. The lower half of this portion bears strong longitudinal striations which die out towards the posterior point.

The right jugal is detachable and, owing to the

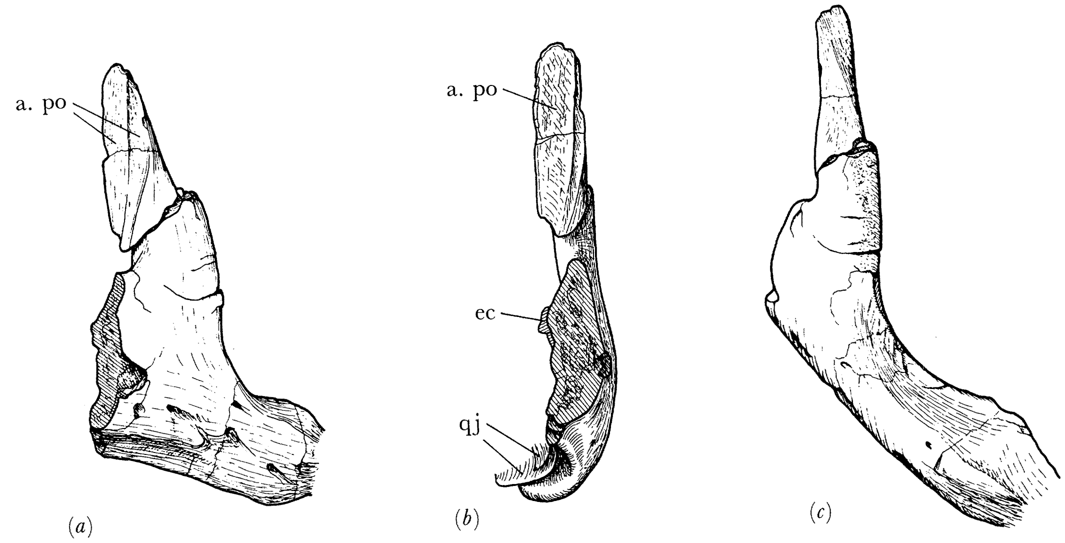

Figure 8. *Sphenosuchus acutus* Htn. (*a*) Anterolateral, (*b*) anterior and (*c*) posterodorsal views of rear part of left jugal, to show postorbital contacts, magn. × 1.5.

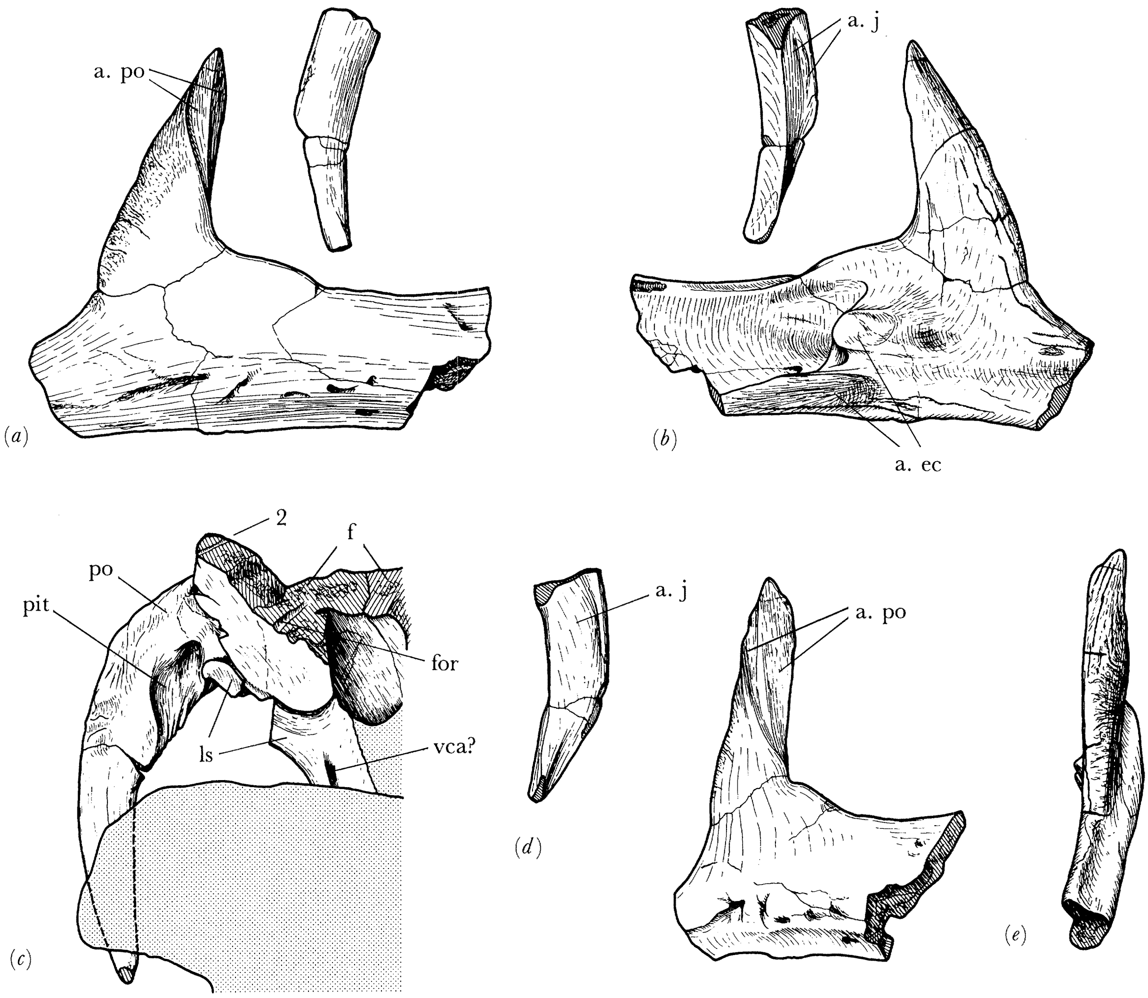

Figure 9. *Sphenosuchus acutus* Htn. (*a*) Lateral view of right jugal and lower end of postorbital; (*b*) medial view of same; (*c*) anterior view of right postorbital, frontal and upper end of laterosphenoid; (*d*) anterolateral view of right jugal, posteromedial view of lower end of postorbital; (*e*) posterodorsal view of right jugal, magn. × 1.5.

presence of a thin intervening film of matrix, it was also possible to remove the outer half of the right ectopterygoid from the jugal. The anterior part of the bone has a channel along its floor, a continuation of that on the maxilla. The low inner wall rises up behind, bordering a blindly ending posterior pocket, on the medial side of which is set the upper facet for the ectopterygoid (figure 9*b*). The articulation is divided into two areas by a horizontal canal. Just behind its anterior entrance a branch canal leads backwards and outwards into the jugal. The upper facet is nearly circular, smooth, very lightly convex in its anterior half and similarly concave posteriorly. The lower facet is of about the same depth but considerably longer, slightly concave dorsoventrally and faintly striated longitudinally, the striations rising a little posteriorly.

The lower part of the *quadratojugal* (figures 7 and 13) is seen in place on the left side, and the upper part on the right. Although the middle region is not *in situ*, there can be no doubt that the bone extended as a thin sheet all the way up the anterior edge of the quadrate. Some thin pieces of bone lying within the anteroventral corner of the left lateral temporal fenestra, extending across the jugal–quadratojugal contact on the inner side, and another piece which was found immediately in front of the left jaw articulation, clearly represent the middle and upper portions of the left quadratojugal. In addition, a fragment found within the posterior side of the left orbit proved to be from the upper end of the same bone. Comparison with the right side shows that it is undoubtedly the portion which bears the socket for the anterodorsal corner of the quadrate.

The thin, pointed upper end of the bone is slightly dislocated from the narrow slot on the squamosal which received it (figure 7*h*, *i*). Its upper border arches gently dorsally and is finely striated vertically on both sides (matrix has been left on the outer side to strengthen the bone). The thickened anterodorsal corner of the quadrate fits into a socket in the expanded rear edge of this section, a continuation of the cavity below the squamosal (figure 7*d*–*h*). This socket is 2.5 mm deep, has a short inner lip and a longer outer one and is longitudinally striated. On the right side the quadratojugal has been pulled backwards below relative to the quadrate and partly fragmented (figure 7*i*). For a short distance below the socket the left quadrate shows only a lateral overlap area for the quadratojugal; the quadrate has a sharp anterior edge in this region. There is then a transition zone in which the quadrate has a more rounded anterior edge, presumably fitting into a shallow groove in the quadratojugal, to a thinner region which is convex forwards in profile. The small fragment found within the left jaw angle (figure 7*c*) agrees perfectly in cross-section with the broken upper edge of the left quadratojugal preserved *in situ* and there is little doubt, from its shape, that it came from the angle between this part of the bone and the quadrate. This piece is 6 mm high, but was originally 3 or 4 mm taller, part being removed before its size was appreciated. The posterior border of the fragment is thickened and bevelled externally at 45° along a gentle curve.

At about one third the height of the quadrate the margin of the quadratojugal thickens to form a slightly concave socket which faces upwards, outwards and a little backwards, and which receives a similarly thickened and somewhat laterally projecting convexity on the anterior border of the quadrate (figures 7*a* and 13*d*). The bulge which this feature makes is visible in posterior view, and is partly preserved on the right quadrate also. This retraction stop (Walker 1972, 1974) is in fact the ventral continuation of the curved bevel described above, into which fitted the projecting curve of the quadrate. Below the stop the quadratojugal curves a little medially, thinning out over a dorsoventrally striated area on the quadrate. The anterior termination of the quadrate is thickened and curved in a quarter-circle, fitting behind a raised rim on the inner surface of the quadratojugal (figure 7*b*). The smooth edge of the quadrate here is composed of grey, minutely porous bone, indicating that it was coated with cartilage. The lower end of the quadratojugal extends well forwards and thins out medial to the jugal, rising as it does so; it is angulated to conform to the contours of the latter. The anterior border curves back a little at first as it ascends, then rises vertically from behind an upward projection of the jugal.

The foramen normally found between quadrate and quadratojugal is absent, but in comparison with the thecodontian *Stagonolepis* (Walker 1961) its former position can be seen to have been at the embayment immediately behind the stop (figure 13*d*).

Palatal complex (*restorations*: *figures 3 and 18*)

The premaxillae and maxillae have been described above. The medially inclined contact surfaces on the posterior processes of the maxillae, and the upward and backward curvature of these processes, suggest that, as in modern crocodiles, the *vomers* (figure 10) were situated on the whole a little above the level of the secondary palate. This high position agrees with their location on the 'prefrontals piece', where they are at the highest part of the palatal vault. Preservation of the bone itself begins about halfway along the choanae. Here the vomers are separated by the pterygoids which are tapering and evidently did not extend more than a few millimetres further forwards. The left vomer broadens rapidly towards its contact with the palatine but this effect has been exaggerated by squeezing of the anterior part. It is clear that the median dorsal trough formed by the pterygoids was continued forwards by the vomers. The posterior parts of the vomers, together with the palatines, curve down laterally to form shallow channels on either side of the median pterygoid 'bar' (which is actually hollow). The bones taper out as thin concavo-convex processes in the angles between the 'bar' and the upward-sloping palatines. The arrangement is similar to that seen in *Stagonolepis* (Walker 1961). On the dorsal surface the palatine sends forward an acutely pointed process which fits into a recess in the vomer; the junction appears to be very firm.

The part of the *palatine* (figures 4, 5 and 10) applied to the maxilla is thick, particularly at the rear end of the choana, where it merges medially into the spout-

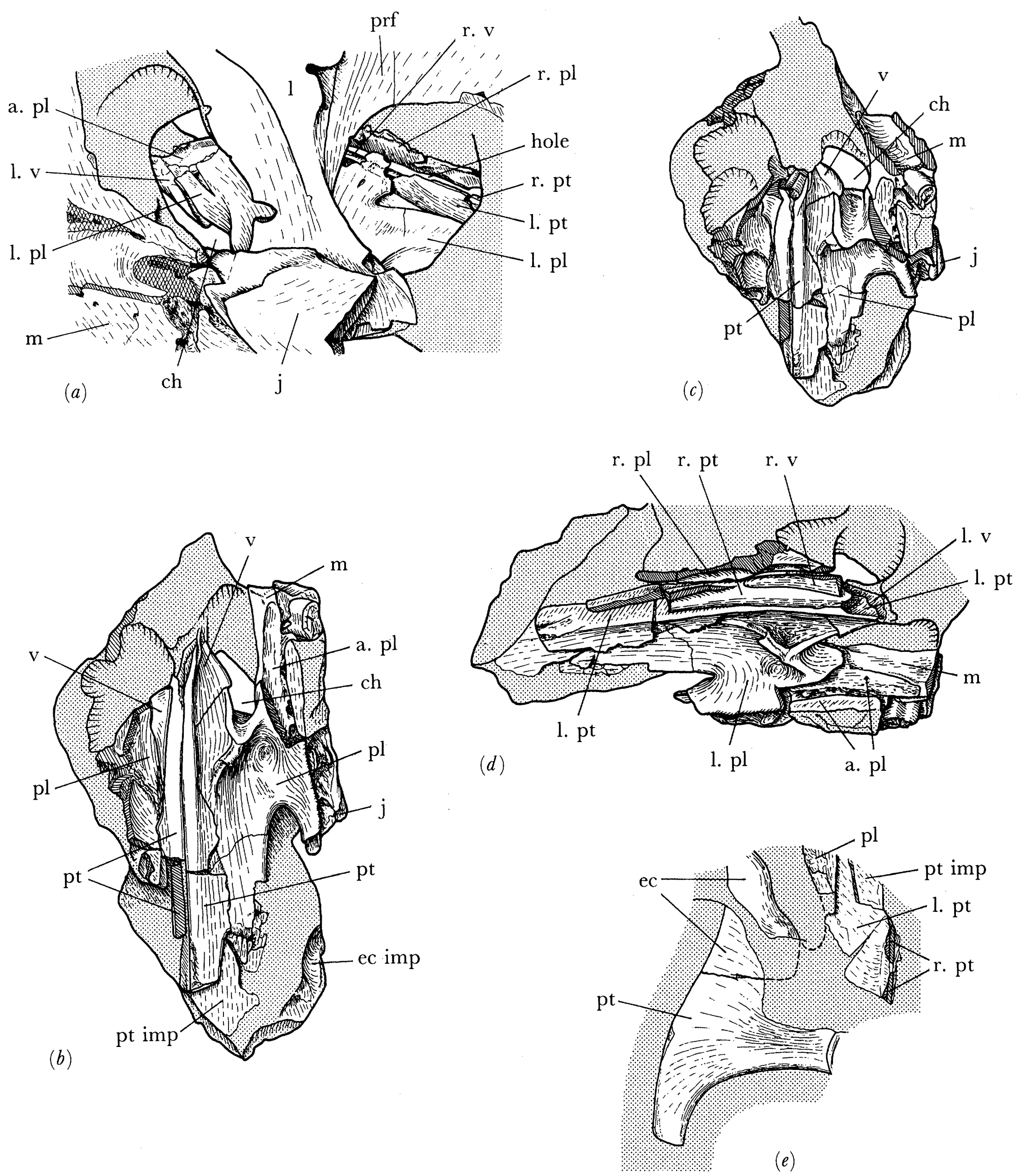

Figure 10. *Sphenosuchus acutus* Htn. (*a*) Part of upper surface of palate and left choana seen through left antorbital fenestra and orbit; (*b*) central part of palate in ventral view; (*c*) anteroventral view of same piece showing 'spout' on palatine; (*d*) oblique ventral view of same piece from right side; (*e*) cast giving upper surface of left side of rear part of palate. All magn. × 1 except (*a*) which is magn. × 1.5.

like projection which carries the choana downwards. The 'spout' is a high overhanging ridge of bone running round the rear end of the choana, forming a channel which curves towards the horizontal posteriorly. From its apex a sinuous ridge runs back with a lateral overhang, merging at its rear end into a shelf along the medial border of the bone. This shelf received a narrow lateral flange from the anterior process of the pterygoid. The lower surface is concave behind the ridge-system, continuing the concavity of the anterior part of the pterygoid. Laterally the edge is thick and rounded. There is a marked pit posterolateral to the choana. The rear end of the bone is damaged and incomplete; presumably it tapered out alongside the pterygoid.

The medial portions of the palatines overlap the pterygoids and vomers, curving up towards the midline, especially in the areas between the ventral ridge-systems. There has been some accentuation by *post mortem* compression, but the resemblance to *Stagonolepis* is very close and confirms that the present disposition of these bones is largely original. The spout-like rear end of the choana and its supporting ridge project down well below the level of the pterygoid bar.

The upper surface of the palate has been exposed over a considerable area (figures 5*a* and 10*a*). The medial part of the palatine is divided into two regions by a deep notch in the inner margin. In front of this notch the palatine expands fanwise medially over the pterygoid and vomer. The thin medial edges are now

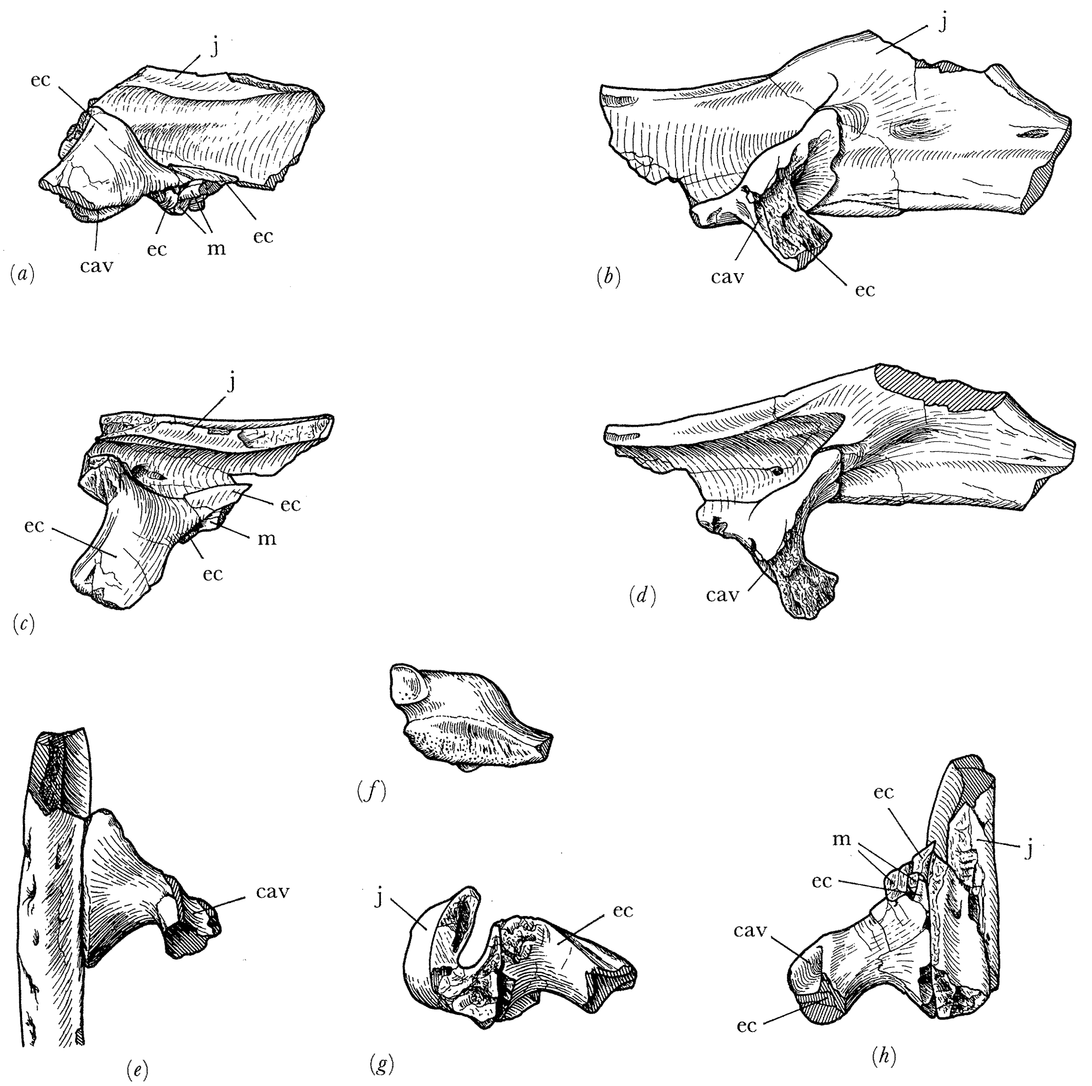

Figure 11. *Sphenosuchus acutus* Htn. (*a*), (*c*), (*g*), (*h*) Medial, dorsal, posterior and ventral views of part of left jugal and ectopterygoid; (*b*), (*d*), (*e*) medial, dorsomedial and ventral views of part of right jugal and ectopterygoid; (*f*) lateral view of right ectopterygoid to show articular facets. Magn. × 1.5.

almost in contact and a little crumpled; originally they no doubt contacted the sides of a cartilaginous expansion of the base of the interorbital septum. Behind the notch the inner margin curves at first medially and then swings laterally to a presumed posterior point.

The posterior rim of the choana is considerably elevated on the upper surface also, but terminates abruptly laterally, leaving a narrow channel leading backwards on to the upper surface of the maxilla, within the lower rim of the preorbital fenestra. The palatine broadens rapidly backwards on the inner side of the lachrymal pillar, and has a pronounced posterolateral corner which has been bent sharply upwards against the lachrymal on the left side. There was evidently some overlap of the maxilla by this process, the extent of which is difficult to assess. The arrangement was evidently similar to that seen in *Stagonolepis* (Walker 1961, fig. 3b), and there is no reason to think that the palatine originally contacted the lachrymal, because of the distortion, and the crushing of the alveoli in this region. A curving ridge on the upper surface projects backwards as a thin edge and encloses laterally a rather deep pocket between itself and the underlying thickened anterior border of the postpalatine fenestra. The structure of this region is, again, strongly reminiscent of that of *Stagonolepis*, but the cavity is more pronounced.

The anterior half of each *ectopterygoid* (figures 10 and 11) is present, but the posterior portion is preserved only as an impression of the upper surface, continuous with that of the left pterygoid on the 'left quadrate piece'. The existence of a fairly large medial pterygoid flange, coupled with the apparent absence of a suture on this impression, led to the statement that the ectopterygoid is a large element (Walker 1968). However, cleaning and casting the impression later revealed traces of a suture in the normal position. The bone is strongly arched dorsally from its expanded distal contact with the jugal and then expands again downwards and backwards. The outer end is deep posteriorly but its upper border drops rapidly forwards and the bone ends in a pointed anterior process which tapers out along the inturned lower border of the jugal with no sign of a maxillary contact. The articular facets are nearly complete on the right side. The posterior edge forms almost a semicircle, interrupted by the horizontal canal between the two articular areas. The upper facet is nearly smooth, very slightly concave anteriorly, with a narrow rim. The lower facet appears to have had a coating of secondary cartilage. It shows a thin, superficial smooth layer, which has many small pores and also numerous irregular sub-vertical grooves which seem to originate from the canal above. Each ectopterygoid contains a smooth-walled cavity, which can be seen to enter anteroventrally at the broken end of the bone on the left side (figure 11*h*). The cavity ends blindly laterally at the summit of the arch, but its medial extent is unknown. The suture with the pterygoid crosses the lateral pterygoid flange in the normal position (figure 10*e*) and is then presumed to have turned forwards to enter the postpalatine vacuity.

The *pterygoids* (figures 10, 13, 14, 17 and 25–27) are complex in form. At present they are in contact in the mid-line from shortly in front of the basal articulation, but this is evidently due to compression because the medial surface of the right pterygoid is rounded in this region. The first original contact of the pterygoids appears to have been at a point opposite the rear ends of the palatines, at the posterior end of the 'prefrontals piece'. Here the flat medial surface of the bone is faintly striated in the lower half and forms a rather indistinct facet with a sharp ventral edge (figure 10*d*). There is a general resemblance to the form of the pterygoid in *Stagonolepis*, in which a sharper ventral edge is developed at the first contact of the pterygoids, though this occurs a little further back than it appears to have done in *Sphenosuchus*.

The palatal rami arch gently dorsally in the longitudinal direction, levelling off in the region between the ventral ridge-systems on the palatines. Laterally narrow flanges are given off which rest in the shelves along the palatines. Passing forwards the medial edges thicken ventrally to form a median ridge which continues forwards as a bar between the palatine ridges. This bar is rounded ventrally, thickens a little between the rear ends of the vomers, and then tapers forwards to its anterior end.

The median dorsal ridge formed by the inner margins of the bones rises gradually forwards; at the posterior end of the palatine 'fans' it thins and declines rapidly (figure 10*a*) between a pair of narrow grooves which have developed on either side of it. The latter are flanked by thin ridges which curve towards each other. Thus the pterygoids are transformed into a channel, open dorsally, which is roughly **U**-shaped in cross section with the median dorsal ridge persisting in a reduced form along its floor. This arrangement of ridges and grooves is, again, very similar to that of *Stagonolepis*. The paired grooves evidently articulated with a pair of ridges on the lower edge of a local expansion of the base of the cartilaginous interorbital septum. These ridges thickened forwards and merged to form an expanded and rounded lower surface which fitted into the channel between the pterygoids and vomers, and which was contacted dorsolaterally by the palatines.

The lateral or transverse flange of the pterygoid is preserved only as an impression of the upper surface on the left side (figures 10*e* and 17). This surface is gently concave transversely, with a rather thick lateral edge which sweeps back to a blunt termination. The posterior border is considerably embayed, the breadth of the bone being reduced to 10 mm at the 'neck', in front of the basal articulation. The right pterygoid is broken off just in front of the 'neck' and shows the smooth posterior end of a cavity within the bone (figure 26*d*). The rounded lower lip indicates an entrance situated ventrally, about 6 mm from the mid-line. A narrow groove which traverses the 'neck' of the pterygoid would have received the prolongation of the palatoquadrate cartilage, as in a young *Sphenodon* (Wettstein 1931, fig. 41a; cf. also *Stagonolepis* and *Ornithosuchus* (Walker 1961, 1964)).

Below the region of the basal articulation there is a large *medial pterygoid flange* (figures 25*a* and 27*c*). This is a flattened process, originally projecting postero-ventrolaterally and in effect constituting a triangular ventral extension of the quadrate wing, into which it merges posteriorly. The lower edge is horizontal; the posterior edge (better preserved on the left side, although twisted) is thin and some 11 mm tall.

The quadrate ramus of the pterygoid is a deep, vertical sheet of bone lying close to the pterygoid ramus of the quadrate although for the most part not originally in contact with it. The anterior margin is curved inward slightly; it rises as a straight edge from the region of the basal articulation to the level of the pituitary fossa (figure 17), overlapping but not touching the lower end of the prootic–basisphenoid flange and the side of the rostrum. This edge was inclined a little backwards. The anterodorsal parts of the pterygoids have been pressed towards each other into the sides of the rostrum (figure 25*a*, *b*). The anterior edge thickens downwards, lying close to the 'anterior pillar' of the basipterygoid process. It then curves medially and posteriorly below the base of the rostrum, round the anterior end of the basipterygoid process, and forms a short upward and backward projection on the inner side of the latter. I have called this projection the 'parabasal process' in *Ornithosuchus* (Walker 1964); the parabasal processes were not in contact in *Sphenosuchus*, however. The statement (Walker 1972) that the basal articulation is 'immovably fixed' was due to misunderstanding of the complex structure of the basipterygoid processes and their relation to the rostrum.

The *basal articulation* lies in a shallow cavity facing upwards, backwards and inwards, lateral to the parabasal process. A '**Y**'-shaped system of low ridges delimits the articular area and the medial pterygoid flange (figure 27*d*). The stem of the '**Y**' extends dorsally and posteriorly from the rear end of the parabasal process. It then divides, the anterior branch running more or less vertically and dying out, the posterior branch, with the stem, forming the upper boundary of the medial pterygoid flange. The basal articulation lay in front of the anterodorsal ridge of the '**Y**'. On the right side (figure 26*d*) part of the basipterygoid facet is still in contact with the lower part of this area, which has been displaced forwards and downwards. It appears to have been simply a flat surface, and is probably visible on the left side also,

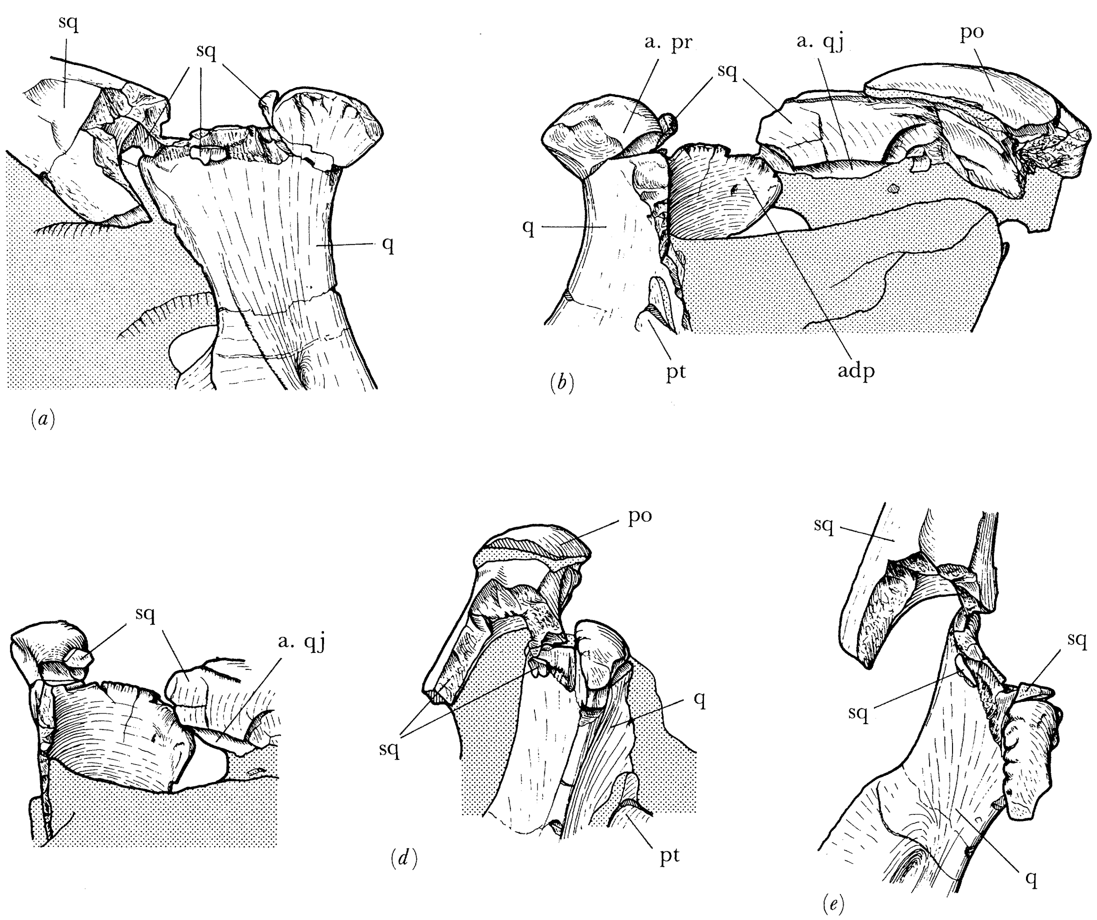

Figure 12. *Sphenosuchus acutus* Htn. Upper end of left quadrate in (*a*) lateral, (*b*) medial, (*c*) anterior, (*d*) posterior and (*e*) dorsal views, magn. × 1.5. Rear part of squamosal removed.

represented by the smooth area adjacent to the incomplete medial edge of the quadrate wing, immediately above the horizontal line of fracturing (figure 25*a*). A very faint ridge running upwards and backwards some 4 mm lateral to the edge probably marks the posterior limit of the articular area, as on the right side. By analogy with a lizard such as *Varanus*, it seems probable that the concavity above the parabasal process was filled in life with a pad of fibrous cartilage, which formed the actual articulation with the basipterygoid facet.

The 'Y'-ridge system is also seen on the left side where it is more pronounced due to crumpling. The pterygoid has been strongly buckled (figures 14*b* and 25*f*), so that the posterior branching ridge plunges into the axis of the fold and emerges again above it.

The main articulation between quadrate and pterygoid was by means of a convex, cartilage-covered surface on the inner side of the basal portion of the pterygoid wing of the quadrate, which fitted into a shallow socket on the outer surface of the quadrate ramus of the pterygoid, just above its lower edge (figures 14*b* and 25*f*). These two areas have been pushed past each other by some 7 or 8 mm on the left side. On the right side, the area where the articular cup might be expected to lie is some 6 mm below and in front of the convexity on the quadrate, but the pterygoid is incomplete here.

It has been possible to excavate between the two bones posteriorly on the left side to reveal about half of the concavity which received the bulge of the quadrate. It is a smooth, shallow, elongate-oval area, facing outwards and downwards. The cross section of the rear edge (figure 14*b*) shows that the upper boundary of the concavity is a laterally projecting lip sharply set off from the extremely thin bone above it. There was thus a gap between pterygoid and quadrate posteriorly, above the socket.

The posterior and posterodorsal edges of the quadrate wing of the pterygoid are not fully preserved, but it seems to have been rather short, rising to an acute apex. The relationship to the prootic–basisphenoid flange is uncertain in detail, but it seems that the posterodorsal corner lay close to the prootic flange below the trigeminal foramen. Restoration of quadrate and pterygoid to their presumed original positions indicates that a notch would have been visible in side view, behind the apex of the pterygoid.

The *quadrate* (figures 7, 12–17, 19, 23 and 25) is virtually complete on the left side and but little distorted, save that the head has been bent a little laterally and its backward curvature has been exaggerated. The right quadrate has been slewed round medially and compressed, accentuating the curvature of its upper end around the outer corner of the supratemporal fenestra. It is also broken by several shear-cracks.

The upper termination is divided into two sections.

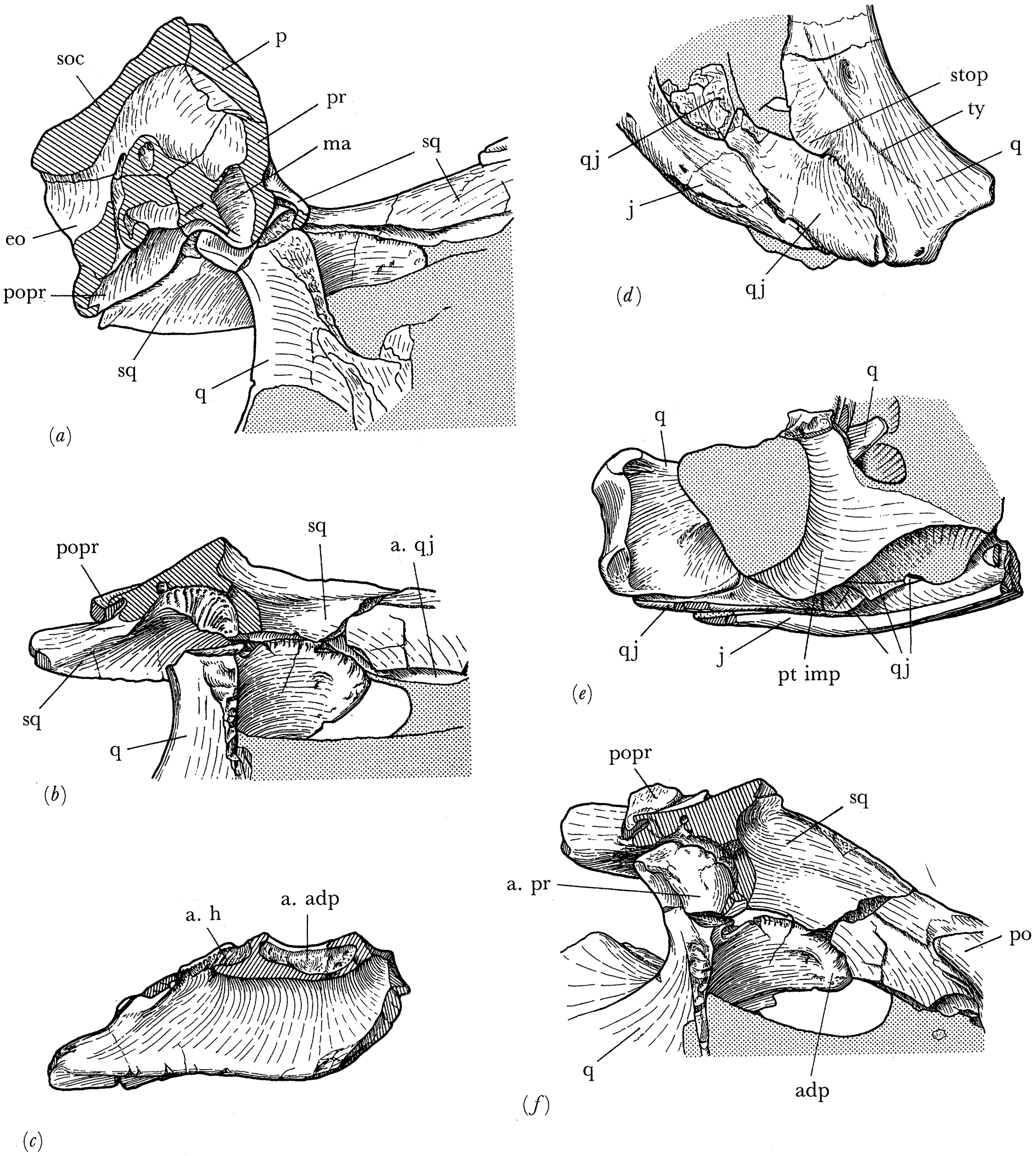

Figure 13. *Sphenosuchus acutus* Htn. (*a*) Medial view of upper end of left quadrate with 'supraoccipital piece' in place; (*b*) the same with 'supraoccipital piece' and quadrate head removed; (*c*) lower view of rear part of left squamosal (socket for anterodorsal process is incomplete on this piece); (*d*) posterolateral and dorsal view of left quadrate and adjacent bones; (*e*) lower view of same piece; (*f*) oblique dorsomedial view of upper end of left quadrate and squamosal. (*a*)–(*c*), (*f*): Magn. × 1.5; (*d*), (*e*): magn. × 1.

The head proper is narrow from side to side and strongly convex anteroposteriorly, dropping abruptly in front to the transverse slot already noted. The articular surface is smooth, grey and minutely porous. It falls away abruptly laterally to a flat surface with short vertical grooves. These notch the edge of the articular surface (which is itself faintly wrinkled) in such a way as to suggest that a thick cartilaginous capping was originally present, an inference which is borne out by the discrepancy in size between the head and its socket. The inner side, on the contrary, curves over medially forming a broad ridge, meeting first the squamosal and then, lower down and anteriorly, the prootic, fitting into a corresponding smooth groove in the latter, external to the temporal canal. Posteriorly, below the ridge, there is a concave area which is closely approached by a small projection from the rear end of the prootic flange (figures 12*b* and 13*a*).

The upper end of the quadrate also has an anterior projection of crocodilian type. Although it is considered that this probably served as a protraction-stop, rather than a true condylar articulation, it was referred to as the 'anterolateral head' (Walker 1974) because of a supposed homology with the anterolateral head of the bird quadrate. This view is now believed to be mistaken. For convenience of reference, therefore, the projection of the sphenosuchid and crocodilian quadrate will be referred to as the *anterodorsal process*.

This process curves round forwards from the transverse slot, following the curvature of the outer

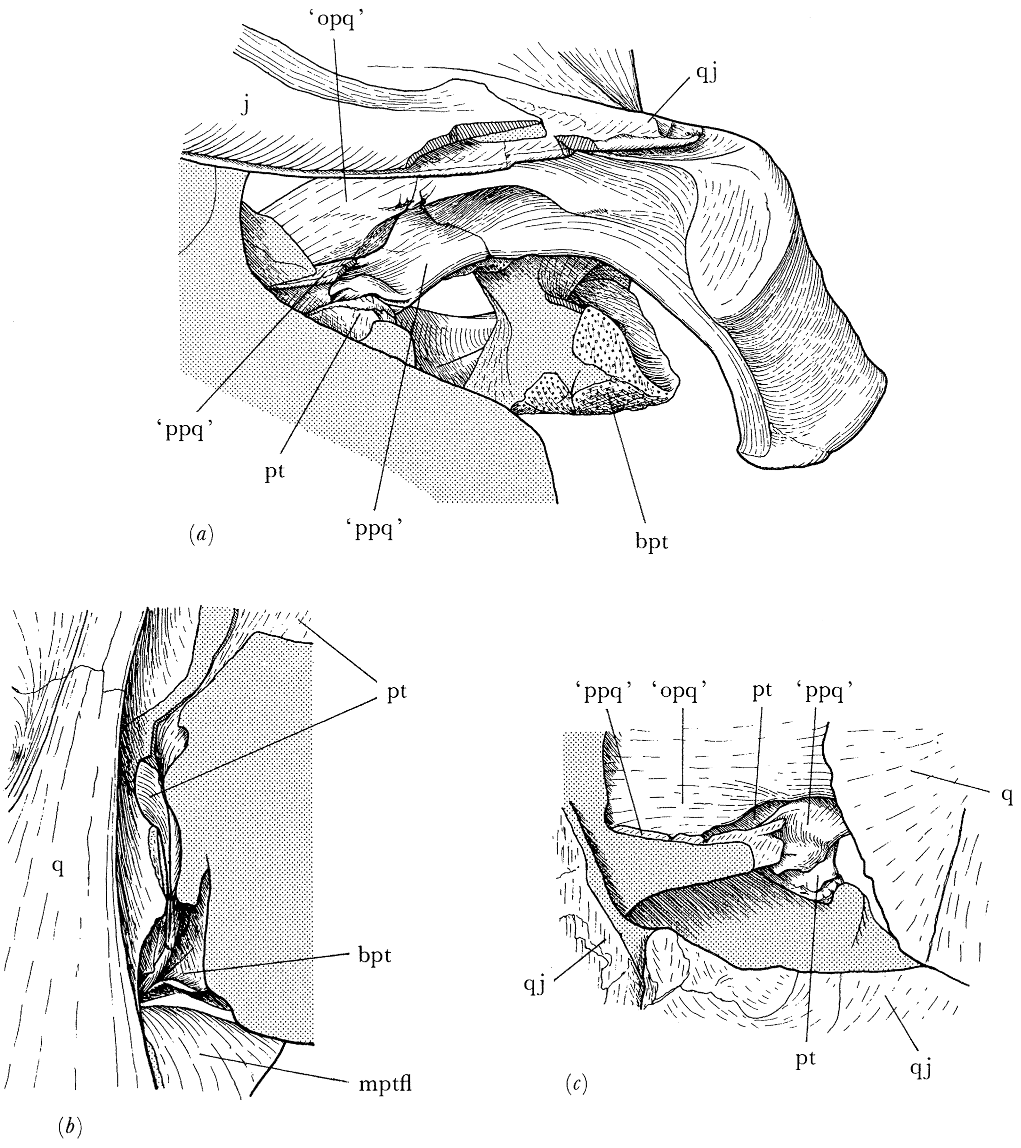

Figure 14. *Sphenosuchus acutus* Htn. (*a*) Ventrolateral view of left quadrate and basipterygoid process; (*b*) posterior view of central part of left quadrate and articular cup on quadrate ramus of pterygoid; (*c*) lateral view of 'orbital' and 'pterygoid' processes of left quadrate, magn. ×3.

corner of the upper temporal fenestra. Its upper edge, narrow at first, arches gently dorsally and thickens to form an elongate-oval prominence which fitted into the cavity underneath the squamosal. The edges of this rounded prominence bear short vertical striations. The articular surface is minutely porous, indicating a former cartilaginous coating. The reception area for the squamosal flange and its apophysis has already been described, also the articulations with the quadratojugal.

The pterygoid wing of the quadrate has been considered (Walker 1974) to consist of separate orbital and pterygoid processes. When prepared, the left quadrate showed a finger-like anterior process at the base of the pterygoid wing (figures 7*a*, 14*a*, *c* and 25*b*). Although sheared through and telescoped at its base, the upper edge of this process and the lower edge of the 'orbital process' appeared to be entire as they emerged from the matrix during preparation. The specimen has been returned to the South African Museum so that I have been unable to re-examine it, but it has occurred to me that, in view of the strong forward drive suffered by the left quadrate and the sharp geniculation of the pterygoid, it is possible that appearances are deceptive and that a narrow strip has been sheared off the lower part of the pterygoid ramus. Two considerations add to this possibility. One is that there appears to be enough actual bone of this region of the right quadrate remaining (figure 17*b*) for the distinction between 'orbital' and 'pterygoid' processes to be seen, had it been present, although it must be admitted that this quadrate has been strongly compressed and sheared and most of the pterygoid wing is represented by an impression. The other consideration is the resemblance of the pterygoid ramus of *Sphenosuchus* to that of a modern crocodile. The ridge running down and back from the base of the 'orbital process' to the anterior surface of the bone (figure 14*a*) bears a distinct resemblance to that termed 'crest B' by Iordansky (1964), leading to the supposition that the area below

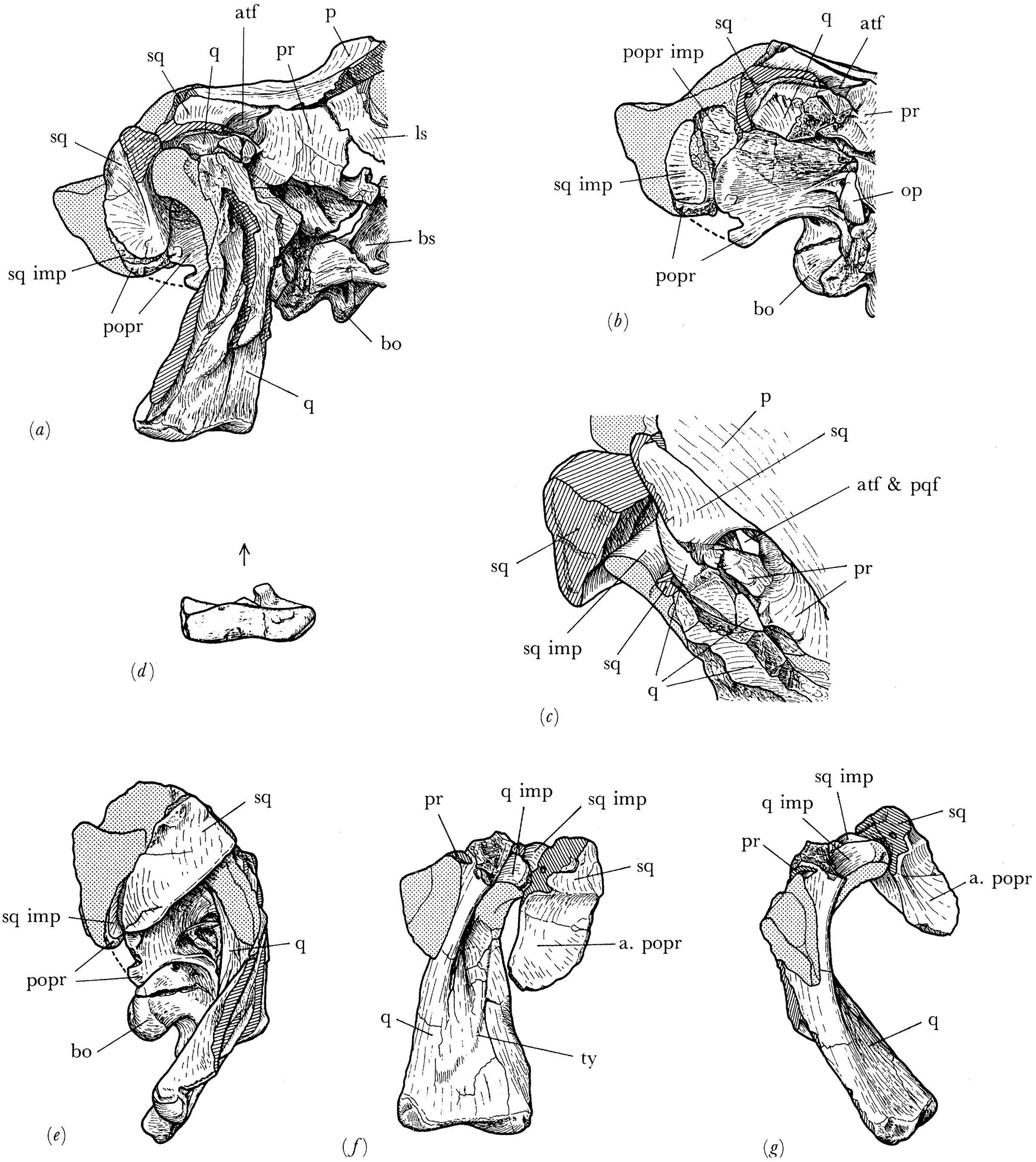

Figure 15. *Sphenosuchus acutus* Htn. (*a*) Anterolateral view of 'right quadrate piece' in place on braincase, showing relationships of squamosal to paroccipital process; (*e*) lateral view of same; (*b*) a similar view with 'right quadrate piece' removed, showing full extent of paroccipital process; (*c*) dorsal view of right quadrate head crushed into anterior temporal foramen, postquadrate foramen seen through latter; (*d*), (*f*), (*g*) condylar, posterior and medial views of 'right quadrate piece'. All magn. × 1 except (*c*), which is magn. × 2.

this crest or break of slope has split off anteriorly to form the apparent 'pterygoid process' of the *Sphenosuchus* quadrate.

Nevertheless, the right quadrate does show an anterior forking of the pterygoid wing, but again, the modern crocodilian quadrate often shows a similar tendency, although the anterior cleft is more open.

The upper edge of the pterygoid wing extends forwards at first, meeting a groove running forwards and downwards across the prootic, and then drops abruptly downwards. The distal end expands a little to a rather square termination which is thickened, indicating a former cartilaginous extension. The middle part of the ramus is laterally convex, becoming flattened distally. The impression of the right side on the 'laterosphenoids piece' (figure 17*b*) appears to show a small projection halfway down the upper edge. However, there is no indication of this on the well-preserved left side, and since the upper boundary on the right side is rather vague, the projection may be an irregularity of the matrix or part of the apex of the pterygoid which projected above the quadrate. The upper margin is thus not notched or channelled for the exit of the trigeminal nerve as in the modern crocodilian skull, confirming that the ramus was not very close to the prootic–basisphenoid flange.

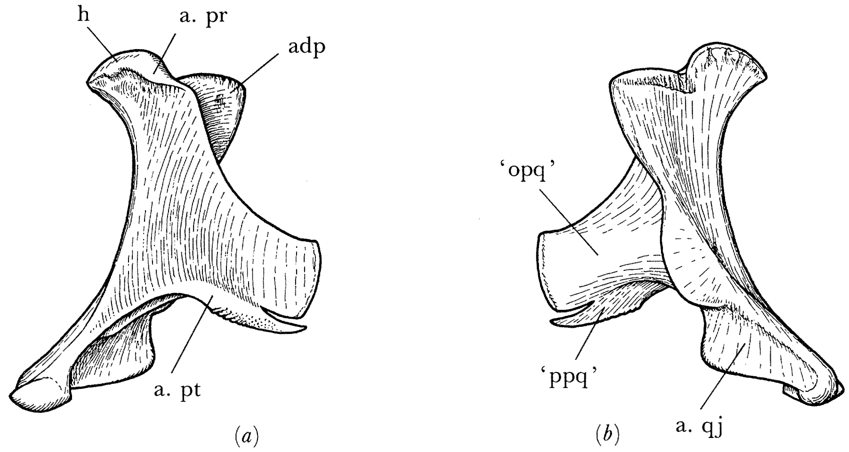

Figure 16. *Sphenosuchus acutus* Htn. Restoration of the left quadrate in (*a*) medial and (*b*) lateral views, taking into account the possibility that the appearance of an elongated pterygoid process is partly due to post-mortem shearing. The pterygoid wing is shown unforeshortened. (Magn. × 1.)

The lower portion of the pterygoid wing curves medially and thickens in its proximal half, bearing the articular area for the pterygoid. This consists of a low convexity facing upwards and inwards, originally covered in cartilage. The existence of this coating is attested by the denticulations along the lower margin below and in front of the articular area, and the numerous fine canals on the inner surface. The lower portion becomes very thin anteriorly and seems to have been a millimetre or two longer than the upper portion (a tiny fragment of the point remains on the right side (figure 17*b*)). It seems that both 'processes' lay in the same plane anteriorly, or nearly so, but posteriorly the development of 'crest B' led to divergence, and a longitudinal hollow developed between 'crest B' and the lower edge of the ramus. The latter curves down posteriorly to the inner condyle, whereas 'crest B' runs ventrolaterally across the anterior surface of the quadrate and dies out abruptly at the middle of this surface; its lower end is grooved and roughened for tendinous origin.

It seems probably that the cartilage-coated lower part of the pterygoid ramus (i.e. the 'pterygoid process') was continuously in contact with the pterygoid. The main upper portion (or 'orbital process') was slightly separated from the quadrate posteriorly but came very close to it anteriorly with the dying out of 'crest B'. The blunt anterior termination, the probable existence of an epipterygoid, and the groove on the 'neck' of the pterygoid combine to indicate the existence of an area of cartilage in front of the main pterygoid wing.

The central part of the bone forms a strong pillar posteriorly, merging into the inner border below and curving back strongly above to form the posterior edge of the head. A pit is situated in a shallow depression lateral to the pillar just below mid-height. Lateral to this the impression of the attachment of the lateral border of the tympanum is clearly seen on the left quadrate (figure 13*d*). This line can be traced, becoming fainter, to a point 7 mm from the lower end, and upwards to above the projecting lateral wing, where it approaches to within 2 mm of the anterior edge. Throughout its gently curving course it maintains a fairly constant distance of *ca.* 9 mm from the inner border. The middle part of this line can also be seen on the right quadrate (figure 15*f*).

The articular surface for the lower jaw consists of two very oblique, widely separated parallel condyles trending anteromedially, separated by a broad, shallow concavity. The inner condyle is narrow and is prolonged forwards beyond the general line of the articular surface. The outer condyle, better preserved on the right quadrate, is rather broader.

A small piece of bone and impression, 10 mm tall and a maximum of 5.5 mm wide, lying lateral to and just touching the anterodorsal corner of the quadrate wing of the left pterygoid, is probably part of the *epipterygoid* (figure 25). It appeared at first to be an ascending process of the pterygoid like that of some thecodontians, which had been sheared off and dropped down. Later preparation of this area made it seem very unlikely that the corner of the pterygoid was incomplete; also, there is no indication of an ascending process on the impression of the right pterygoid. The medial surface of the fragment is difficult to examine, but posteroventrally, where it is thin and slightly divergent, indications of a porous texture are present, suggesting that it overlay cartilage here. Its straight anterior edge is parallel to and almost in contact with that of the quadrate wing, above which it rises for about 7 mm, as far as the impression is preserved. It increases a little in breadth upwards, is slightly convex laterally from front to back and concave medially, conforming closely to the shape of the adjacent pterygoid. The posterior half is very thin; a low ridge crosses the inner surface obliquely, marking off a divergent posteroventral area which has a porous surface. It seems likely that this piece of bone is an ossification at the anterodorsal corner of a residual area of the palatoquadrate cartilage. Also, it lies lateral to the pituitary fossa and below the groove along the lower border of the laterosphenoid which denotes the course of the ophthalmic branch of the trigeminal nerve. Thus, apart from its unusual height above the basal articulation, it is in the appropriate position for an epipterygoid.

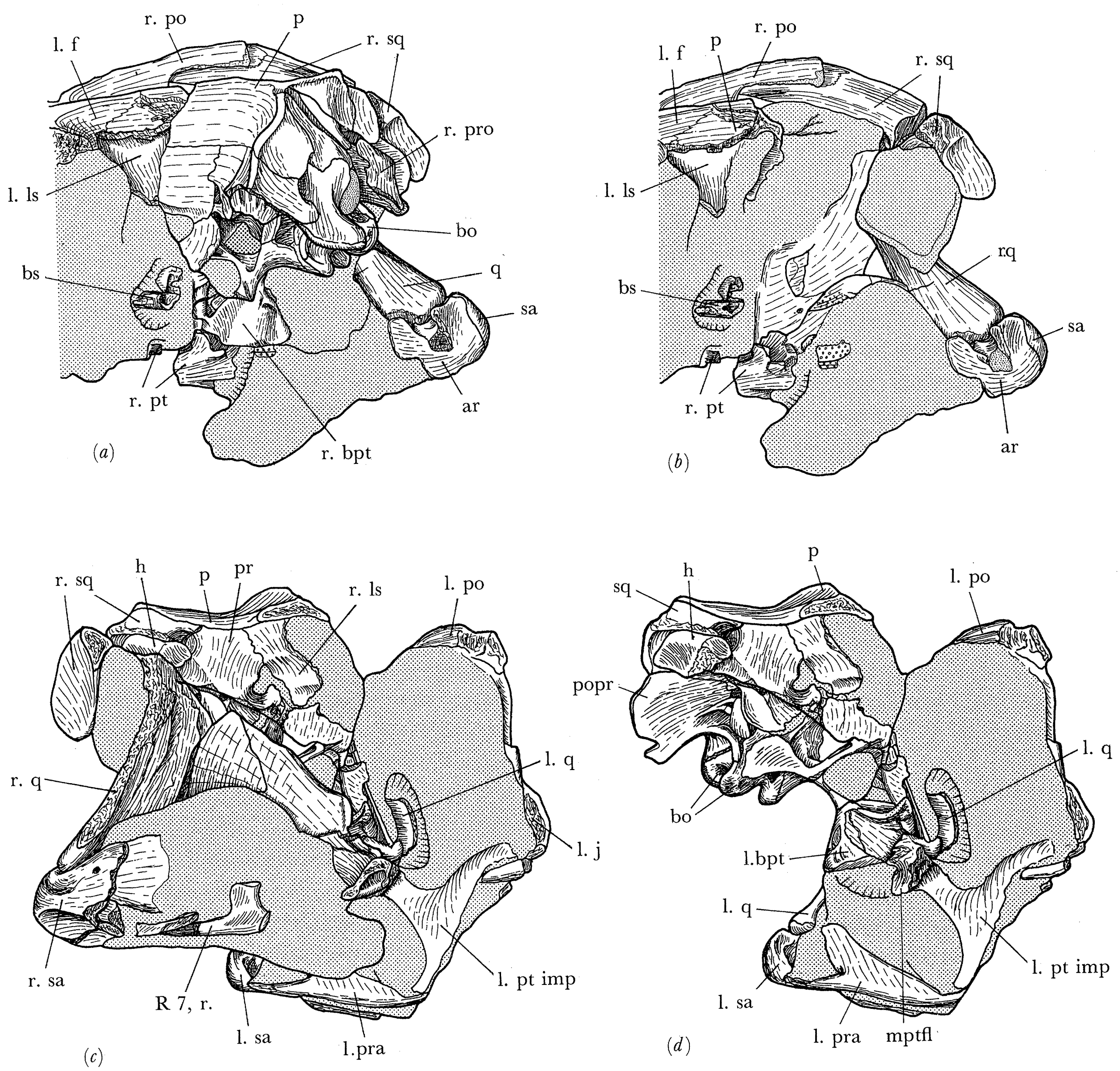

Figure 17. *Sphenosuchus acutus* Htn. (*a*) Assembly of pieces including braincase from the left side, right pterygoid, basipterygoid process, quadrate and articular seen in medial view; (*b*) same, but with 'braincase piece' and 'right basipterygoid piece' removed; (*c*) assembly from right side; (*d*) same, but with right quadrate and pterygoid removed. Drawn before completion of preparation and removal of rear parts of lower jaws. Magn. ×0.75.

Braincase–external surface (*figures 59–62*; *restoration*: *figure 28*)

The *basioccipital* (figures 19–24) is a relatively longer element than it appears externally, because its anterior half is largely concealed by a sheath of bones consisting of the basisphenoid, the pro- and opisthotics and the exoccipitals. The condyle displays a small notochordal pit. The basal tubera project posteroventrally and their rugose anterior surfaces are overlain by extensions from the basisphenoid. The suture with the latter bone follows the converging anterior edges of a roughly triangular aperture in the lower surface of the basioccipital (figure 20), the third side of which is formed by the transverse ridge of bone connecting the bases of the tubera. This aperture lies at the posterodorsal extremity of a median channel on the underside of the basicranium, which extends forwards between the basipterygoid processes to the base of the rostrum. The aperture gives access to a pair of large cavities, termed here the *basioccipital recesses*, which occupy the greater part of the interior of the anterior half of the basioccipital and extend back within the tubera. These cavities are incompletely separated from each other by a longitudinal ridge of bone in the roof of the basioccipital. They lie entirely within the latter bone. (The roof of the right-hand cavity has been broken at its anterior end by the slewing-round to the right of the basisphenoid plate. There is thus a hole dorsally communicating with the cranial cavity.)

The condylar portion of the basioccipital is bevelled off obliquely to receive the exoccipitals, which also send narrow tongues down the sides of the tubera. Emerging in front of these the basioccipital is exposed laterally in a small depressed area bounded by

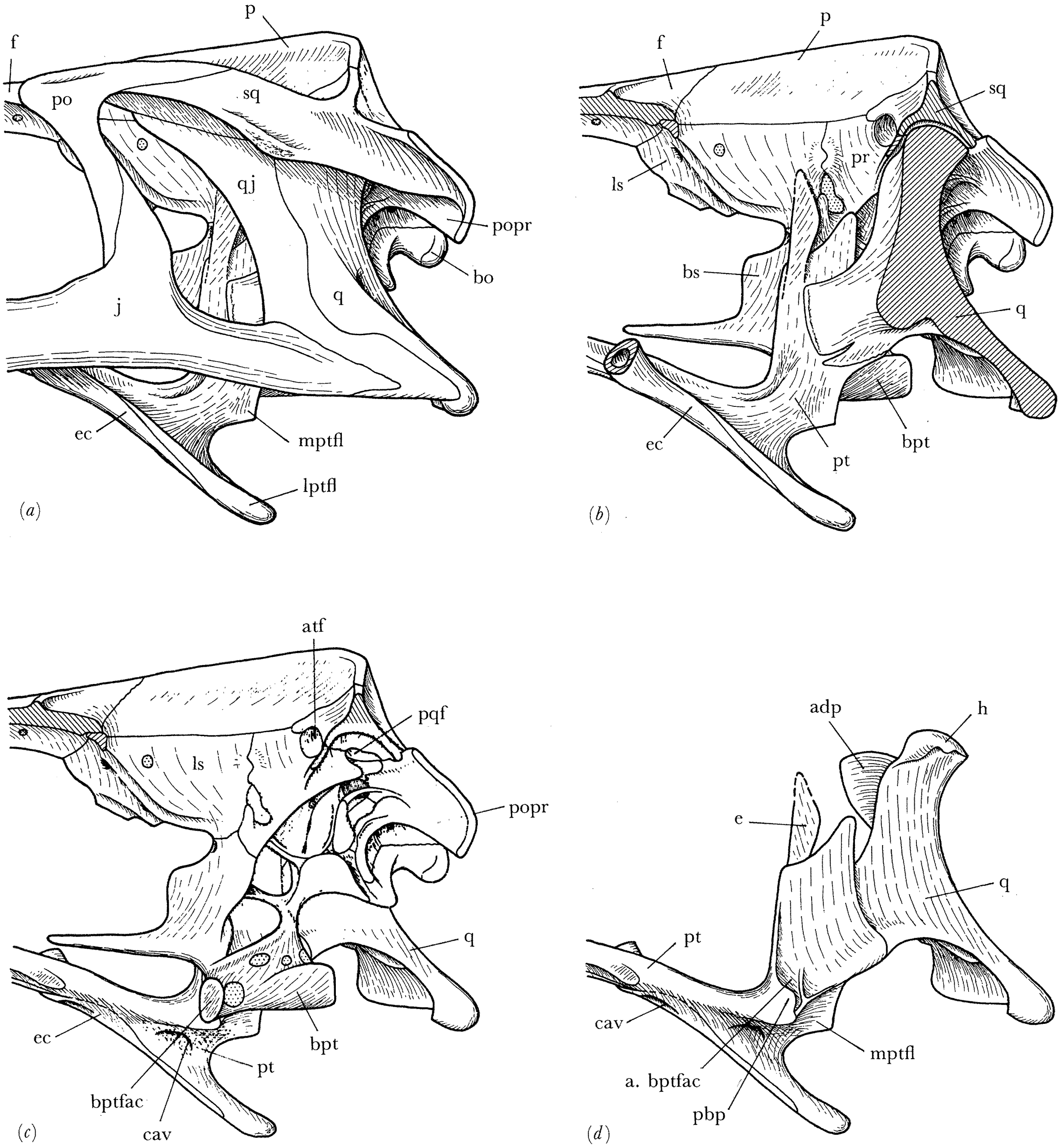

Figure 18. *Sphenosuchus acutus* Htn. Restoration of the palatal complex in relation to the braincase. (*a*) lateral view with cheek-bones in place; (*b*) with cheek-bones removed, left quadrate sectioned vertically through posterior pillar; (*c*) with palatal complex of left side removed; (*d*) braincase removed, palatal complex of right side seen in medial view. Magn. ×1.

exoccipital, opisthotic, and basisphenoid. This area is prolonged ventrally as a narrow groove in the basioccipital, flanked by the thin edge of the basisphenoid and the curving ridge formed by the basioccipital and exoccipital. The groove indicates the position of the lateral eustachian tube, and the depression represents the crocodilian rhomboidal sinus. In front of this again the bone expands laterally at the rear border of the lagenar region at the lower end of the cochlear recess, forming two little tuberosities which articulate with the lower extremity of the opisthotic. It is also excavated to make up the medial half of the cup for the lagena. Here it is overlapped laterally by the basisphenoid, meets the prootic anterodorsally and the opisthotic posterodorsally at thick contacts, and extends up the inner wall of the cochlear recess as a '**V**' between them (figure 22). The basioccipital probably formed a narrow transverse gutter at the base of the metotic foramen in front of a small triangular projection of the exoccipital, but this would have been concealed by the opisthotic in lateral view.

The *exoccipital* (figures 19–24) is fused with the opisthotic and no certain trace of a suture between them remains. It is assumed that the paroccipital process is formed by the opisthotic and that the metotic

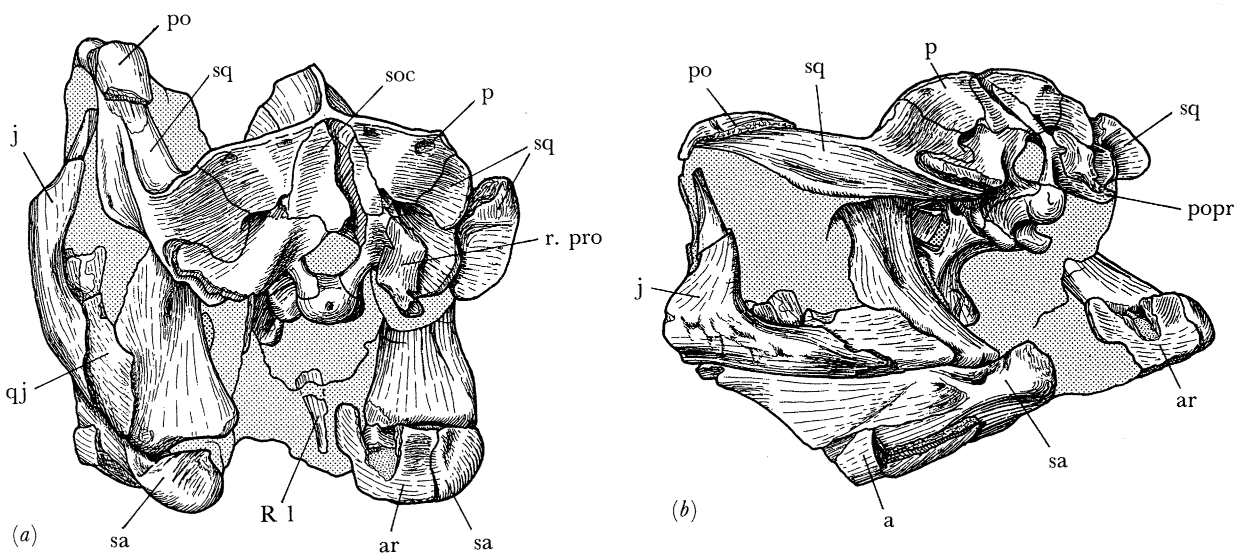

Figure 19. *Sphenosuchus acutus* Htn. Rear part of skull, drawn before completion of preparation and removal of rear parts of lower jaws. (*a*) View normal to plane of occiput; (*b*) left posterolateral view, magn. ×0.75.

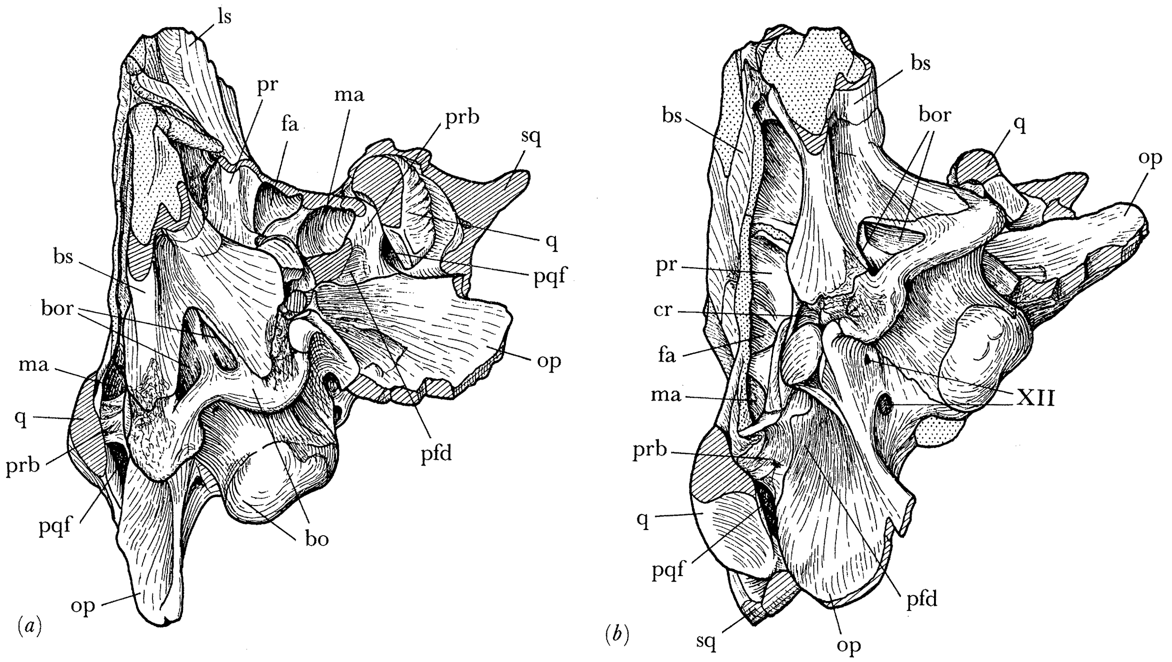

Figure 20. *Sphenosuchus acutus* Htn. Ventral views of 'braincase piece'. (*a*) slightly from left side; (*b*) slightly from right side, magn. ×1.5.

('vagus') foramen marks the line of junction between otic capsule and exoccipital anteroventrally. (The term *metotic foramen* is used in this paper to denote that structure in the adult skull which corresponds to the embryonic metotic fissure, in order to avoid the ambiguity of 'vagus foramen' for a cleft which transmits several elements.) In *Sphenosuchus* the metotic foramen is visible as a slit both internally and externally, but in typical crocodilians the metotic foramen is concealed externally by ossification of the embryonic subcapsular process through which various nerves (including the vagus) and the internal carotid artery pass, and which have both internal and external foramina in addition to the metotic foramen. The subcapsular process projects forwards below the otic capsule and forms a floor to the recessus scalae tympani (Shiino 1914). Although the details have never been described, it is probable that this process ossifies as the anterolateral and ventral parts of the exoccipital (Parker 1883; de Beer 1937; Müller 1967; Bellairs & Kamal 1981). The strong lateral ridge on the exoccipital gives reason to think that this process had developed to some extent in *Sphenosuchus* also. Its significance will be discussed later.

Allowing for over-riding at the left exoccipital/supraoccipital contact, the exoccipitals would have been separated by *ca.* 2 mm in the mid-line dorsally on the occiput. On the left side there is a small, backwardly projecting flange from the dorsolateral rim of the foramen magnum which presumably articulated with the proatlas. Dorsally the exoccipital meets the supraoccipital, and dorsolaterally it perhaps meets the

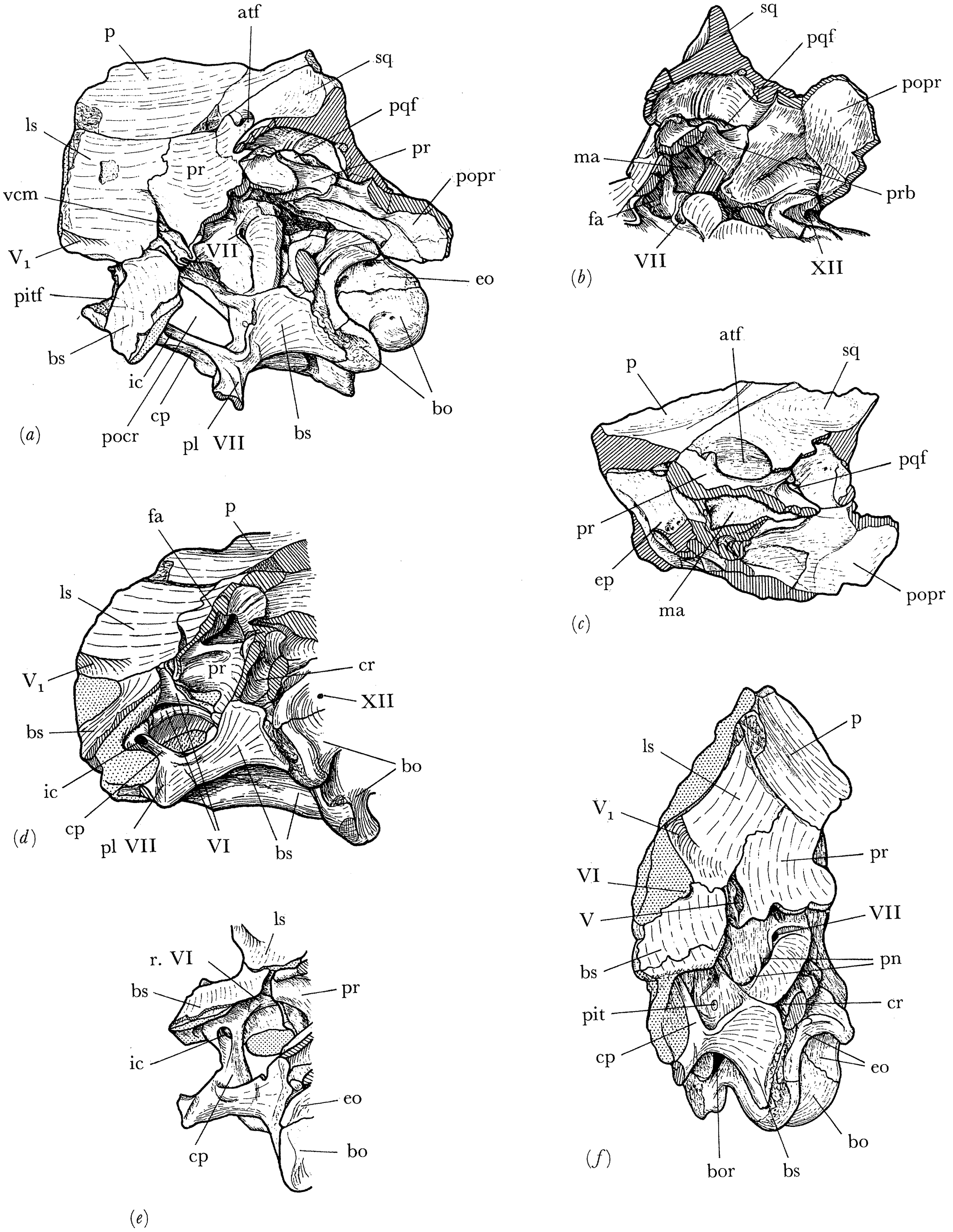

Figure 21. *Sphenosuchus acutus* Htn. Left side of braincase. (*a*) general lateral view with 'supraoccipital piece' in place, showing maximum of prootic articular area for quadrate head; (*b*) ventrolateral view, showing maximum of medial side of squamosal socket for quadrate head; (*c*) anteroventral view of 'supraoccipital piece', showing mastoid antrum below anterior temporal foramen; (*d*) ventrolateral view of part of 'braincase piece' showing foramen for internal carotid artery and 'tubes' for abducens nerves; (*e*) a more posterior view of the carotid pillar; (*f*) anterolateral view with 'supraoccipital piece' removed, showing pneumatic cavities along course of palatine nerve and left pit in basisphenoid plate. Parts (*d*) and (*f*) drawn before final preparation. Magn. × 1.5.

epiotic, although this portion of the bone is more probably of opisthotic origin. The lower parts of the exoccipitals are pierced externally by two foramina for branches of the hypoglossal nerve, a smaller anteroventral foramen behind the lateral ridge which runs down to the tuber, and a larger posterodorsal one at the base of the paroccipital process. The anterior part of the bone is expanded strongly sideways, forming a curving ridge which joins the lower edge of the paroccipital process to the side of the tuber. Allowing for distortion, the anterior surface of this ridge probably just failed to touch the opisthotic behind the lower end of the cochlear recess; it sends forward a flat-ended triangular projection which rests on the basioccipital (figure 23*b*). Above this contact a small flange with a groove behind it projects dorsolaterally from the anterior border of the ridge (figures 22*a*, *c* and 24), and is believed to indicate the position of the stapedial artery where the latter curved backwards above its origin from the internal carotid artery.

The front surface of the exoccipital is a large triangular area originally facing anterodorsally and a little laterally. This area (figures 21*a*, 22*a* and 23*b*) is the floor of the recessus scalae tympani which contained the perilymphatic sac and through which passed nerves IX, X and XI, and (probably) the posterior cerebral vein. The internal boundary of the triangle is at the metotic foramen, a fissure slanting steeply downwards and forwards and much compressed on both sides of the braincase. The lateral border is the edge of the curving ridge mentioned above. The posterior limit is less sharply defined, namely a line running posterolaterally from the upper end of the metotic foramen and crossing the base of the paroccipital process obliquely, behind which the surface curves more or less sharply upwards. This line probably corresponds to the junction between exoccipital (subcapsular process) and opisthotic. The anterior half of the triangular area is almost perfectly flat; the posterior half slopes back a little relative to it and is very slightly concave.

The *supraoccipital* (figure 19) is an inverted shield-shaped element which sends a short median process downwards to enter the foramen magnum. Dorsally the posterior surface becomes shallowly concave from side to side, interrupted by a very slight median convexity which rises to a low boss at the dorsal apex. This part of the bone is thickened and fits into a smooth socket below the tri-junction of the parietal crests (figure 30). The flanks of the supraoccipital articulate firmly with the parietals except at the ventrolateral corners. Here short lateral extensions enter the inner extremities of the post-temporal fenestrae. These extensions are separated from the main body of the supraoccipital by fine suture-like grooves which continue the lines of the supraoccipital/parietal sutures. They thus appear to be discrete elements which are partly fused with the supraoccipital (the left groove is not quite complete) and since in the young of both birds and crocodiles there are paired epiotic ossifications which fuse with the supraoccipital (Parker 1883; Pycraft 1898*b*, 1899*a*, *b*; Jollie 1957; Müller 1967; Bellairs & Kamal 1981) it seems reasonable to identify these elements as epiotics.

The *epiotic* (figures 19, 22, 24 and 30) has a small exposure on the occiput, and above it is the small foramen mentioned in the description of the parietal. Close to the inner corner of the post-temporal fenestra the bone loses its smooth surface and becomes grey and porous. A striated area on the opisthotic runs out a short way laterally from this region indicating the former presence of a tongue of cartilage. The unfinished surface continues to just within the fenestra and is then replaced by normal bone, forming a small, crescentic area on the inner wall of the temporal canal and tapering out in front between parietal and prootic. This area appears to be an element distinct from the prootic on the left side, whereas on the right it seems to be partly continuous with that bone. It would be difficult to decide from the specimen alone whether this area is prootic or epiotic in nature, but comparison with the modern crocodilian skull strongly suggests that it is part of the epiotic, the squeezing which the right side has undergone probably accounting for the situation on this side. The suture between prootic and opisthotic crossing the floor of the temporal canal ends at right angles against the convex lower margin of the crescent, as in the crocodilian skull. In the latter a somewhat similar area is part of the fused supraoccipital–epiotic bone.

In the modern crocodile the epiotic surrounds the sinus superior utriculi and the upper parts of the anterior and posterior vertical semicircular canals. Similarly in the juvenile partridge (*Perdix perdix*) the epiotic contributes to the junction of the same two canals, encloses more than half of the loop of the anterior vertical canal, and takes a share in the formation of the posterior vertical canal. This is a somewhat larger proportion than Jollie (1957, p. 401) reports in the case of the chick. Thus it seems reasonable to assume that these areas lay in the epiotic in *Sphenosuchus*.

The lower part of the epiotic forms a rounded buttress on the inner surface of the cranium, and on the broken left side (figure 22) it can be seen that this is simply a thin shell of bone surrounding a canal about a millimetre in diameter, which housed the sinus superior of the utriculus. The inner surface of the 'supraoccipital piece' (figure 30*a*) exposes the forking of the canal into two branches of finer bore for the anterior and posterior vertical semicircular canals, which have been partly cleaned out. The anterior canal continues to rise for a short distance above the fork before arching forwards. The canal is directed, on the whole, more anteriorly than laterally, and at the fork it arises partly from the medial side of the posterior vertical canal, rather than from directly in front of it as in the crocodile. The posterior vertical canal is directed more laterally than posteriorly and appears to run close within the curve of a reniform cavity on the internal surface of the cranium.

The relationships between the paroccipital process portion of the *opisthotic* (figures 15 and 19–24) and adjacent dermal bones have already been described. The processes are directed downwards, outwards and backwards and are strongly expanded distally. Neither process is complete, but that of the right side lacks only a small part of its distal extremity. The posterior surface is convex proximally in the dorsoventral direction, becoming more flattened distally; the anterior surface is correspondingly concave, facing as a whole a little downwards as well as forwards. Directly behind the fenestra ovalis the concavity is accentuated over an area which is also distinguished by its extremely smooth surface. The lower boundary of this area is a sharp ridge which continues the crista interfenestralis backwards and downwards and dies out at the rear of the metotic foramen. The posterior limit is indefinite. The concavity crosses the prootic/opisthotic suture behind the S-bend in the latter, and is more clearly defined on the lower surface of the prootic buttress

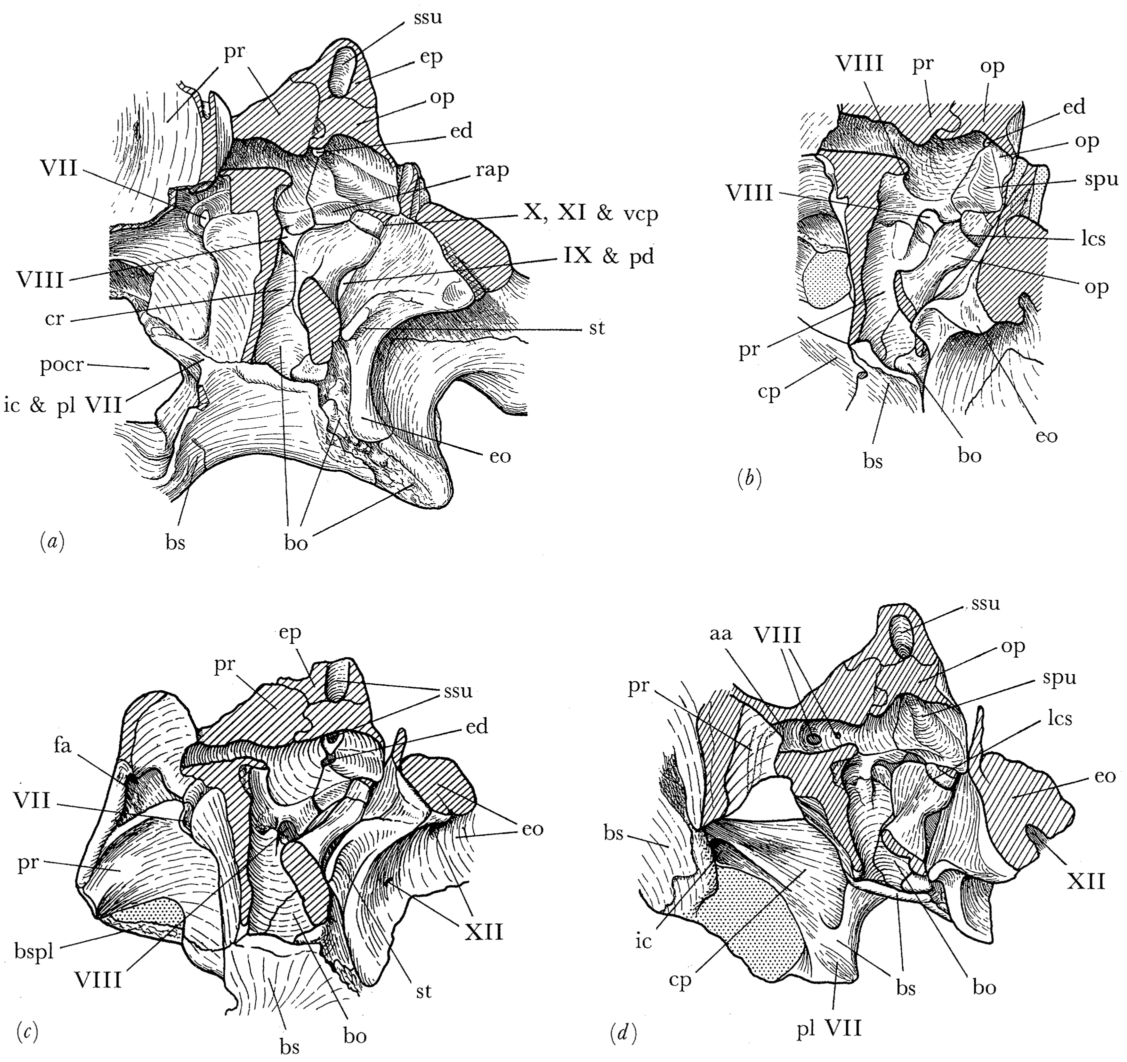

Figure 22. *Sphenosuchus acutus* Htn. Details of left otic capsule. (*a*) Lateral, (*b*) posterolateral, (*c*) ventrolateral and (*d*) dorsolateral views. (*a*) and (*b*) drawn after removal of matrix from interior of braincase. Magn. × 2.5.

(defined below). This concavity (figure 20) is worthy of note because it is considered to be the homologue of the avian posterior tympanic recess, a much deeper cavity in the bird skull. It is convenient to refer to it as the *postfenestral depression*.

The suture with the prootic crosses the floor of the temporal canal towards its rear, running outwards and slightly backwards from the epiotic. Just in front of the squamosal it runs round the thick posterior border of the prootic buttress into the tympanic cavity, makes an S-bend and then enters the middle of the upper border of the fenestra ovalis.

The *inner ear* consists essentially of three intercommunicating cavities: the vestibule, the cochlear recess and the recessus scalae tympani, although the last is not part of the otic capsule proper. It is well preserved on both sides, albeit somewhat distorted; on the left side a parasagittal fracture exposes a roughly vertical section through the capsule enabling more of the internal details to be seen (figures 22, 24 and 30*a*). Externally the prootic and opisthotic exhibit a nearly vertical prominence which houses the lower part of the cochlear recess. Behind and above this there lies a deep, approximately triangular cavity (figure 23*b*, *c*) divided into two unequal parts by a slender bar of bone from the opisthotic, the *crista interfenestralis* (Säve-Söderbergh 1947, p. 513). The area above the bar is the fenestra ovalis into which fitted the head of the stapes, that below it is the fenestra pseudorotunda (de Beer 1937, p. 431) across which was stretched the secondary tympanic membrane. The lower part of the cavity (recessus scalae tympani) contained the perilymphatic sac; in its depths can be seen the slit-like metotic foramen which passes through into the cranial cavity, and above this the foramen perilymphaticum (de Beer 1937, p. 401) communicating with the cochlear recess. The entrance to the vestibule is within the fenestra ovalis, its anterior border lying more deeply or medially within the fenestra than the posterior border. Medial to the crista interfenestralis the vestibule communicates freely with the cochlear recess.

The *vestibule* is a sub-spherical cavity divided into two approximately equal parts by the prootic/opisthotic suture which descends in a vertical meridional curve. About halfway up the inner wall this contact is briefly interrupted to admit the epiotic at an area which is just large enough to carry the sinus superior of the utriculus (figures 22*c* and 24*b*). Immediately below this aperture a small foramen for the endolymphatic duct enters along the suture. From this point a well-marked groove, taken to indicate the position of the sinus posterior utriculi, extends posterolaterally across the floor of the vestibule towards the recess for the posterior ampulla. The lower end of the left posterior vertical canal is seen on the 'supraoccipital piece' (figure 30*a*) entering the upper side of a small cavity which indicates the position of this ampulla. The cavity is separated by only a thin wall from a channel leading into the upper end of the metotic foramen. The external semicircular canal enters at the anterior side of the cavity and would have curved round medially above the posterior ampulla at this point, within the posterior vertical canal, and run anteromedially within the vestibular cavity to the base of the sinus superior utriculi. The lumen of the external canal has been nearly closed up, and the ampullary cavity reduced in size, by the inward and forward sliding of the opisthotic along its contact with the prootic.

The entrance to the vestibule faces downwards and outwards and is surrounded (except ventrally) by a pronounced rim. Here there is a low threshold outside which is a 'step' down to the suture of the opisthotic 'with itself'. The latter is a phenomenon which has received little attention, but which occurs in lizards and crocodiles at least and in the juvenile stages in some birds. It is the result of the formation by the opisthotic of a loop of bone (Parker 1883) surrounding the foramen perilymphaticum, for which reason it will be referred to as the *perilymphatic loop* (Walker 1985). (The term 'cochlear loop' of Miall (1878, p. 21) is inappropriate since the loop does not surround the cochlea; 'opisthotic loop' is not entirely satisfactory because in many birds the 'exoccipital' intervenes to break the continuity of the opisthotic.) In *Sphenosuchus*, as in crocodiles, the perilymphatic loop also forms the posterior wall of the cochlear recess, meeting the prootic laterally and medially. The loop is a continuation of the crista interfenestralis which arises as a sharp ridge along the anterior surface of the opisthotic, at the root of the paroccipital process. From there it passes forwards as a gentle arch of slender bone, the anterior end of which has been a little shortened by shearing on the right side. The upper side of the crista is longitudinally grooved. It expands at the contact with the prootic to form the thick posterior wall of the lower part of the cochlear recess. The latter cavity extends in a gentle curve downwards and slightly forwards from the vestibular entrance. The recess is of tubular form, with a slight inward curvature ventrally towards the lagenar region, which is a little expanded. The lower end of the opisthotic completes the posterior wall of the lagenar region and apparently just touched the basisphenoid. The outer surface of the opisthotic is of unfinished bone, lobate in outline and convex dorsoventrally. The posterior surface is concave, forming the anterior wall of the cavity occupied by the perilymphatic sac. Prootic and opisthotic curve away from each other at the lower end of the cochlear recess, leaving a small open space lateral to the lagenar expansion. This aperture has been a little exaggerated by loss of bone from its margins.

The perilymphatic loop then extends dorsomedially and broadens out to form a rather flat triangular area just within the foramen perilymphaticum. The anterior boundary of this area is the suture with the prootic running up the centre of the medial side of the cochlear recess. At the top of this section the opisthotic forms the rear border to a notch in the prootic behind the foramen for the posterior branch of the auditory nerve. As in the crocodilian skull, this notch was probably occupied in life by residual cartilage or membrane and did not transmit any structure. From this point the edge of the triangular area turns abruptly back almost at 90° and runs along the foot of the step leading into the vestibule. The prootic/opisthotic suture is offset a little posteriorly behind the notch just noted, so that the opisthotic first meets the prootic at the base of the step. Behind this the opisthotic sutures 'against itself' at what may be called the *loop-closure suture*. This has been partly forced open on the left side. The lateral surface of the step is grooved longitudinally. There is little doubt that this groove (figures 22*a* and 24*b*), which runs from near the posterior auditory foramen to the region of the posterior ampulla, crossing the threshold into the vestibule posteriorly and joining up with the oblique groove already referred to, indicates the course of the branch of the auditory nerve which supplied the posterior ampulla and the macula neglecta (Retzius 1884; Glatt 1975). The posterior edge of the triangular area is thickened and rounded and forms the inner border of the perilymphatic foramen and the anterior border of the metotic foramen. This edge, which it is convenient to call the *opisthotic ledge*, is swollen below at its middle, giving the 'dumb-bell shaped piece of bone' referred to by Haughton (1924). The loop-closure suture turns laterally through an obtuse angle near the posterior side of the vestibular entrance and crosses the opisthotic ledge just behind the central swelling. The metotic foramen, which passes out posterolaterally, would originally have been a wider slit. At its lower end the opisthotic now has a touch contact with the exoccipital, but originally there appears to have been a small gap between them floored by basioccipital.

The *prootic* (figures 15 and 20–24) is a relatively large bone whose upper portion is broadly exposed on the side wall of the braincase. The capsular portion will be described first. On the left side the vestibule has been somewhat flattened but the cavities for the anterior and external ampullae and the region of the recessus utriculi seem little affected. Some bone is missing from the roof and side walls of the two anterior ampullary recesses where the 'braincase piece' joins the 'supraoccipital piece'. A slight annular constriction partly separates off the region occupied by the anterior ampulla, whose floor is at a higher level. The external ampullary recess lies directly behind that of the anterior ampulla, and is indistinguishable ventrally and medially from that approximating to the recessus utriculi. Both the anterior and external ampullary recesses were originally roughly spherical. The depression approximately corresponding to the recessus

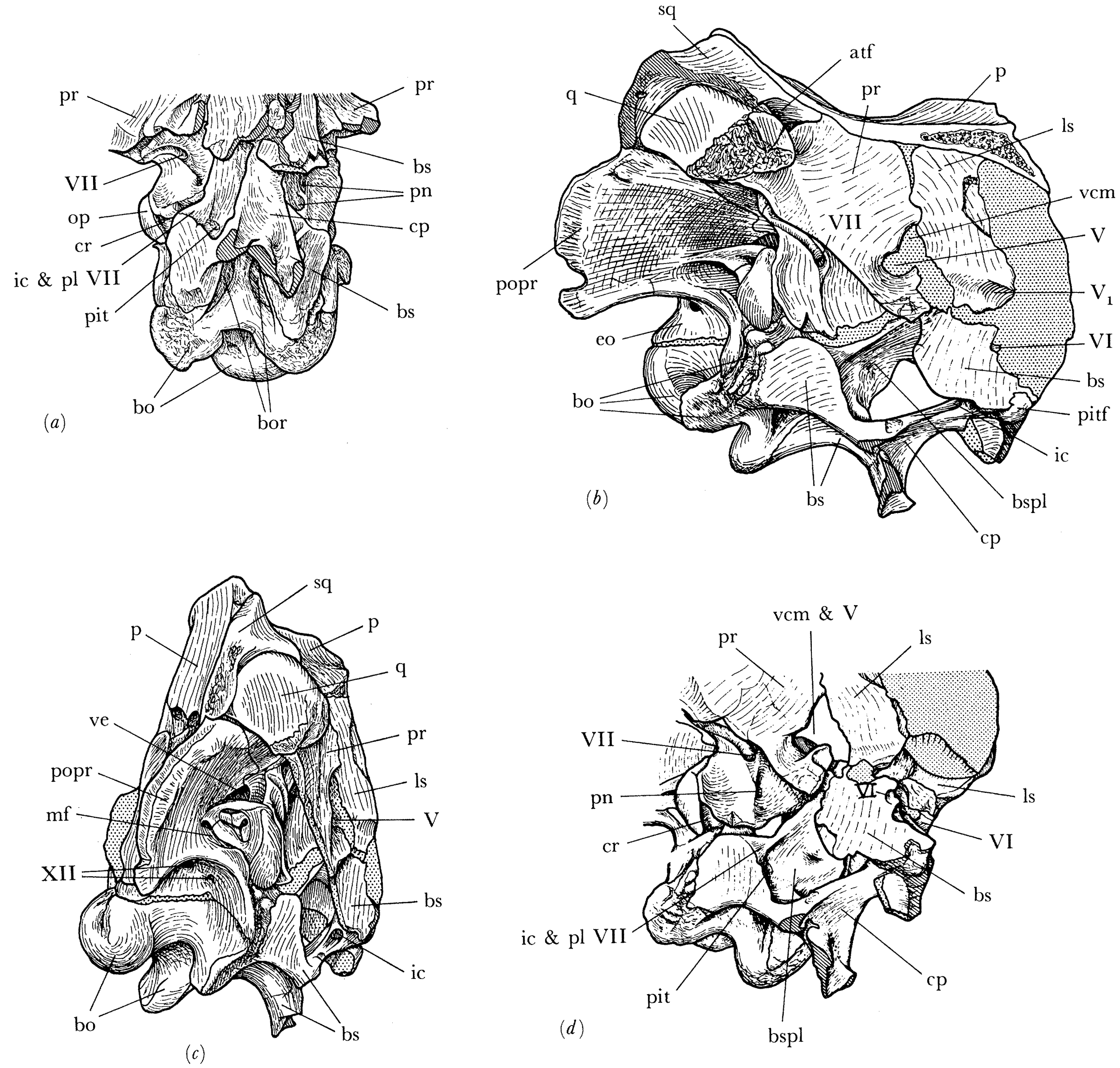

Figure 23. *Sphenosuchus acutus* Htn. Right side of braincase. (*a*) Anterior view, showing right pit in basisphenoid plate; (*b*) general lateral view; (*c*) posterolateral and (*d*) anterolateral views. (*b*) and (*c*) drawn before clearance of interior of braincase. Magn. × 1.5.

utriculi is barely distinguishable from that below the saccular region; presumably perilymph intervened below the membranous labyrinth in these areas. A relatively large foramen in the floor of the former concavity transmitted the branch of the anterior acoustic nerve which supplied the two anterior ampullae and the recessus utriculi. Close behind this foramen is a very small one for the branch of the same nerve which innervated the anterior part of the macula sacculi (Retzius 1884; Glatt 1975). This foramen, which like the one anterior to it enters somewhat from the medial side, must have lain near the anterior extremity of the sacculus.

On the 'supraoccipital piece' the anterior vertical canal is seen at the edge of the thin, broken wall of bone between the mastoid antrum and the cranial cavity (figure 30*a*). The canal resumes on the 'braincase piece', running down into the anterior end of the recess for the anterior ampulla. The external canal runs in a straight line from the opisthotic through to the prootic, a short length being exposed on the latter bone. It rises forwards at about 20° to the horizontal. There is an abrupt right-angled inwards bend in front, from which it enters the top of the recess for the external ampulla. The prootic, epiotic and opisthotic meet on the broken surface at an area of grey, rather sugary-looking bone, which is evidently a little less well ossified than the rest of the capsule.

The anterior half of the cochlear recess forms a deep groove in the thickened posterior edge of the prootic. On the left side the proximal end of this groove is slightly offset by a minor fracture. Distal to this a low ridge extends a short way down the recess; behind it the groove for the cochlear nerve adjoins the opisthotic. The channel for the cochlea is narrower lateral to this ridge and curves inwards a little ventrally. Fine annular corrugations cross it and, lower down, these have an increasing tendency to radiate from the ridge and to

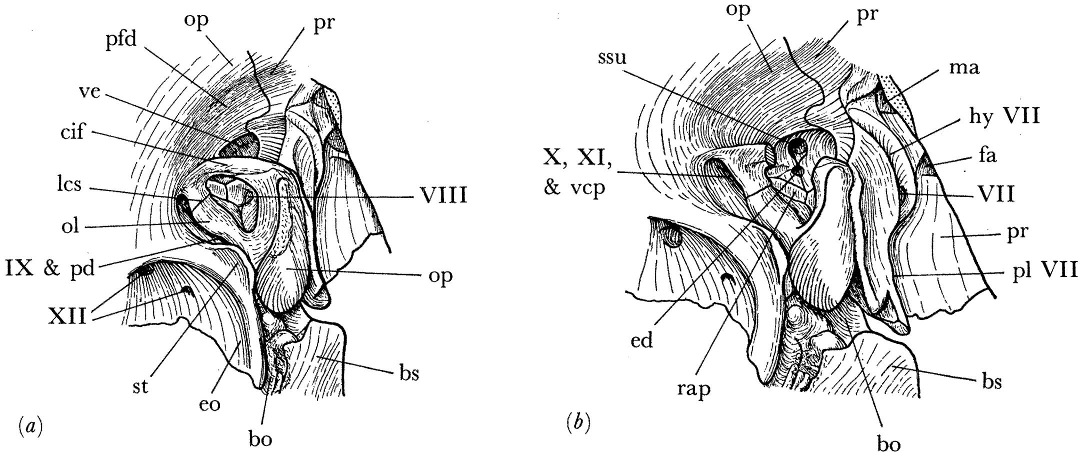

Figure 24. *Sphenosuchus acutus* Htn. Details of right otic capsule. (*a*) Posterolateral view; (*b*) a slightly more lateral view than (*a*), with crista interfenestralis imagined as cut through and partly removed. Magn. ×2.5.

curve downwards distally, where they die out before reaching the basioccipital. Similar corrugations also occur on the right prootic. The foramen for the posterior branch of the auditory nerve is a relatively large circular aperture, widely open behind to the opisthotic on the left side. This is believed to correspond more closely to the original condition, because the foramen has clearly been squeezed on the right side, as has the groove leading into it on the inner surface of the cranium.

The remainder of the bone is divided into two areas by a ventrolaterally projecting flange which commences below the head of the quadrate and descends in a curve until it meets the basisphenoid. It is continued by the latter, but there seems to have been a small but definite increase in its width below the junction. A comparable structure in lizards has been termed the 'crista prootica' (Versluys 1898). Because in *Sphenosuchus* the basisphenoid contributes almost as much to the flange as the prootic, it does not seem appropriate to use this term for it in the present instance, and it will be referred to as the *prootic–basisphenoid flange* or, where the context is clear, simply as 'the flange'. The posterior margin of the area below the flange is embayed dorsally to form the anterior border of the fenestra ovalis. Below this it curves out laterally to a thin edge which meets the opisthotic along the crest of the cochlear prominence. The broad base of this portion rests on the thick anterodorsal edge of the basioccipital, meeting the thin edge of the basisphenoid lateral to it. The latter contact runs horizontally for a short distance, then turns upwards behind the outer edge of the thin plate of basisphenoid at the back of the postcarotid recess (defined below), disappearing beneath the flange. Between this contact and the flange there is a depressed, triangular area of prootic which swells out behind at the anterior wall of the cochlear recess. At the upper end of the groove which traverses this change of level is set a prominent foramen for the facial nerve, from which a marked groove for the hyomandibular branch of this nerve leads upwards and backwards over the fenestra ovalis. The anterior rim of the foramen is notched for the passage of the palatine branch, which followed the groove noted above and ran down to the posterior corner of the postcarotid recess. The course of the nerve is clearly marked on the left side (figure 21*f*). Directly medial to it there are two deep pits on the left side and one on the right entering the bone posteromedially, tending to penetrate, that is, between the cochlear recess and the body of the bone. The right anterior pit is represented only by a shallow depression. These pits, the *precochlear cavities*, are regarded as pneumatic in origin.

The prootic–basisphenoid flange overhangs strongly laterally, to the extent of *ca.* 5 mm on the prootic and more than this at the top of the postcarotid recess. The cavity below the flange is penetrated by a number of pneumatic sinuses with thin intervening partitions, which can be accurately matched on the two sides. The spout-like lower border of the trigeminal foramen is represented below by a broad ridge, flanked before and behind by depressions. The posterior of these is separated by a thin bony partition from a very deep cavity above the facial foramen (figure 21*d*). It is proposed to call this the *facial antrum* because it is fairly constantly present in modern crocodiles. The entrance is triangular, with one apex running down to the foramen. This cavity reaches far dorsally into the base of the flange and extends forwards nearly to the trigeminal foramen and upwards and backwards in front of the recess for the anterior ampulla. Behind the facial antrum and barely separated from it dorsally is the *mastoid antrum* (figures 20*a* and 21*b*). This lies above and partly in front of the fenestra ovalis and is clearly homologous with the more extensive cavity which has received this name in modern crocodiles ('antrum mastoideum': Hasse 1873, p. 690; Wettstein 1937–54; Müller 1967; 'cellules epitympaniques': van Beneden 1882). The entrance, which is entirely surrounded by prootic, appears originally to have been approximately circular. The cavity expands dorsally, filling the entire rear portion of the prootic and lying below (or medial to) the anterior half of the temporal canal (figure 21*c*). Its bilobed upper extremity approaches closely to the supraoccipital, but does not communicate with it.

The flange ends behind as a short, posterolaterally directed process, faintly striated above, which nearly touched a concavity on the quadrate. Below this is a strong buttress notched above and behind by the postquadrate foramen. It is convenient to call this the *prootic buttress*; it separates the entrance to the mastoid antrum from the postquadrate foramen and probably braced the prootic articular area for the quadrate, which lies directly above it. The dorsal end of the postfenestral depression forms a shallow concavity in the lower surface of the buttress; its posterior border is the thick, rounded lower margin of the postquadrate foramen. The groove for the hyomandibular branch of VII runs back across the lower end of a strong ridge at the anterior side of the depression and ceases owing to the change in level (figure 24); thus the postfenestral depression passed up and back medial to this nerve and the stapedial artery, as does the posterior tympanic recess in the bird skull.

The anterior end of the prootic is thickened medial to the flange and fits against a correspondingly broad surface on the basisphenoid immediately lateral to the internal foramen for nerve VI (figure 30*c*). This portion sends a short process upwards which tapers out in a recess in the laterosphenoid, in front of the lower half of the trigeminal foramen. The lower end of the prootic overlaps the basisphenoid at the upper corner of the postcarotid recess, both bones combining to form a web spanning the channel beneath the flange.

The trigeminal foramen is centrally constricted, the upper portion probably serving for the exit of the middle cerebral vein. Above this, the edge-to-edge junction with the laterosphenoid runs at first sinuously at a thickened contact which bulges laterally, and then up and slightly back to meet the parietal. The lateral surface of the bone is gently concave, curving round behind at a broad, saddle-shaped area to form the floor and inner wall of the temporal canal. Here it makes a substantial buttress to receive the anterior end of the squamosal. Other contacts within the temporal canal have been described under *squamosal*, *parietal*, *epiotic* and *opisthotic*. The articular surface for the head of the quadrate consists of a broad groove beginning in front of the postquadrate foramen and running down and forward across the posterior corner of the flange (figures 15*a*, 21*a* and 23*b*). The shallow anterior part of this groove was previously incorrectly labelled 'canal for stapedial artery' (Walker 1972, fig. 1b). The medial wall of the groove is well developed lateral to the temporal canal but declines abruptly in front of this.

The *basisphenoid* (figures 17 and 20–27) is by far the most complex element in the skull, consisting of little more than a system of bony lamellae surrounding a number of pneumatic sinuses or recesses. There is no evidence of a separate presphenoid or parasphenoid and the bone will be described as a single entity. The posterior portion sheathes the anterior half of the basioccipital as described and forms a thin lateral wall to the lagenar recess. In front of this the lower part of the bone contracts in width and assumes a thin, W-shaped cross-section. The median channel on the lower surface occupies the central part of the 'W', whereas the paired channels on the upper surface probably carried the internal carotid arteries. Above and in front of the W-shaped portion lies a large air space, which may conveniently be regarded as divided into two parts by a strut of bone which conveyed the internal carotids into the base of the pituitary fossa. This strut is here called the *carotid pillar*, and the recesses in front of and behind it will be referred to as the *precarotid* and *postcarotid recesses*, respectively. The carotid pillar interrupts the continuity of the W-shaped section, which resumes again in front of it, curving down into the roots of the large basipterygoid processes. The central portion of the 'W' continues down and forwards as a crest of thin bone which unites the basipterygoid processes in the mid-line, and which will be termed the *interbasipterygoid lamina*. The channels in the dorsal surface of the 'W' curve down to form the posterior ends of the elongated apertures which give access to the cavities within the basipterygoid processes.

The postcarotid recess is an almost rectangular aperture in side view, passing completely through the basisphenoid from side to side. Its posterodorsal wall is a thin plate of bone, the *basisphenoid plate*, which slopes upwards and forwards to the dorsum sellae. The edges of this plate appear at first glance to converge dorsally, but this is largely due to loss of bone; the plate would originally have been for the most part parallel sided. The lower ends of its edges curve smoothly laterally where they join on to the flanks of the bone, forming notches which indicate the course of the internal carotid arteries and the palatine branches of the facial nerves (figure 23). The edges of the plate are bevelled off posterodorsally to receive the anterior edges of the prootics. This contact is broad below and tapers dorsally. On the right side, just medial to the notch for the internal carotid, is a narrow cavity caused by squeezing. Below it lies a small, shallow, almost circular pit, which is matched by a similar structure on the left side (figures 21*f* and 23*a*, *d*). The pits are floored by grey, granular bone, in contrast to the smooth, well-ossified bone surrounding them. They do not abut against the cavities in the basioccipital; on the right, part of the basioccipital and prootic have broken away internally and one can see from within the cranial cavity that there is a thin wall of basioccipital resting against the posterior surface of the lower end of the basisphenoid plate. The pits are evidently residual areas of incompletely ossified bone, which has shrunk slightly on the drying out of the skull. They appear to be homologous with similar residual areas in the basisphenoid of the young of certain modern birds, e.g. the sandwich tern, *Sterna sandvicensis*, and the penguin *Eudyptes chrysolophus*.

The front surface of the basisphenoid plate merges at its lower end with the upper surface of the 'W'. Although on the right side the channel in this upper surface has been accentuated, it is continuous with the notch at the edge of the plate and gives every appearance of having carried the internal carotid. The outer limb of the 'W' on the other side is more distorted. The channel dips in a roughly semicircular arc and the carotid then ran up the groove in the outer edge of the pillar to enter the lower end of the pituitary fossa (figures 21*d*, *e* and 23*c*).

The carotid pillar tapers to half its breadth at the foramina for the carotids. These are set towards the

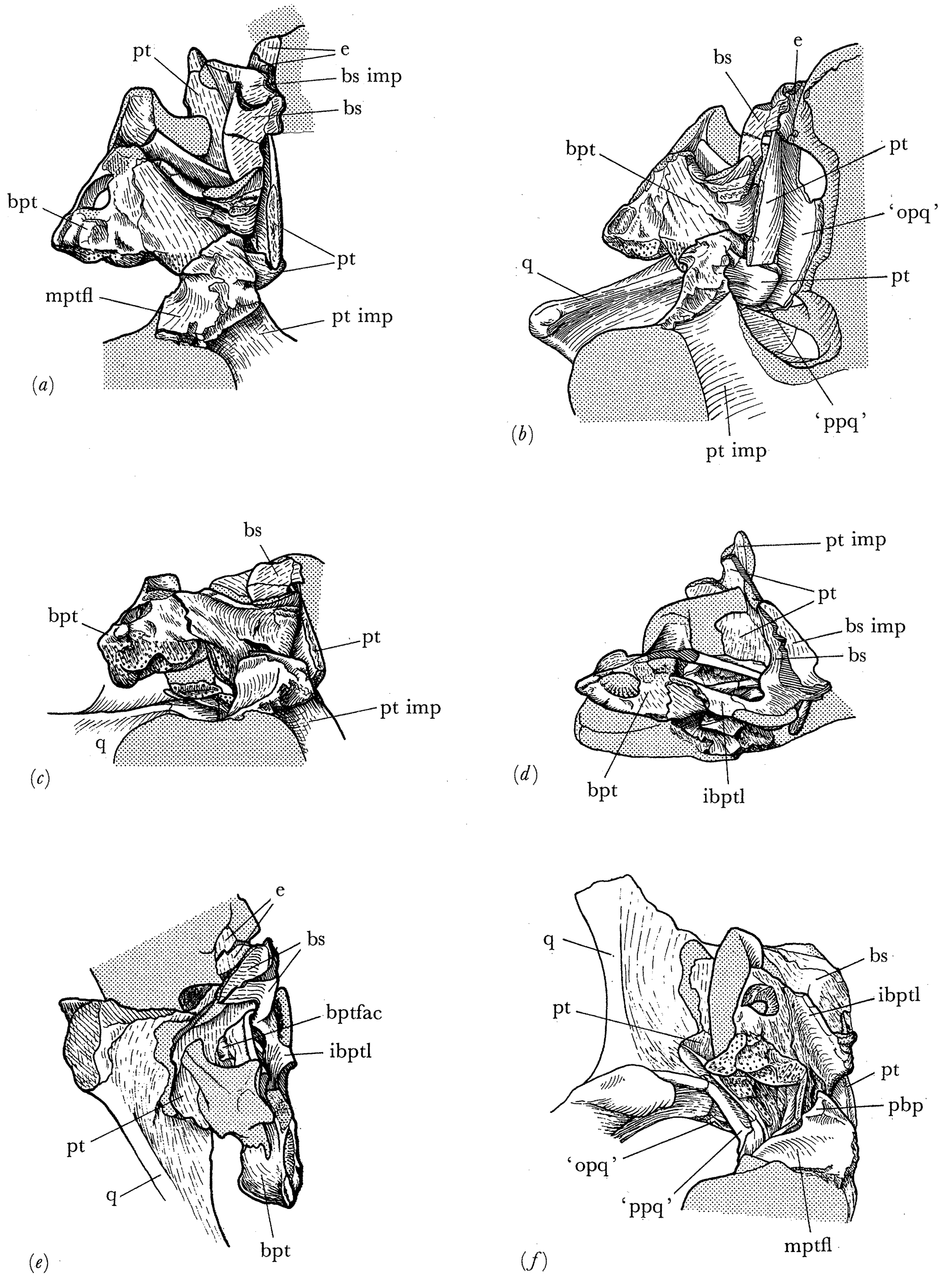

Figure 25. *Sphenosuchus acutus* Htn. The left basipterygoid process in relation to quadrate and pterygoid, as preserved. (*a*) medial, (*b*) anteromedial, (*c*) ventral and (*d*) dorsal views; (*e*) posterodorsal view showing basipterygoid facet; (*f*) posteroventral view. Magn. × 1.5.

posterior side, as are the grooves leading up to them. The foramina join below the fossa and here one can see through them from side to side. The pillar broadens out anteriorly and posteriorly above to merge with the lower part of the cup which contains the pituitary fossa. The latter is a thin-walled structure lying between the basisphenoidal continuations of the prootic flanges, and has been very much compressed. It appears to have been sub-triangular in shape as seen from above, the broadest side lying posteriorly, and the other two sides converging forwards to a rounded anterior end. It is *ca.* 5 mm deep, excluding the confluence of the carotid canals at its base.

It seems that there was a small increase in width of the flange as it passed on to the basisphenoid, although it is difficult to be certain of this. The flanges appeared when prepared to have lost very little bone, except posteriorly on the left prootic, and the basisphenoidal parts agree very closely in their maximum depth. It is certain that this represents the full depth on the left side, because the flange here is continued on the 'left quadrate piece' (figure 17). (The groove which runs along the anterior half of the upper edge of the 'right basipterygoid piece' (figure 26*c, d*) is probably a break; cleaning the mud from this edge failed to reveal any trace of bone.) The increase in width is not great, but it does seem to indicate the presence of an incipient projection of the basisphenoid, like that variously called in birds the 'alisphenoid wing' (Pycraft 1898*b*), 'tympanaler Flügel' (Erdmann 1940) or 'alaparasphenoid' (Jollie 1957).

The roof of the postcarotid recess is occupied by a pair of strong, cylindroidal ridges which arch forwards from the top of the basisphenoid plate to merge with the rear wall of the pituitary cup (figure 21*d*). These ridges are in fact tubes of bone which carried the abducens nerves. The latter led off in front from the summits of the arches and emerged at small foramina lateral to the posterior wall of the pituitary fossa; the left tube has been broken open (figure 23*d*). There is now a narrow slot, due to breakage, between the tubes, but the gap would originally have been greater and almost certainly roofed by bone. There was evidently a high arch forming the dorsum sellae at the summit of the recess. At the sides of this region broad facets articulate with the laterosphenoids, although the inner edges have been broken away. The left side preserves more or less the original relationships between basisphenoid, laterosphenoid and prootic in front of the trigeminal foramen, although the latter has been squeezed nearly shut. The articular surface on the laterosphenoid faces ventromedially and is convex both anteroposteriorly and transversely. The facet on the basisphenoid to receive it, at the side of the dorsum sellae, must originally have been of considerable depth.

The precarotid recess communicates with the cavities in the basipterygoid processes below and with the cavity in the rostrum in front. A pair of small depressions at the anterior base of the pillar are probably pneumatic in nature. The legend to a previous figure (Walker 1972, fig. 1b) described the basipterygoid processes as 'suspended from separate anterior and posterior struts' and showed the cultriform process on a level with the pituitary fossa. This was based on the belief that the cultriform process had been sheared through and dropped down *post mortem*. Subsequent preparation and study made it clear that this was incorrect. Interpretation of the structure of the rostral region is made difficult by the fact that several pieces join together at its posterior end and some bone has been lost. Understanding is facilitated by comparison with the structure of a thecodontian such as *Stagonolepis* (Walker 1961). In this form there is a deep median groove beneath the basisphenoid and the midline of this groove slants forwards and downwards to a point between the basipterygoid processes, beyond which it curves upwards for a short distance and then runs out horizontally as the base of the cultriform process. If the basisphenoid were hollow, its thin lower wall when sagittally sectioned would conform in profile to the above line, and this is in fact the configuration found in *Sphenosuchus*. The interbasipterygoid lamina is equivalent to the groove between the basipterygoid processes of *Stagonolepis*; it is seen in broken section in the 'left quadrate piece' (figure 25). It could formerly be seen to curve down a little further to the right beyond its median culmination and hence it is a midline structure; unfortunately some bone was lost from the edge after the drawings were made. The lamina curves upwards and thickens in front (partly due to shearing) and, after a short gap, resumes on the 'laterosphenoids piece' as the cultriform process. It is an added difficulty that this region is seen mainly from the left side, whereas the left basipterygoid process and the lamina are mainly visible from the opposite side (figure 17). In its present position the lower edge of the cultriform process points towards the highest part of the pterygoids in the anterior part of the palate, just as it does in *Stagonolepis*, and this affords further evidence that it has not been significantly displaced.

The paired 'anterior struts' as shown in the earlier figure are in fact simply the posterior ends of the sides of a median rostral air space (the *rostral recess*) beneath the pituitary cup, a space which extended forwards into the cultriform process also. However, to term them 'struts' is not entirely inappropriate, because their posterior edges are thick and rounded, and it is convenient to continue using this term in quotation marks when dealing with problems posed by the preservation of this region. The lower edges of the prootic–basisphenoid flanges curve inwards and downwards in front and merge with the sides of the rostrum just in front of its rear edges (i.e. the 'struts'). The sides of the rostrum become thinner anteriorly and in front of the basipterygoid processes they have been compressed between the thickened anterior edges of the quadrate rami of the pterygoids. On the left side this edge has cut into the side of the rostrum and fractured it (figure 25*a, b*).

It appears at first sight that the upward convergence of the 'struts' is entirely the result of this compression, but the situation in front of the pituitary fossa shows that, on the contrary, it is largely original. The actual merging of the 'struts' must have occurred directly above the part remaining on the 'left quadrate piece' but has unfortunately been lost. The convergence of the 'struts' at *ca.* 30° is in fact a continuation of the situation seen at the basisphenoid flanges, which approach each other closely in front of the pituitary fossa (figure 23). The sides of the fossa are almost complete on the 'braincase piece', but in front of this the upper edge of the rostrum is damaged, although there was evidently a fairly high median septum of bone here (figure 17*a*).

The fragment on the 'laterosphenoids piece' (figure 26*e–h*) consists of a portion of the cultriform process with part of the thin-walled hollow rostrum above it at its proximal end. Fortunately this area preserves the dorsal junction of the side walls. These apparently converged at *ca.* 30° originally. The median upper portion divides anteriorly to give a vertical groove (pressed shut above) which continued downwards as the open anterior end of the rostral recess. The anterior edge of the left wall is wavy and horizontally striated, suggesting a cartilaginous contact, and it is clear that the posterior edge of the cartilaginous interorbital septum rested in this channel, rising more or less vertically from the cultriform process. The latter is sub-triangular in cross section posteriorly, becoming attenuated forwards so that at its broken anterior end it has become '**Y**'-shaped, the stem of the '**Y**' being a thin, sharp-edged keel, with the arms diverging to form a groove for the interorbital septum. The posterior end is penetrated by a tapering cavity. Originally more of the left wall was preserved, and there was a complete, or nearly complete, horizontal septum separating the upper and lower air spaces at the rear end. Unfortunately some parts of these very thin laminae were lost during preparation. The septum continues anteriorly as a pair of ridges on the inner surfaces, which ran obliquely down and apparently joined at the floor of the groove in the upper surface of the process, a little behind the anterior end of the lower pneumatic space. The position of these ridges marks the limit of the cartilaginous interorbital septum, and indicates that posteriorly its base was in contact with the air space within the cultriform process. The resemblance throughout the rostrum to the conditions in birds, especially juvenile birds, is extremely striking.

Although it is clear that the lower surface of the interbasipterygoid lamina continued forwards as the lower edge of the rostrum, and the 'struts' continued as the sides of the rostrum, it is not quite so evident as to how the convex upper surface of the lamina passed forwards into the inner surfaces of the rostrum, assuming that there was no fenestration of the sides of the latter. Interpretation of this transition is difficult on present evidence, and there may have been a more complex system of internal ridges than as shown in figure 28*b*. The inner surfaces of the 'struts' seem to have been separated by some 5 mm at their lower ends, bordering a triangular aperture some 9 mm high.

The *basipterygoid process* (figures 25–27) is a large, hollow structure, approximately tetrahedral in shape (rather like an old-fashioned flat-iron, except that the lower surface is convex), originally forming an almost complete shell of bone with an elongated dorsal aperture open to the precarotid recess. The upper walls are made of thin, lamellar bone perforated by several foramina, but the lower or ventrolateral wall is minutely porous and extremely fragile except anteroventrally where the bone is stronger and thicker.

The medial walls appear to have been essentially parallel and a few millimetres apart, but it is possible that the processes diverged a little as a whole from their posterior apices at the foot of the carotid pillar. The right process has suffered mainly from compression, whereas that of the left side has also had its lateral side pushed forwards to that the posterior wall is strongly oblique. The medial wall, approximately triangular, is an expansion of one of the inner limbs of the '**W**' referred to above. Anteriorly the surface is smooth, curving over medially to form the interbasipterygoid lamina. Posteriorly it is complexly sculptured or fluted, but much of the extremely thin bone has been lost from the right side and the left has been defaced by chisel marks, so that it is not possible to give a complete account of it. The posterior edge broadens downwards and forms a rounded buttress between medial and posterior faces. Its lower end, seen in broken cross section, has a wall about 1.5 mm thick containing elongated thin-walled cavities, *ca.* 0.25 mm in diameter × 1 mm long, sandwiched between two thin lamellae. The interior of the buttress also appears to have consisted of larger spaces between very thin partitions. It is not easy to interpret and harmonize the lower edges of the two sides owing to loss of bone and the fragmentation and distortion of the lower surfaces. However, it does seem that there was a thin flange or bevelled edge running round the posterior half of the process.

About halfway up the posterior border of the medial face is an oval foramen 2.5 mm in length, set close to the edge. The bone surface curves posterodorsally into the cavity and now, in fact, closes up the foramen on the right side. Comparison with the left side, however, indicates that originally there would have been at least a slit-like aperture at the back of this depression.

The posterior wall is incompletely preserved on each side but the two sides complement each other to a large extent. It appears to have been essentially triangular in shape, with the lower edge curving outwards and upwards to a posterolateral projection. The posterior and dorsolateral walls have been strongly buckled on the right side; however, there appears to have been no definite separation between them. The lower edge projected as a broad flange posteriorly and to a lesser extent laterally. A large foramen, originally some 4 mm long × 2 or 3 mm wide, is set obliquely about halfway up the posterior wall and 2 mm from its inner edge, and there are indications on the left side of three further smaller foramina extending roughly in a line towards the posterolateral corner. It is possible that the outermost of these corresponds to one seen at the rear of the dorsolateral wall on the other side.

The ventrolateral wall has fortunately been preserved in a broken but fairly complete condition on the right side, although difficult to distinguish from the matrix. The medial half of this wall is mostly preserved on the 'right pterygoid piece' (figure 27*d*) and the lateral half on the 'right basipterygoid piece' (figure 26*b*). When these two pieces are fitted together it is clear that one is dealing with a structure which is continuous with the medial wall. The ventrolateral wall is gently convex, continuing with a slight accentuation the curvature of the inner surface of the quadrate ramus of the pterygoid. It seemed at first that the two bones were joined edge-to-edge, and this was one of the reasons for stating that the basal articulation was fixed (Walker 1972). However, later preparation showed that the ventrolateral wall extended farther dorsally within the pterygoid (figures 26*a*, *b* and 27d), and there is no question of its being fixed to that bone, although they may have been in contact. This preparation was undertaken somewhat reluctantly as it involved removal of part of the impression of the right pterygoid, of which little actual bone remains. It was, however, rewarded by the discovery of more of the dorsolateral wall with its lower edge, and a large part of the basipterygoid facet, which is damaged on the opposite side. The portions of the ventrolateral wall preserved indicate that its posterior edge was disposed at right angles to the medial edge, and hence to the mid-line. There may have been a groove broadening

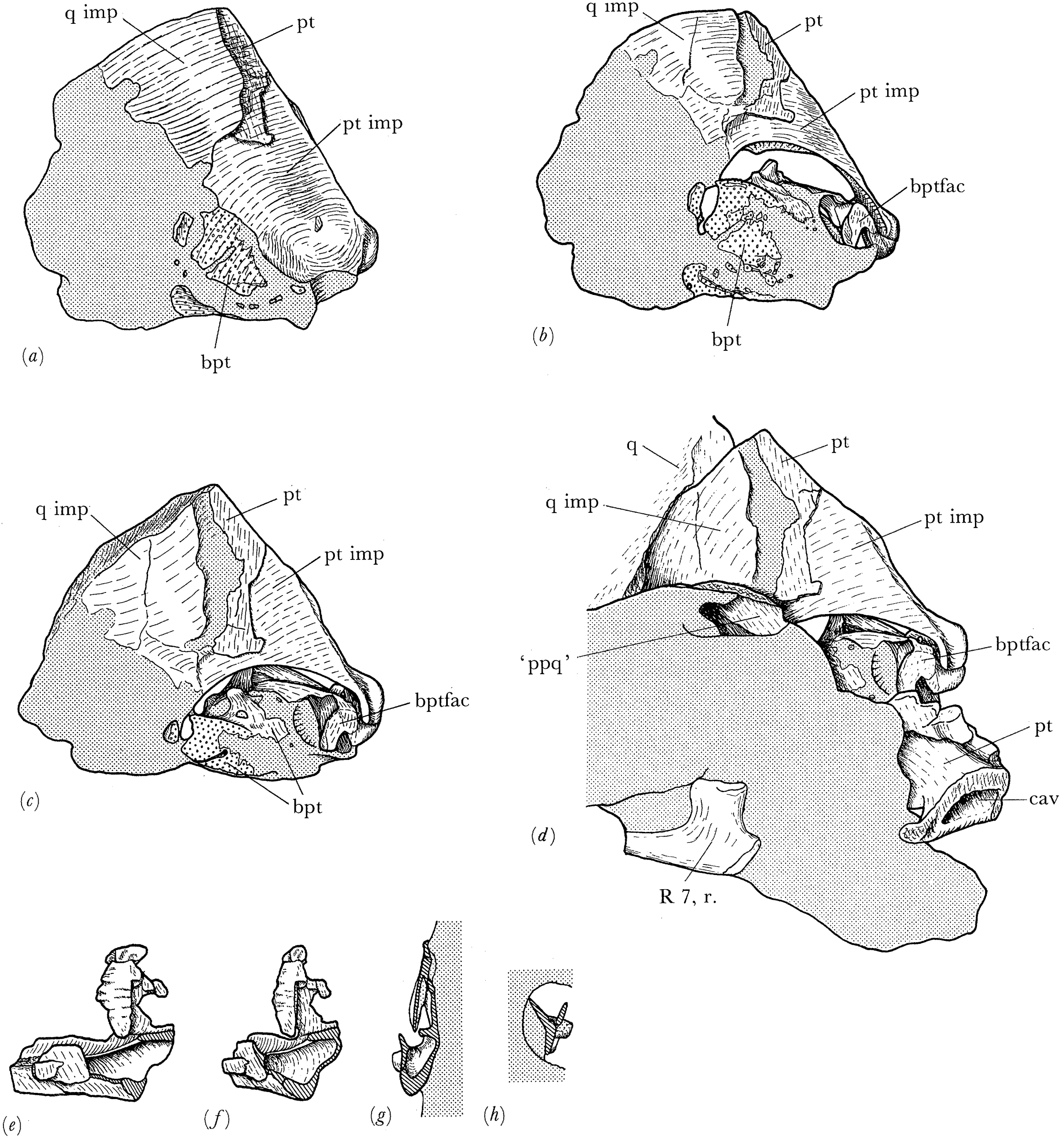

Figure 26. *Sphenosuchus acutus* Htn. (*a*)–(*d*): Lateral views of right basipterygoid process in relation to pterygoid, as preserved. (*a*) ventrolateral view before preparation; (*b*) the same, after removal of some of the impressions. Shows maximum extent of ventrolateral wall of basipterygoid process, also basipterygoid facet; (*c*) lateral view, showing crumpled dorsolateral wall of basipterygoid process; (*d*) a similar view to (*c*), with basipterygoid process in place within right pterygoid; the lateral pterygoid flange is broken away; (*e*)–(*h*) lateral, posterolateral, posterior and anterior views of rostrum and cultriform process of basisphenoid. (*a*)–(*d*): Magn. × 1.5; (*e*)–(*h*): magn. × 2.5.

backwards near the inner edge, represented by a convex impression on the 'right pterygoid piece' (figure 27*d*), but this may simply be an effect of preservation. The ventrolateral wall merges with the dorsolateral wall in front, the projecting edge between them dying out halfway along the process.

The dorsolateral wall consists mainly of lamellar bone. On the left side it is now nearly in the same plane as the posterior wall. A groove indicating the course of the palatine branch of the facial nerve begins laterally below the lower angle of the postcarotid recess and runs down behind the rear border of the process, curving round below on to the medial surface (figures 21 and 27*b*). The upper edge of the dorsolateral wall is thickened to form a strengthening rib slanting downwards and forwards. A sharp bend anteriorly in this rib on the left side (figure 25*e*) has been caused by the forward push on this side. To correct it the anterior 'strut' has to be imagined as rotated anticlockwise (seen from above) about its vertical axis. The slanting rib then joins on to the lateral side of the 'strut'. A longitudinal groove runs along below the rib on the lateral surface, passing over the basipterygoid facet and dying out. Posteriorly it ceases without joining up with the groove for the palatine nerve. The groove may have been for the sphenopalatine (sympathetic) nerve

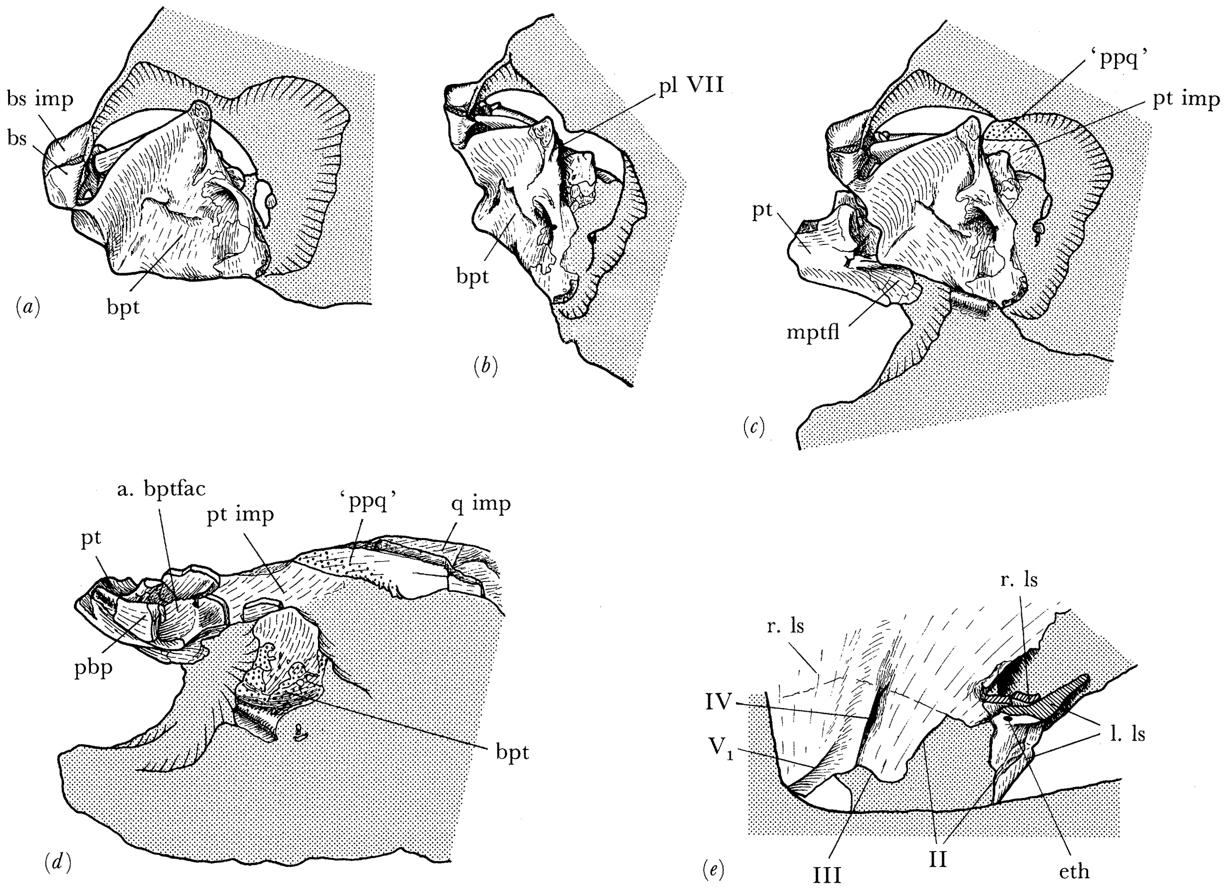

Figure 27. *Sphenosuchus acutus* Htn. (*a*)–(*d*): Medial views of right basipterygoid process in relation to pterygoid, as preserved. (*a*), (*b*) Medial and dorsomedial views; (*c*) a similar view to (*b*), showing basipterygoid process in place within right pterygoid; (*d*) dorsomedial view of basal region of right pterygoid and impression of ventrolateral wall of basipterygoid process with some adherent bone; (*e*) details of lower anterior parts of laterosphenoids. (*a*)–(*d*): Magn. × 1.5; (*e*): magn. × 3.

which passes over the basipterygoid process in at least some birds (Toerien 1971), or for a branch of the internal carotid artery which does likewise (personal observations).

The anterior part of the dorsolateral wall is convex laterally, becoming concave posteriorly and curving out to the edge which separates it from the ventrolateral wall. On the right side there is a small foramen in this lower area and behind it an apparently oval larger one perhaps 3 mm long, set obliquely at the point where the dorsolateral wall curves round into the posterior wall (figure 26*c*). There are indications of an additional large foramen, perhaps 3 or 4 mm long, or possibly two smaller ones, above and in front of the two just mentioned.

The lateral wall extends forwards and joins on to the upper end of the basipterygoid facet. One of the most puzzling questions concerns the structure of the lower part of the lateral wall in this region. On the left side thin, porous grey bone extends ventrolaterally without an obvious break right into the axis of the 'kink' in the pterygoid (figure 25*f*), and it seems scarcely possible that this can represent an original extension in this orientation. Since additional bone of the same type is present more dorsally, it is assumed that the extension is a continuation of the lateral wall which has been bent downwards. However, the rear edge of the facet must have projected quite strongly laterally so that there may have been a foramen in the lateral wall behind it.

The interior of the process has been partly cleared on the right and almost completely on the left. Internal ridges on the medial and lateral walls curve down forwards and join to form an oblique septum bracing the basipterygoid facet and dividing the lower part of the cavity into two pockets (figure 25*d*). On the left side the smaller anterior pocket has been almost filled by a tongue of bone from the anteroventral end of the process which has been forced laterally by compression against the basal region of the pterygoid. This has also resulted in some lateral deflection of the anterior half of the lower edge of the process. However, neither of these effects seems adequate to account for more than a part of the lateral curvature of the lower edge anteriorly, a curvature which is also suggested by appearances on the right side. On the right process the ridge on the medial wall is represented by a ventrally deepening groove on the impression (figure 27). Here also the anteroventral corner of the process seems to have been strongly deflected laterally. Certainly, the anterior pocket within the process lay above a single thick edge and this seems to have curved out and forward to meet and brace the lower end of the basipterygoid facet. This interpretation agrees with the fact that the 'nose' of the

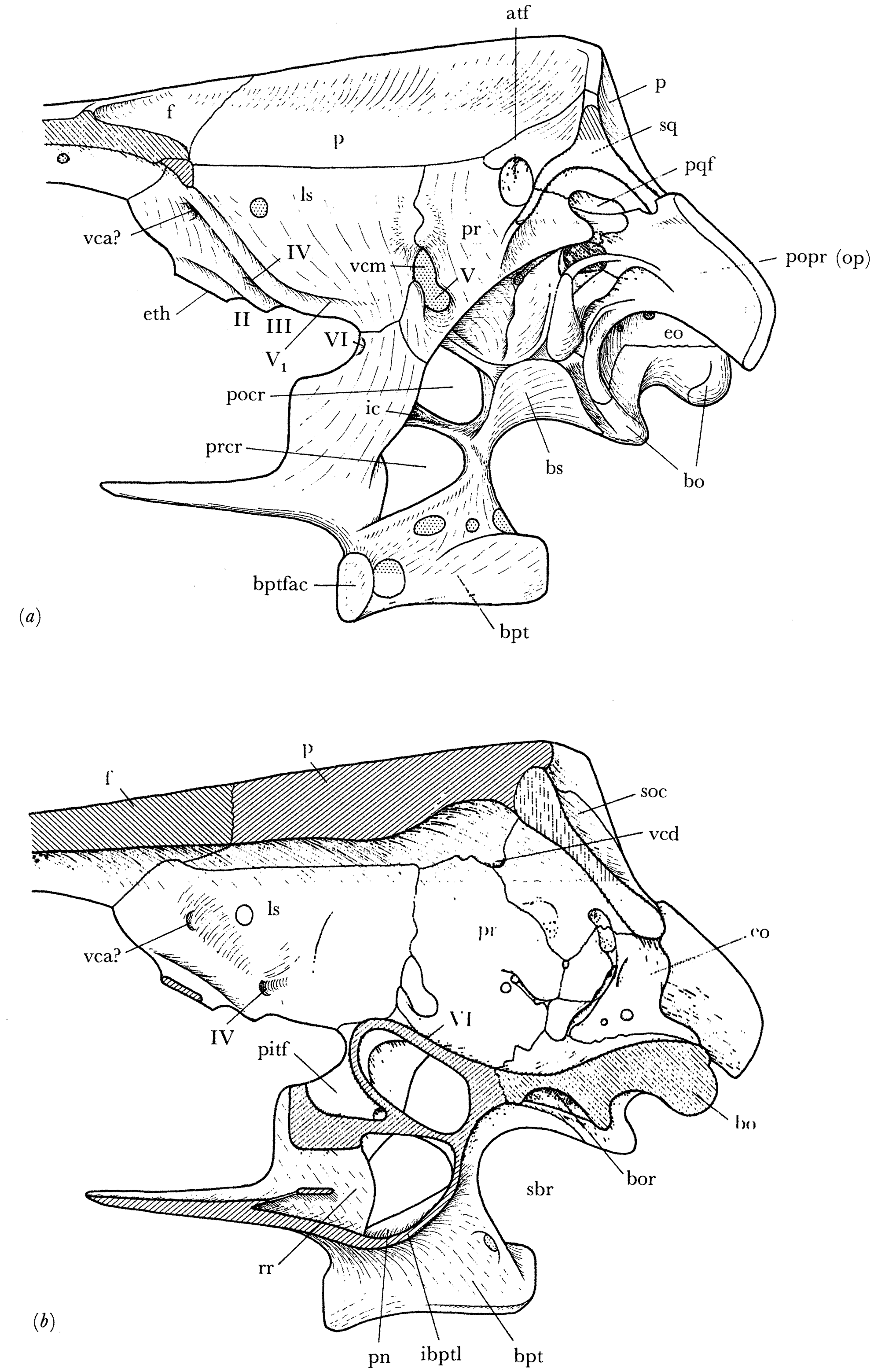

Figure 28. *Sphenosuchus acutus* Htn. Restoration of the braincase. (*a*) Left lateral view; (*b*) sagittal section. Magn. × 1.5.

process is broad at its dorsal end, curving round continuously from medially to anterolaterally facing, but tapers ventrally owing to the arching over of the interbasipterygoid lamina at the base of the rostrum. There must also have been room anteroventrally between the two processes to accommodate the parabasal processes of the pterygoids.

In side view the rear edge of the rostrum slants backwards at first as it ascends, then curves forwards again to merge into the lower end of the basisphenoid flange.

The upper half of the *basipterygoid facet* is preserved on the right side, although it has been pushed upwards, inwards and backwards by the pterygoid (figure 26*d*). Originally it would have faced anterolaterally and probably a little upwards. On the left it is represented by an apparently flat, unfinished surface in close proximity to and directly facing the pterygoid (figure

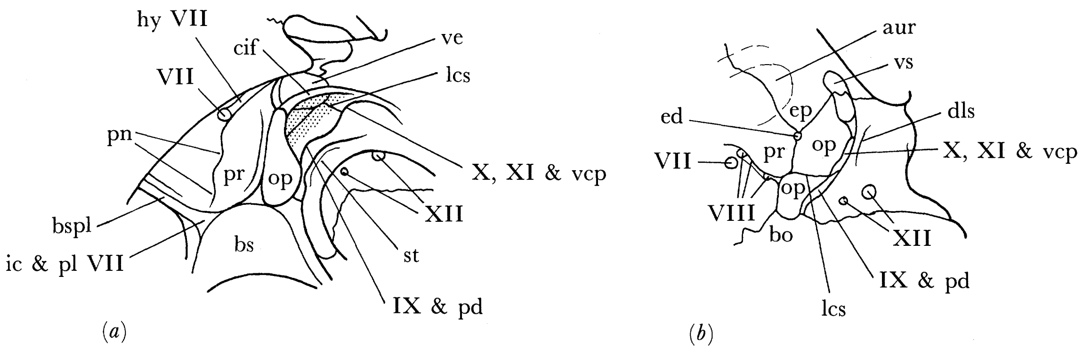

Figure 29. *Sphenosuchus acutus* Htn. Key diagrams of otic region of braincase. (*a*) Lateral view of left side, foramen perilymphaticum stippled; (*b*) medial view of right side. Magn. ×1.5.

25*e*) and consequently very difficult to examine. The posterior edge is broken off on this side. The lower part of the facet is not preserved but the oblique buttressing of this lower region implies that it was well developed. Estimating the total height from the extent of the fractured surface of the right pterygoid gives about 7 mm, while a breadth of 4 mm is suggested by both sides. The facet is not marked off by a rim either dorsally or anteriorly, but displays a slightly roughened surface on the right side. The unfinished surfaces of the facets would presumably have been covered with pads of cartilage in life.

The *laterosphenoid*† (figures 6, 9, 17, 21, 23 and 27) is better preserved on the right side; on the left its anterior half is mainly represented by the rather distorted inner impression. The bone is divided into two regions by a prominent buttress which trends upwards, outwards and forwards and culminates in an elongated, tapering lateral process, originally some 12 mm long on the right side. This process runs out below the junction of frontal and parietal, at the anterior end of the supratemporal fenestra, and was probably not visible from above in the undistorted skull. It lies in a shallow groove in the undersurface of the posterolateral process of the frontal, bounded in front by the postorbital, and its tip makes contact with a shallow recess on the inner surface of the latter bone (figure 7*h*). The outer 5 mm or so of the tip is poorly ossified, consisting of grey–blue, porous bone whose canals are filled with crystalline calcite.

Behind the buttress the laterosphenoid is convex dorsoventrally above, continuing the curvature of the parietal, and expanding forwards from the suture with the prootic. In the anterior part of this area where the bone is thin there is a circular foramen, 2 mm across, of unknown function. A sharp ridge rises in front of the trigeminal foramen, curving upwards and declining along the buttress. The shallow groove between this ridge and the margin indicates the course of the profundus nerve. A few millimetres in front of the buttress on the right laterosphenoid there are two foramina leading upwards and forwards; the larger upper one (figure 6*e*) was probably vascular, while the smaller elongated one, joined to the lower edge by a closed slit (figure 27*e*), was for nerve IV. A little in front of (or medial to) the latter a few millimetres of thickened, finished edge are preserved in a rectangular break in the margin, and indicate the position of the optic foramen. Behind this is a second re-entrant of about the same size into which passes the lower end of the slit. Although the ventral margin is incomplete it seems likely that little is missing, and the more posterior re-entrant probably corresponds fairly closely to the location of the oculomotor foramen. Whether nerves II and III were surrounded by bone or (as seems more probable) lay in notches in the margin, cannot be decided from the present specimen.

In front of these notches the medial parts of the laterosphenoids project as a pair of short processes, the outer surfaces being angled at about 120°, the inner curving smoothly round. These processes now overlap, the left member being lower down. They evidently met the rear end of the interorbital septum along their inner edges, forming a pair of flat surfaces, probably of no great length, facing forwards and downwards. The left member of the pair is the better preserved and is pierced by a small foramen running upwards and forwards close to the mid-line. This probably transmitted the ethmoidal artery. Reconciling of the two sides is difficult because of the distortion and incompleteness of the left side, but a short section of relatively thick finished margin below the small foramen noted above is evidently a more medial structure than anything now visible on the right side and seems to have been part of a median notch running up from the confluent optic foramina. Dorsally the edges of the laterosphenoids are thin, diverging gradually before curving round to meet the frontals. The identification of these foramina is discussed more fully below. There is no indication of a separate orbitosphenoid ossification.

Braincase: internal surface (figures 28b, 30 and 60)

The *basioccipital* has a long exposure on the braincase floor. The posterior portion forms a trough between the exoccipitals, expanding in front of this into the lower ends of the metotic foramina and sending a prominent salient upwards between prootic and opis-

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† The term 'laterosphenoid' for an ossification in the pila antotica was firmly established for the crocodile by Gregory & Noble (1924) and has since been widely used for archosaurs. Its use for a non-homologous element in snakes is later (de Beer 1926). The attempt by Rieppel (1976), followed by Bellairs & Kamal (1981), to revive the term 'pleurosphenoid' (Goodrich, 1930) for the crocodilian bone is therefore mistaken. If a new term is required, it should be applied to the 'laterosphenoid' of snakes. De Beer himself (1926, p. 315) refers to the crocodilian ossification as the 'true laterosphenoid'.

thotic at the lower end of the cochlear recess. The strongly indented contacts with the prootics converge and descend forwards to the straight transverse junction with the basisphenoid. The anterior part of the bone is gently concave from side to side and from front to back, reaching its lowest point between the metotic foramina.

The inner surface of the *exoccipital* is concave dorsoventrally but more or less straight in the fore-and-aft direction. Its lower portion is pierced by the hypoglossal foramina, of which there are two on the left side, whereas on the right there are two small foramina close together anteriorly, which must join in the braincase wall, as well as the larger posterior foramen. Anterodorsally the bone (or the opisthotic) participates with the epiotic (or supraoccipital) in the formation of a deep cavity at the back of the upper part of the otic pyramid. This cavity is 5 mm long by 2 mm wide, reniform in shape with a smooth internal surface. A number of small foramina open into its upper and lower ends. It is open medially and gives off at its lower end a narrow groove, now less than a millimetre in diameter but wider originally, which runs into the upper end of the metotic foramen. It probably housed a venous sinus on the posterior cerebral vein. The anterior end of the exoccipital curves inwards a little and builds a thin wall behind the upper half of the metotic foramen. There was evidently a small recess, as in the modern crocodilian skull, facing inwards and backwards behind this wall. This recess is identified by Hopson (1979, Fig. 1: 'vcp') as receiving a diverticulum of the longitudinal venous sinus.

The *metotic foramen* itself is a narrow, elongated fissure running obliquely up and back behind the otic pyramid and separating for the most part the opisthotic from the exoccipital. The basioccipital enters the lower end.

No suture is discernible between *supraoccipital* and *epiotic* on the inner face of the cranium. Of the two, apparently only the epiotic is exposed within the cranium of modern crocodiles (Parker 1883; Müller 1967). However, the single element present in the adult is very thick in these forms and has a reduced internal exposure due to the strong contact between the exoccipitals above the foramen magnum. It would seem probable that, in the present specimen, the supraoccipital occupies the median or posterior part of the internal surface of the single bone distinguishable, and the epiotics make up the anterolateral parts.

The roof of the cranial cavity curves steeply upwards in the mid-line from just within the foramen magnum. The suture with the parietal runs forwards, downwards and outwards to meet the prootic/epiotic suture. Just before it does so a small foramen enters along the suture between the two bones. This foramen is considered to mark the anterior emergence of the vena capitis dorsalis from the medial wall of the temporal canal. The canal entering above the epiotic on the occiput probably also communicates with this foramen, carrying a tributary vein. On the right side of the cranial cavity the foramen continues forwards as a groove running along the parietal/prootic suture. On the left side the groove appears to have been prolonged downwards towards the trigeminal foramen by a broad, shallow depression, which probably represents the transverse venous sinus.

The epiotic forms a very prominent, rounded buttress, inclined slightly backwards above, and ending below in an acute salient between pro- and opisthotic at the summit of the otic pyramid. The course of the anterior vertical semicircular canal within the bone is shown by a low ridge which curves over forwards and downwards on to the prootic, over the top of the floccular recess (figure 30*b*). The latter is a well-marked depression above and in front of the otic pyramid; a group of three or four small foramina emerge from the epiotic at the posterior end of this cavity.

The *opisthotic* supplies the posteroventral part of the otic pyramid. The small foramen for the endolymphatic duct lies between pro- and opisthotic adjacent to the lower point of the epiotic. The suture then runs down the lower half of the pyramid, is offset forwards a little, then continues down to meet the upward 'V' of the basioccipital. The loop-closure suture of the opisthotic runs back more or less horizontally (figure 30*d*) from the vicinity of the posterior auditory foramen, curving into the metotic foramen and passing round the opisthotic ledge to the exterior.

The *prootic* contributes the anterior part to the floccular recess and meets the basisphenoid at a straight contact. There is a fairly well-marked groove anteroventrally below the pyramid. The facial foramen is set at the anteroventral end of this groove. Immediately behind and above it, close together below the vestibular overhang, are the two foramina for the anterior branch of the auditory nerve. The foramen for the posterior branch lies a short distance behind, connected to them by the groove, which enters the posterior foramen very obliquely.

The elongated upper surface of the *basisphenoid* is almost flat. It expands gradually forwards and rises at about 30°. The anterior end is incomplete. The left side is a little obscured by the prootic, which has hidden the exit of nerve VI on this side. The foramen for the corresponding nerve of the right side is set close to the prootic contact. The central part of the anterior half shows three or four chevron-shaped or converging grooves with their apices pointing forwards (figure 30*c*) in the mid-line. These probably represent branches of the basilar artery as this vessel passed backwards below the brain.

The roof of the cranial cavity is formed by the *parietal*, which also extends about one-quarter the way down the sides. The highest part of the vault is at the posterior end, just in front of the supraoccipital. From here forwards the roof declines gradually to a point within the rear halves of the *laterosphenoids*. Because of the way in which the pieces fit together and loss of bone it has not been possible to clear all of the interior of these elements. The summit of the cranial cavity rises forwards a little below the anterior part of the parietal and then remains essentially horizontal; the thickness of the bone above it gradually decreases. The cross section of the cavity at the rear ends of the laterosphenoids is approximately elliptical, with the greater

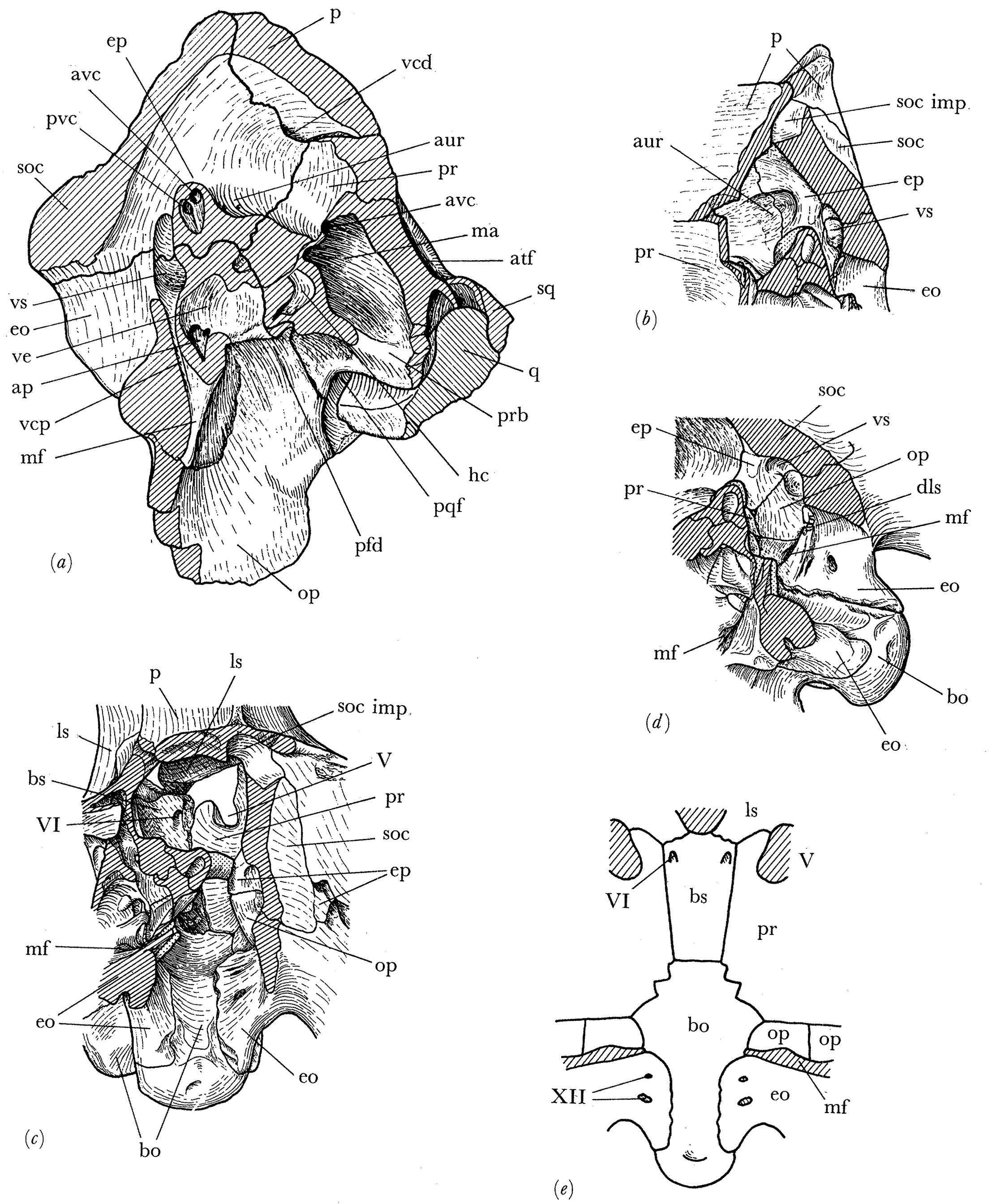

Figure 30. *Sphenosuchus acutus* Htn. Interior of braincase. (*a*) Medial view of 'supraoccipital piece', showing broken section of left otic capsule; (*b*) inner view of right side, showing ridge formed by anterior vertical semicircular canal; (*c*) posterodorsal and a little from the left showing braincase floor and right otic pyramid; (*d*) posteromedial view showing right otic pyramid; (*e*) diagram of sutures on the braincase floor. In (*b*)–(*d*) the left otic capsule is seen in broken cross section and a bridge of matrix, since removed, spans the gap between the otic pyramids. All magn. × 1.5 except (*a*), which is magn. × 2.5.

axis vertical, the maximum width being attained a little above mid-height, within the laterosphenoidal portion. A broad ridge runs up the inner side of the right laterosphenoid, separating a shallow posterior concavity, possibly for the optic lobe, from a deeper anterior one for the cerebral hemisphere.

Lower jaw (*restoration*: *figure 31*)

The lower jaw was made up of at least seven bones: dentary, splenial, coronoid, angular, surangular, articular and prearticular, but two coronoids may have been present. Preservation and restoration are discussed on pp. 9 and 10.

The right *dentary* (figure 32) is the better preserved, but the lateral bulge near the symphysis has been reduced by the compression and the lower parts of the teeth are very much flattened. This bone shows the full number of teeth and alveoli, namely fifteen. The upper portion is gently concave laterally behind the two large teeth, in the region opposite the largest maxillary teeth. The lower half of the anterior end is liberally supplied with large vascular foramina. Above these, at the

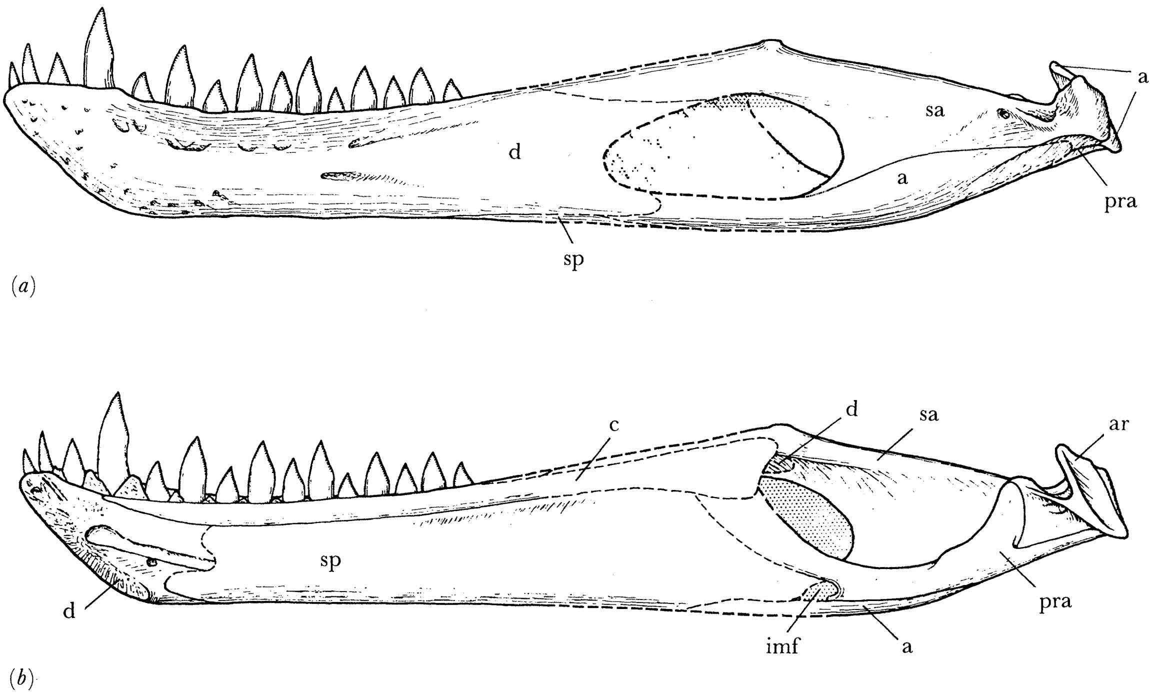

Figure 31. *Sphenosuchus acutus* Htn. Restoration of the lower jaw in (*a*) lateral and (*b*) medial views, magn. ×0.75.

bottom of the concave area, a series of six or seven large foramina open obliquely upwards from a large canal within the bone. From the last of these foramina a groove runs upwards and backwards sub-parallel to the upper border. It is evidently homologous with a groove and foramen in a similar position in the crocodilian skull, and is useful in helping to fix the position of the dentary/surangular contact.

On the medial side the dentary is covered by the splenial up to the rear end of the symphysis. The meckelian canal emerges between dentary and splenial and terminates in a median expansion which lies at about the middle of the triangular symphysial area and acts as a centre from which a series of weak ridges radiates forwards and downwards. The symphysis is rather weak. The break in the middle of the 'right dentary piece' gives a cross section at the ninth and tenth teeth (figure 32*f*). Starting behind the break, approximately below the socket for the tenth tooth, the meckelian canal gives off a larger canal or sinus which passes forward dorsolaterally, sending branches upwards to the foramina in the external concavity. The sinus has a strong bony floor and terminates behind the fourth tooth.

At the fractured posterior end of the right dentary (figure 32*c*, *g*), four layers of bone can be seen at the dorsal side. The outer and inner of these are certainly dentary and splenial, respectively. The posterior side of the last alveolus makes only a shallow recess in the dentary, and a thin bone with a broken upper edge intervenes between dentary and splenial, running along at the base of the flat inner surface of the dentary and tapering out against the splenial about halfway along the inner side of the last alveolus. These relationships are so exactly crocodilian that there can be no doubt that the tapering bone is the anterior tip of the surangular, which formerly extended up to the dorsal border. The shallowness of the last alveolus indicates that its rear wall was partly made up by the surangular, as in *Alligator*, *Caiman*, *Osteolaemus* and *Crocodylus*, and in the phytosaur '*Machaeroprosopus*' (Camp 1930). The fourth layer is only a short portion of a thin plate and is probably part of the upper border of the surangular which has been forced downwards.

Some 15 mm of a thin, flat bone is preserved at the anterior end of the 'left jaw counterpart piece'. This seems to be the rear end of the left dentary. A slight channel below the overhanging rod-like part of the surangular probably received its upper edge. The bone may thus have passed back within and below the surangular as does the dentary in modern crocodiles.

The *splenial* (figure 32) must originally have been somewhat convex medially and the upper half of the posterior end would have been less concave than it is now. Contrary to an earlier statement (Walker 1970), made before the dentaries were separated, the bone takes no part in the symphysis, but thins to a feather-edge in front. It sheathes the inner side of the dentary up to the bases of the teeth, where it meets the coronoid. It also seems to have formed the inner wall of the last three or four alveoli, as in the crocodile, but concealment by the coronoid makes it difficult to settle this point. A narrow, obliquely striated shelf along the upper edge at the rear end suggests that the coronoid continued back along this region. The lower edge thickens posteriorly and takes up an increasing share of the lower surface of the jaw, so that the suture with the dentary passes round to the lateral side at the limit of preservation. Here the splenial underlies the angular. Presumably the lateral exposure of the splenial was short, and as in the thecodontian *Stagonolepis* or a Recent crocodilian, the lower edge of the splenial passed round again to the inner side of the jaw behind this point, in this section lying against the inner surface

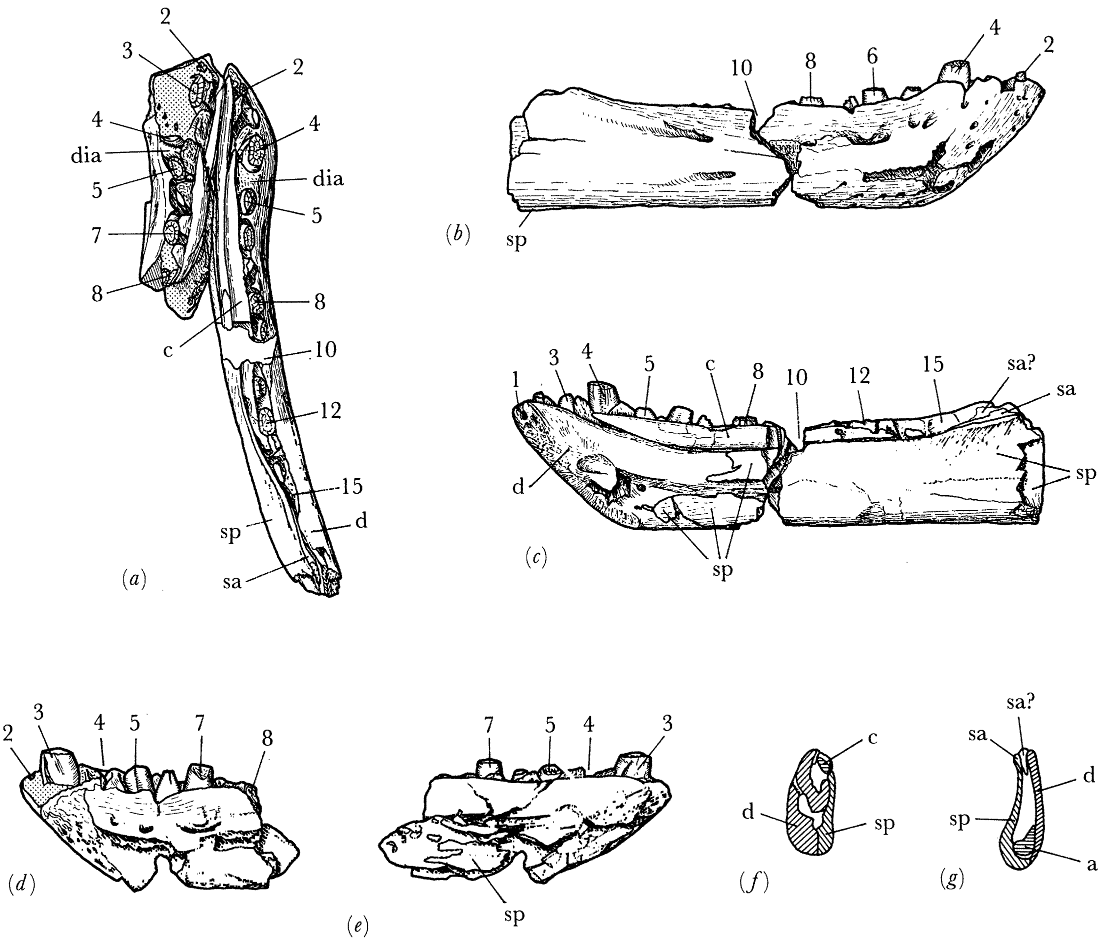

Figure 32. *Sphenosuchus acutus* Htn. (*a*) upper view of anterior ends of lower jaws in symphysis, before separation; (*b*), (*c*) lateral and medial views of 'right dentary piece'; (*d*), (*e*) same of 'left dentary piece'; (*f*) cross section at anterior end of posterior half of 'right dentary piece'; (*g*) cross section at posterior end of same piece. Magn. ×0.75.

of the angular. Posterodorsally the splenial is assumed to have lain against the downwardly projecting flange on the inner side of the dentary and its continuation on the surangular, almost to the beginning of the small ascending flange on the upper edge of the latter. The posterior part of the bone would have extended back to the prearticular as a thin sheet. Ventrally there is evidence for the existence of an infra-meckelian foramen between them.

The *coronoid* (figure 32). A slender splint of bone lying anteriorly above the dentary and splenial seems to have continued back to the area where the coronoid is usually found. Because a coronoid is present in different groups of thecodontians, the Triassic crocodile *Orthosuchus* (Nash 1975), and is retained in living crocodiles, it is highly likely that it occurred in *Sphenosuchus* also. Furthermore, Romer (1971) has figured a long, splint-like coronoid in the Middle Triassic thecodontian *Chanaresuchus*, and this reaches back to the area where the coronoid occurs in other thecodontians. A slender, elongated coronoid is found also in the mesosuchian crocodiles *Pelagosaurus* (Eudes-Deslongchamps 1864), *Steneosaurus* and *Metriorhynchus* (Andrews 1913). Thus it is probable that only a single element was present in *Sphenosuchus*. The bone is of oval cross section and covers the interdental plates. The anterior end tapers to a point, medial to the fourth tooth, slightly overlapping a bevelled-off surface on the dentary. A similar surface at the rear of the splenial suggests that the coronoid formerly lay above this region. Presumably it continued back along the medial face of the surangular, and ended below the small flange on the latter. Probably it met the prearticular posteroventrally. The left coronoid was found displaced and in a fragmentary condition within the matrix covering the anterior end of the palate.

This bone was earlier termed a 'supradentary' (Walker 1970), after Osborn's usage in *Tyrannosaurus* (1912). However, the 'supradentary' of *Tyrannosaurus* (which may in fact be part of the splenial) occupies all of the inner face of the dentary above the meckelian canal, whereas the coronoid of *Sphenosuchus* is essentially dorsal to the dentary and resembles very closely the coronoid of mesosuchian crocodiles.

The central part of the *surangular* (figures 32–34) is nearly flat, with a thickened upper edge which becomes a stout rod over the top of the mandibular fenestra. Just behind the broken anterior end there is a small flattened medial area above which lies a low coronoid flange. In the crocodilian jaw this flattening lies approximately in a vertical plane. Assuming a similar attitude for the area in *Sphenosuchus* implies that the outer surface faced a little upwards. This agrees with the evidence from the cotylus for the quadrate, which seems to have been horizontal in the transverse direction. The surangular tapers to a thin edge below

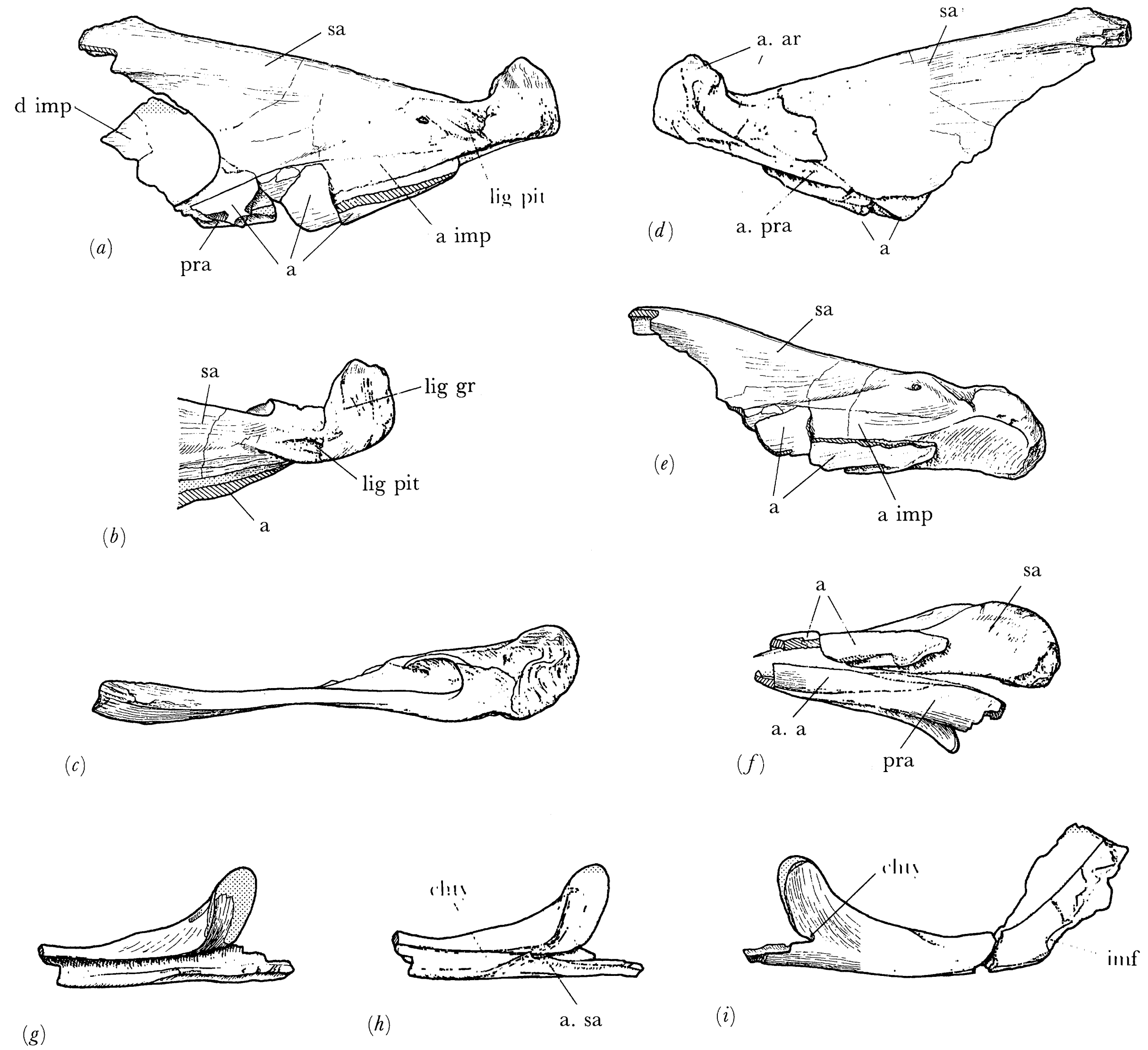

Figure 33. *Sphenosuchus acutus* Htn. (*a*) Lateral view of left surangular and angular; (*b*) dorsolateral view of rear end of surangular; (*c*) upper view of same bone; (*d*) medial view of same, omitting small piece with anterior end of prearticular; (*e*) ventrolateral view of same; (*f*) lower view with prearticular as originally occurring; (*g*) lateral view of rear portion of left prearticular; (*h*) a slightly more dorsal view of same to show groove for chorda tympani nerve; (*i*) medial view of prearticular. Magn. × 1.

the fenestra and is overlapped externally by the angular. Passing backwards the bone develops a lobate, slightly concave ventral area set nearly at right angles to the upper portion and partly covered by the angular. A prominent ligament pit on the side of the bone lateral to the cotylus deepens posteriorly and ends in a very irregular surface.

The thick posterior end of the surangular is deeply excavated medially to receive the articular. In front of this socket the bone has a concave anterior surface. The thin precotylar portion with its thickened upper edge projects forwards from the lateral side of this concavity; on the medial side a thinner, shorter projection runs forwards a short way along the lateral surface of the articular and must have approached very closely to the prearticular above Meckel's cartilage. Below the socket for the articular there is a firm, edge-to-edge contact with the prearticular, but in front of this they diverge leaving a ventral space floored by the angular.

The surangular supplies a little more than half of the concavity for the outer condyle of the quadrate. It contributes approximately the outer third to the curious hoof-like retroarticular process, meeting the articular on the posterior surface in a sinuous subvertical suture. The upper end of this contact makes a conical prominence, the anterior surface of which, behind the cotylus, is deeply grooved along the suture. Another shallow, sinuous groove, believed to mark the course of a medial jugomandibular ligament like that of birds, starts from the groove in the anterior surface of the cone and runs laterally, curving at first backwards and then forwards and ending at a slightly roughened area above and behind the lateral ligament pit referred to above. The posterior and lateral surface of the surangular portion of the retroarticular process is strongly marked by subvertical striations.

The *articular* (figure 34) is only preserved on the right side, together with the posterior ends of the surangular and prearticular. This 'right articular piece' has been distorted so that the originally transverse axis of the

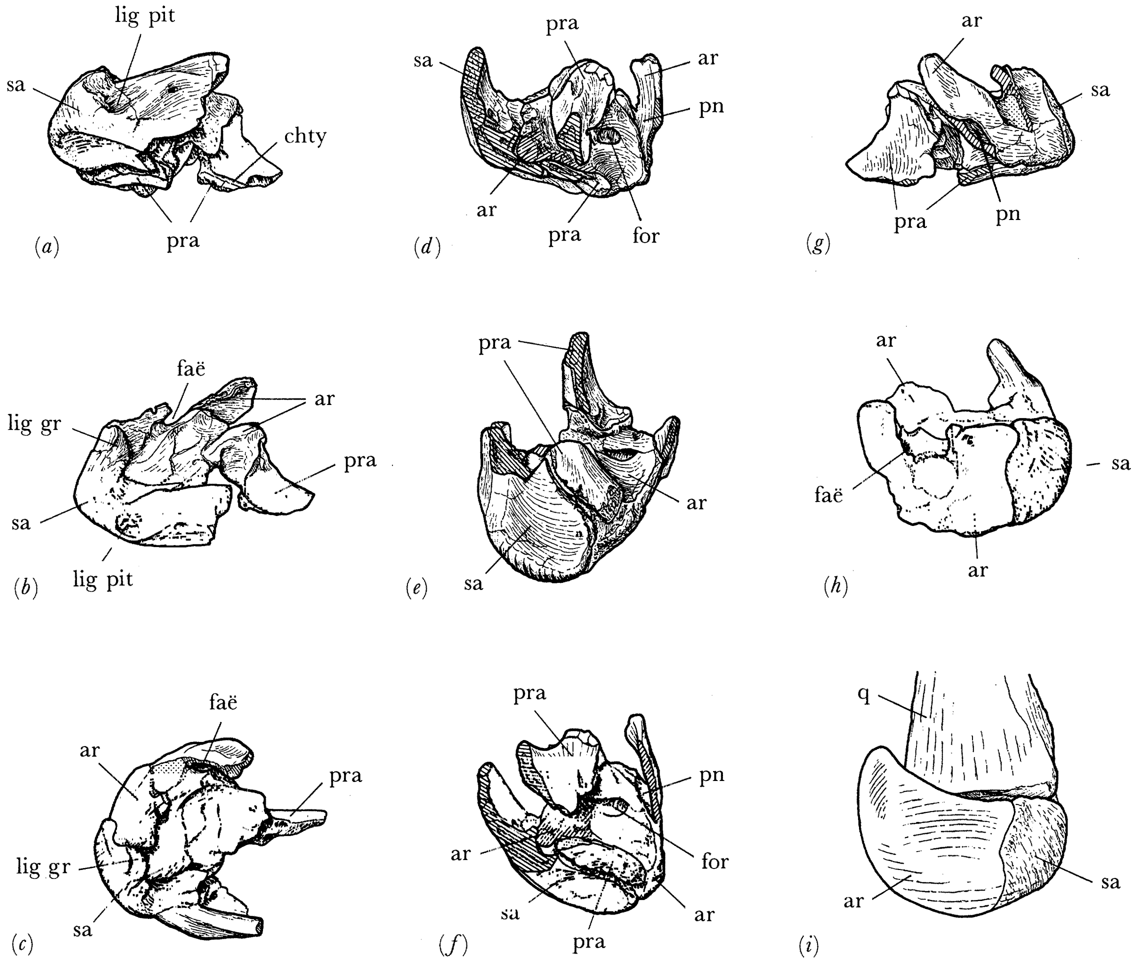

Figure 34. *Sphenosuchus acutus* Htn. The 'right articular piece' in (*a*) lateral; (*b*) dorsolateral; (*c*) dorsal; (*d*) anterior; (*e*) ventral; (*f*) anteroventromedial; (*g*) medial and (*h*) posterodorsal views. (*i*) restored posterior view of right lower jaw in articulation. Magn. × 1.

cotylus is now oblique. The lobed area formed by the surangular and the rear end of the prearticular has been bent medially. The internal ascending process of the articular and the flange which forms its ventral continuation have been bent forwards, accentuating the concavity of the medial surface which lies in front of them. Originally, the inner edge of the internal ascending process must have been directed almost due medially, and the posterior surface of the retroarticular process would probably have been, on the whole, slightly concave.

Regarding the transverse axis of the cotylus as horizontal, the lower surface of the bone is divided into two regions, one of which lies above the lobed area and faces ventrally and a little laterally, while the other is an exposed concavity which faces ventromedially and anteriorly, being overhung by the inner condylar region of the cotylus and bordered behind by the base of the internal process. Laterally, the articular fits into the recess in the surangular which sends a flange medially a short way below it. The posterior process of the prearticular underlies the remainder of the ventrolateral surface, except for the posterior rim. The inner concavity of the articular is pierced by a large foramen, 3 mm in diameter, which enters a substantial cavity, surfaced by smooth bone, lying within the medial side. In front of this is an elevated region anterior to the inner condylar depression. The posterodorsal process of the prearticular covers the anterior and medial surfaces of this prominence, both bones having been a little telescoped. The articular becomes gradually less well ossified and increasingly permeated by matrix anteriorly and, decreasing rapidly in height, obviously passed forwards into Meckel's cartilage. The outer side of the poorly ossified region was covered by the inner projecting tongue of the surangular.

The posterior surface of the bone is damaged; its lateral portion is concave. The upper edge is thick laterally and elevated 2 or 3 mm above the level of the articular surface. There is a gap towards the medial side due to loss of bone but it is evident that the upper edge curved up gradually to the internal ascending process, forming a thin sheet of bone continuous with this process (figure 34*h*, *i*). The latter is a little over a millimetre in thickness, slightly concave anteriorly and convex posteriorly. It is a little thicker at its upper end, which is incomplete but has probably not lost very much, and rises to a height of 6 mm above the articular surface. Some 5 mm of the finished inner edge of the process is preserved at the upper end. Below this the edge is damaged. It converges below with another thin sheet of bone, likewise incomplete medially, which runs down posteroventrally from the inner side of the cotylus. This latter sheet forms the ventromedial concavity and is perforated by the large foramen already noticed. The two sheets bound the internal cavity in front and behind and evidently originally converged to form a continuous projecting rim to the ventromedial concavity. The lowermost part of this rim is still present; its inner edge originally followed a curved course dorsally to join up with the ascending process. The lower end of the rim curves posteriorly and laterally behind the tip of the prearticular, and is continued by the surangular, forming the posterior boundary of the lobate depression. The rim is incomplete; it thickens considerably behind the prearticular and evidently formed a downward projection at this point to which the prearticular probably contributed.

On the dorsal surface the articular surface for the quadrate is clearly marked as an area of grey, minutely porous bone, in strong contrast to the 'normal' bone behind it and to the articular surface on the surangular. There are two moderately deep depressions, strongly oblique like the condyles of the quadrate, with a saddle-shaped area between them. The inner concavity has a strong medial rim, now partly broken away. In front of it the surface rises strongly upwards. The convex posterior surface of this elevation is covered by a continuation of the same grey bone. Between the cotylus and the posterior wall formed by the surangular and articular is a narrow area, some 2 mm wide. This area changes into a groove towards the medial side and turns abruptly downwards into a large pneumatic foramen, posteromedial to the inner condylar depression, which enters the cavity within the bone and is bounded by the two converging sheets already mentioned.

The main part of the *prearticular* (figures 33 and 34) is of L-shaped cross section, tilted a little so that the inner limb faces a little ventrally as well as medially. It forms the lower edge of the jaw posteriorly and is just visible in lateral view, but further forward the angular takes over this position. The posterior end of the bone divides into two processes. Of these, the posterior process underlies the articular and meets the surangular; its inner edge curves round into the ventromedial concavity of the articular. The posterodorsal process is thick anteriorly, where it lies against the anteromedial side of the prominence in front of the cotylus, but tapers to a fine edge posteriorly. The angle within the 'L' is occupied by the groove for Meckel's cartilage. The chorda tympani nerve entered in the angle between the two posterior processes and passed forwards in a well-marked groove below the thickened upper edge of the 'L' (figure 33*h*), on the medial side of the cartilage. The lower part of the bone tapers forwards as it diverges from the surangular, at the same time curving upwards. It evidently ended in a point, below an infra-meckelian foramen, as in *Stagonolepis*. The lower portion also shows a recessed area for the overlap of the angular. The inner flange of the 'L' curves upwards, becoming thinner, and forming the anterior boundary of the adductor fossa. The latter appears to have been narrow, but deep. The upper edge of the bone has two grooves for tendon insertions, one just on the lateral side in front of the upward expansion of the articular, the other just to the medial side at about the middle of the bone.

The *angular* (figures 32 and 33) binds together the prearticular and surangular, being obtusely angulated at its rear end to overlap them both. Its thin dorsal edge at first follows a slight ridge (the ventral boundary of a muscle-insertion field) on the surangular, then diverges posteriorly. The bone bends round a strong ridge on the surangular and dies out about halfway along the lower surface of the lobed area. How far it extended back over the latter is uncertain. Further forwards loss of bone makes details uncertain, but the lower edge of the angular evidently came to lie below that of the prearticular, and continued the curve of the latter upwards and forwards. Its broken anterior end is seen at the rear end of the 'right dentary piece' (figure 32*g*), and is sub-triangular in cross section, the outer side lying against the dentary, the lower side above the splenial. Between these two regions the angular would have formed the lower border of the mandibular fenestra, with the lower branch of the dentary tapering out against it laterally and the splenial in contact with its inner edge. Meckel's cartilage lay in a trough in the prearticular posteriorly (figure 33*g*), but further forwards, where the prearticular diverges from the surangular, the angular covers the ventral space between them, and in the floor of the adductor fossa the cartilage was sheathed roughly equally below by prearticular and angular, its upper surface being exposed.

Dentition (figures 4, 10 and 32)

The teeth and alveoli have been considerably damaged by the distortion of the skull. The interalveolar septa have mostly been crushed and broken, and the roots of the teeth compressed. Almost all the crowns of fully erupted teeth were broken off and were presumably present in the adjoining matrix but few have survived. However, numerous teeth in various stages of eruption are present, and preparation of these has enabled the general form of the teeth to be determined. Difficulty is caused by the loss of the serrated portions from fully erupted teeth, and the inaccessibility of the replacing teeth within the alveoli. The critical transition region has been exposed in a few instances, however. Previously (Walker 1970), the crowns were said to be 'lanceolate, much like those of *Hesperosuchus*' but, with the possible exception of some of the dentary teeth, this does not seem to have been the case.

The premaxillary teeth, of which restoration of the snout seems to demand as many as five or six, are very small, apparently uniform in size and subcylindrical in shape. Their crowns are very poorly preserved. The tip of a replacing tooth (penultimate tooth on left side) shows a fine serrated ridge on its posterior side. The small chip which fits on to the right premaxilla indicates that the last tooth projected at least 7 mm. The penultimate premaxillary tooth, at about 2 mm, is only a little over half the diameter of the first maxillary tooth.

The fourth right maxillary tooth shows that the rounded anterior border passes into a serrated edge distally without any constriction or interruption of the smooth convex profile. Other teeth, notably the fourth left maxillary, show that the serrated posterior edge of the crown was concave in profile, while the eighth of the right side shows that this concavity passed proximally by a gentle reversed curve into a rounded border, again without a constriction or more than a gradual change in profile. The main part of the tooth was originally oval in cross section, with a long root, and slightly recurved. The crowns are dark in colour and lenticular in cross section, the thickest part being in advance of centre. The anterior serrations extend about half as far proximally as the posterior ones. The maxillary teeth (13) increase in size rapidly to the third. This tooth, and the two succeeding it, are very large and no doubt passed down outside the constricted region of the dentary behind the fourth dentary tooth. They are estimated to have projected about 15 mm from the jaw margin. The remaining teeth decrease in size backwards, at first rapidly and then more gradually. The interdental plates are extremely strong in the region of the three largest maxillary teeth, extending down to 6 mm below the maxillary shelves.

The first two dentary teeth are very small and of about the same size as those on the premaxilla. Then follow two large teeth, subequal in size, larger than the remaining dentary teeth but only about three quarters the diameter of the largest maxillary teeth. These teeth are estimated to have projected about 14 mm. The fourth tooth is followed by a diastema of spongy bone, some 3 mm long, instead of the usual thin partition between the sockets. The remaining eleven teeth are subequal in size. In general, the dentary teeth seem to have been like those of the maxilla, but there are indications that the crowns of some of these teeth may have had a more lanceolate shape.

The presence of two large anterior dentary teeth on each side is a functional parallel with the jaws of *Ornithosuchus* (Walker 1964). This arrangement ensures that at least one of the teeth is fully operational on each side at any time. In the present fossil the third left and fourth right dentary teeth are apparently fully erupted, whereas the fourth left and third right are being replaced. These large teeth evidently approached the anterior palatal vacuities as the jaws closed, but their size can hardly be the main reason for the existence of these spaces because the palate is set high up between the large maxillary teeth and only the tips of the dentary teeth could have reached it; furthermore, the cavities extend far dorsally and anteriorly and are quite out of proportion to the size of the dentary fangs. The raised rostral part of the dentary would presumably have been surrounded by the premaxillary teeth. The last four maxillary teeth were unopposed.

The replacement pattern is of the usual archosaurian type, with a marked alternation between mature and replacing teeth. This is clearly exhibited by the maxillae, where on the right side long first, third and fifth teeth alternate with short replacing second and fourth teeth, and on the left side a short fourth tooth lies between long third and fifth teeth. Thus the waves of replacement in the maxillae are approximately in phase, whereas in the dentaries the waves are very clearly seen to be 180° out of phase, as far back as the eighth tooth.

(*b*) *Postcranial skeleton*

Vertebrae

The column appears to have been complete at least as far as to the eighteenth vertebra. However, the skull and anterior cervicals seem to have been separated from the rest of the skeleton, and as the posterior cervicals are identified by comparison with those of *Hesperosuchus* (Colbert 1952), it is possible that a missing vertebra has not been allowed for. The lack of the fourteenth vertebra is probably caused by the loss of a piece of matrix; however, since a rib is also missing at this point there is a possibility that it reflects a real break, either by removal of a vertebra or by backward displacement of the rear vertebrae and their ribs as a whole.

The nearly complete right half of the *proatlas* (figure 35), and a fragment of the left, were originally preserved lying on the right paroccipital process. Identification of the larger bone is based on comparison with the proatlas of *Osteolaemus*, the right half of which it closely resembles. It is a thick, rhomboidal bone, 12 mm along the anterior edge. The upper surface is gently concave, curving up to the midline. The lower surface is convex, with a central oblique thickening. The medial edge is thick, with sutural irregularities for its fellow. The posterolateral corner is a little produced, to rest on a process of the atlas neural arch. A notch at this corner appears to be original.

The elements of the *atlas* and *axis* (figures 35 and 36) lay close behind the skull and were somewhat disarticulated. A poorly preserved area of spongy bone below the left half of the atlas neural arch, which it was not possible to preserve, perhaps represented the atlas intercentrum, or alternatively this element was indicated by a small area of impression closer to the condyle. The left half of the atlas neural arch cannot be separated from the atlas centrum, which was hidden within the matrix. The arch is not quite correctly located, being rotated a little laterally and tilted up anteriorly. The right half, however, is free and can be placed in position. There is an anteroposteriorly concave arched articular surface which rested on a rounded anterolateral projection on the atlas centrum. Anteriorly the usual articular area for the occipital condyle is seen. Above this is a short upward process to receive the proatlas with, behind it, an inwardly and slightly dorsally sloping projection which roofed over the neural canal. These paired processes probably did not meet in the mid-line and were slightly overhung by the neural spine of the axis. A tapering postzygapophysis preserves traces of the articular area, facing downward and inward. The left arch appears curiously robust compared with the right, and this does not seem entirely attributable to loss of bone.

The centrum of the atlas is poorly preserved. It has an irregular wedge-like shape and is 12 mm in width and 10 mm long. There is a shallowly concave anterior face, originally cartilage covered, for the occipital condyle. The floor of the neural canal is nearly flat,

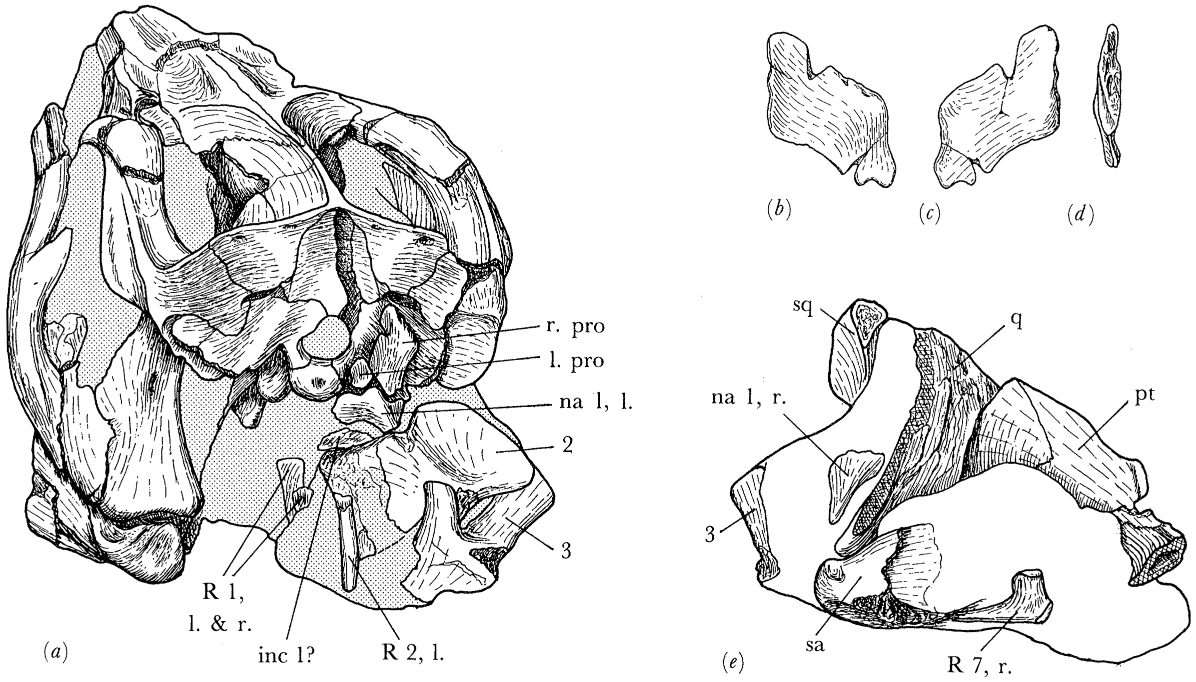

Figure 35. *Sphenosuchus acutus* Htn. (*a*) Occipital view of skull and anterior part of vertebral column, as originally occurring; (*e*) right side view of some of the detachable pieces, magn. × 0.75; (*b*)–(*d*) upper, lower and medial views of right half of proatlas, magn. × 1.5.

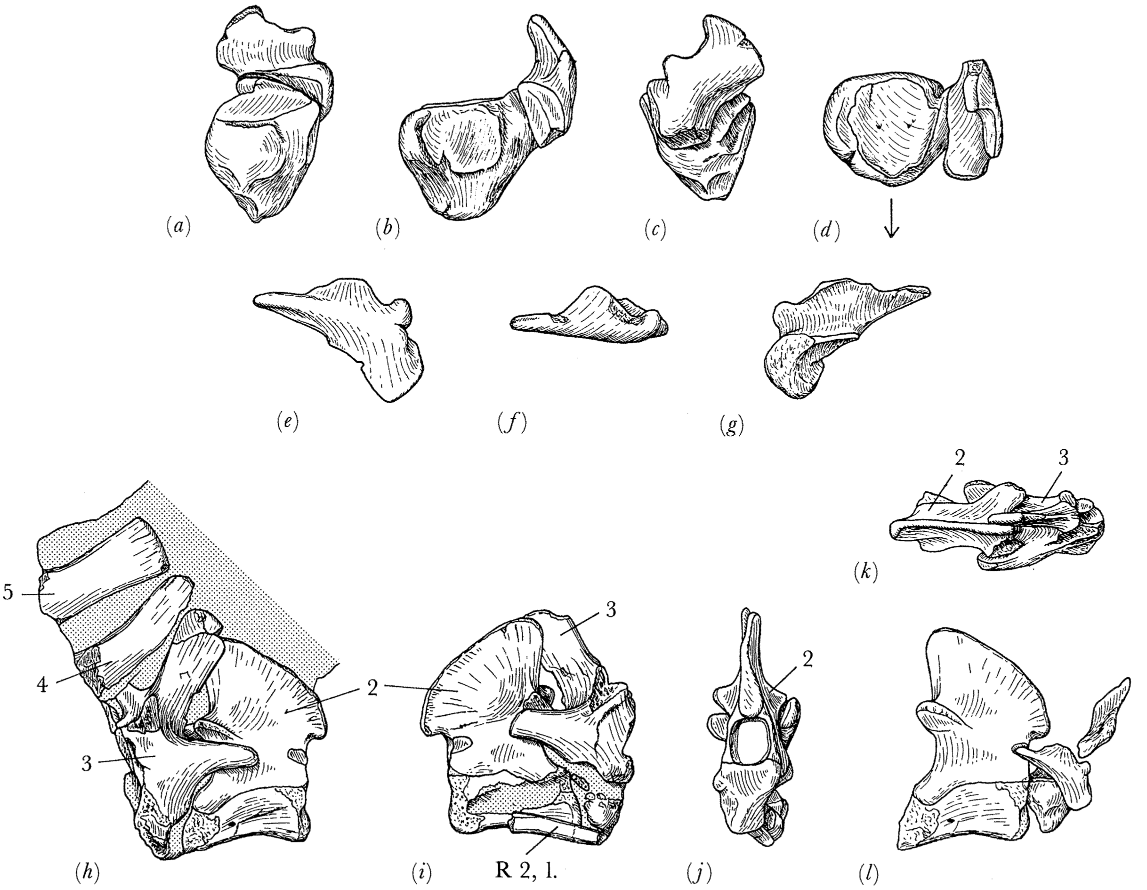

Figure 36. *Sphenosuchus acutus* Htn. (*a*)–(*d*): Right side, anterior, left side and upper views of atlas centrum and left half of neural arch; (*e*)–(*g*): lateral, dorsal and medial views of right half of atlas neural arch; (*h*) right lateral view of axis and parts of cervicals 3–5; (*i*) left lateral view of axis and part of cervical 3; (*j*), (*k*): the same, anterior and dorsal views; (*l*) assembly of proatlas, atlas and axis, right lateral view. (*a*)–(*g*): Magn. × 1.5; (*h*)–(*l*): magn. × 0.75.

with a pair of small foramina. The posterior surface is composed of incomplete, spongy bone, nevertheless the dorsal portion fits quite well into a concavity at the anterior end of the axis centrum, and the floor of the neural canal narrows backward into the axis in a manner which suggests continuity. Articulated in this way, there is a narrow, wedge-shaped ventral gap which scarcely leaves room for a separate axis intercentrum. Accordingly, the atlas centrum and axis intercentrum are believed to have been fused, as in modern crocodiles. There is no sign of rib facets, but preservation is poor. A posterior groove running down the left side, discovered during cleaning, may be a tooth-mark.

The *axis* has been a little crushed, and the centrum has been opened up on the left side. The ends are not well preserved. The centrum was apparently narrow but not keeled, and lacked a hypapophysis. It measures 22 mm long × 11 mm high. A scar anterodorsally may represent the diapophysis, but preservation is poor. The prezygapophyseal facets are broken off. The neural spine is blunt anteriorly, rises steeply backward, and thickens again at the posterodorsal apex. The postzygapophyses are strong and inclined at *ca.* 45°. The neural canal in this and cervical 3 dips deeply into the centrum as a narrow channel. The total height of the axis is 40 mm.

The cervical column bends dorsally behind the axis. Only the anterior end of the centrum of the third cervical is preserved, and this continues the damage seen on the axis on its left side. The scar of the parapophysis is seen low down at the anterior end on the right side. The diapophysis is present on the left side, projecting down from the neural arch some distance from the anterior end. A slight hint of a hypapophysis is present. The prezygapophyses are strong and project well in front of the centrum. The neural spine is set back a little, is tall and narrow and broadens a little dorsally. The maximum height of the vertebra is 42 mm.

The neural spines of cervicals 4 and 5 are similar to that of cervical 3, but are a little taller and broader.

The column recommences on the main block and three small pieces which fit on to it. These vertebrae (figure 37) are identified by comparison with those of *Hesperosuchus* (Colbert 1952, figs 15 and 16), in which the first seven cervical vertebrae were found articulated. The first reasonably complete vertebra compares very well with the seventh of *Hesperosuchus*, and the one behind it agrees well with that figured as the eighth (although in the text Colbert expresses some doubt as to its position). These vertebrae in *Sphenosuchus* are therefore identified as the seventh and eighth cervicals, and a very incomplete vertebra in front of them is identified as the sixth. Agreement with the cervicals of *Dibothrosuchus* (Wu 1986) is also close. The division between cervicals and dorsals is difficult to establish in most fossil archosaurs. The criterion that the first pair of dorsal ribs are attached to the sternum fails because of the cartilaginous nature of the latter, and the fact that in Recent crocodiles the ninth, or the eighth and ninth, cervical ribs resemble the dorsal ribs closely (Mook 1921). It is assumed that there were nine cervicals in *Sphenosuchus*, as in Recent crocodiles, but it is convenient for descriptive purposes to refer to the more posterior vertebrae by numbering from the skull.

For reasons already noted these vertebrae are poorly preserved. They are tall, with large, strongly projecting zygapophyses, the neural spines somewhat set back, with a tendency to become narrower posteriorly (in side view). The centra are compressed, without keels but with hypapophyses at the anterior ends. That of the seventh is most marked and best preserved; those of the eighth and ninth are damaged, there is only a slight indication on the tenth (or first dorsal) and by the eleventh the projection has probably died out. There is a tendency towards procoely in these vertebrae. The anterior ends of the centra are wider and more concave than the posterior ends; the latter have broader bevelling so that the terminal concavity is smaller in extent, allowing the bevelling to fit partly within the concavity of the centrum behind. These features can be observed from the seventh to the anterior face of the eleventh vertebra (the posterior face not having been prepared). The neural canals dip down into the centra.

The rib articulations are poorly preserved. However, the parapophysis is seen low down at the anterior end of the centrum in cervical 7, evidently rising gradually backwards to the eleventh vertebra, where it is represented by a broad, abraded area quite high up at the anterior end of the centrum. The diapophysis is halfway along the base of the neural arch in cervical 7, rising posteriorly to a scar beginning 4 mm up the side of the neural arch in vertebra 11. In this vertebra a lamella ran from the postzygapophysis to the rear edge of the diapophysis, enclosing a deep cavity behind the latter. Ridges also run postero- and anteroventrally from the scar, the latter probably connecting with the parapophysis. The diapophysis was evidently strong. There is a tendency for a decrease in the length of the centra, from 18 mm in the seventh to 16 mm in the eleventh vertebra.

Only a little of the neural arch and a small part of the anterior end of the centrum of vertebra 12 are preserved. After a gap of suitable length the anterior half of centrum 13 is seen at the posterior edge of one of the loose pieces (figure 38). The posterior half has been taken away by a missing piece of matrix which has presumably also removed vertebra 14, assuming that these vertebrae were each about 18 mm long. The impression of the lower portion of a centrum, about 17 mm long, occurs at the anterior end of the piece with three parallel slender ribs (figures 1 and 38*f*). This is presumably vertebra 15. A small fragment partly counterparts this piece and at its dorsal edge bears the impression of a tiny portion of the rear end of a centrum, presumably vertebra 16, and impressions of the ventral edges of two further centra, vertebrae 17 and 18. These centra are each 19 mm in length. These vertebrae were evidently narrow ventrally, but nothing further can be said about them. Because of incompleteness of the matrix it is difficult to be certain whether the vertebral column originally continued further posteriorly.

An isolated anterior caudal vertebra figured by Haughton (1924, fig. 13) is practically complete (figure

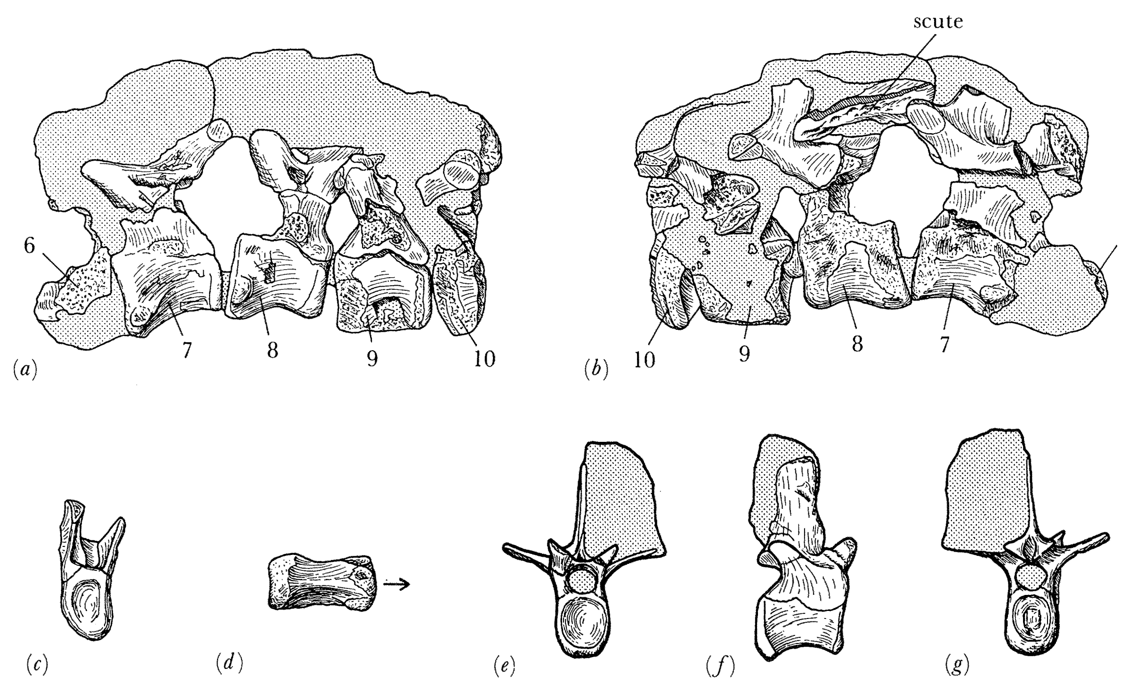

Figure 37. *Sphenosuchus acutus* Htn. (*a*), (*b*) Left and right lateral views of parts of vertebrae 6–10 and scute as occurring; (*c*) posterior view of vertebra 8; (*d*) lower view of same; (*e*)–(*g*) anterior, right lateral and posterior views of anterior caudal vertebra. Magn. × 0.75.

37) and has been prepared a little more, but the harder matrix here prevented complete clearance. The centrum is fairly narrow and somewhat elongated, 15 mm in length, the lower surface being rather flattened. There is a noticeable tendency for procoely, the posterior concavity being smaller, with a wider surrounding bevel. Posteroventrally there are two areas for the articulation of a chevron bone. The right prezygapophysis has been pushed medially a little; the articular surfaces are actually set at a little less than 45° to the horizontal. The transverse processes are inclined a little upward and backward, with no signs of sutures at their bases. The neural spine is thin and tall, but is not narrow and inclined in side view, as figured by Haughton, being in fact rather broad, even without allowing for the damaged anterior edge, and vertical. The maximum overall height is 35 mm, the breadth across the transverse processes being 29 mm.

The number of presacral vertebrae has not been established with certainty in any close relative of *Sphenosuchus*. Crush (1984) assumed that there were 24 in *Terrestrisuchus*, in comparison with *Protosuchus* and *Orthosuchus*; Bonaparte, on the other hand (1971), thought that there might have been as many as 26 in *Pseudhesperosuchus*. Taking a typical thecodontian number of 25, and allowing for some increase in length of the posterior dorsal vertebrae as in *Terrestrisuchus* and *Pseudhesperosuchus*, one arrives at an estimate of 166 mm for the neck (assuming 9 cervicals) and 307 mm for the trunk, a presacral length of 473 mm.

Ribs

A pair of slender, tapering rod-like bones of oval cross section originally lay close behind the skull and below the anterior end of the axis (figure 35). A maximum length of 16 mm is preserved. These are presumably the first pair of ribs, articulating with the atlas intercentrum. Part of the second rib of the left side is preserved in place alongside the axis (figure 36). This is again rod-like. This rib was presumably dichocephalous; the capitulum may have articulated with the odontoid (atlas centrum), the tuberculum apparently met the axis centrum anterodorsally.

A typical mid-cervical rib occurs close to the right lower jaw. This rib (figure 38), presumably from the right side, is most similar to the seventh cervical rib of *Alligator* in the sub-equal sizes of the capitular and tubercular facets, and in having the shaft sub-parallel to the vertebra, but the length of the shaft is more like the eighth of the alligator. The angle between the two processes has been reduced by compression. The capitulum is slightly the longer and was found when prepared to be already 'gnawed' anteriorly. The anterior projection of the shaft, however, was already broken off when received. The articular surfaces are narrow and elongated. The preserved length is 21 mm.

The slender bone lying in front of the shoulder girdle (figures 38*c* and 39) is probably the distal portion of the ninth cervical rib of the right side. The bone was already broken off proximally when embedded. The central part is mostly represented by an impression. The shaft is straight and elliptical in cross section with a tendency to flattening on the concealed side. After a slight constriction the presumed distal end widens to a thin expansion which curves slightly in a presumed posterior direction. There was evidently a thickened posterior edge which was found on preparation to have been partly broken away, leaving a longitudinal slot. The exposed side of the distal expansion has a shallow longitudinal concavity while the concealed side, when temporarily exposed, was seen to have a corresponding convexity. The bone is thus not bilaterally symmetrical

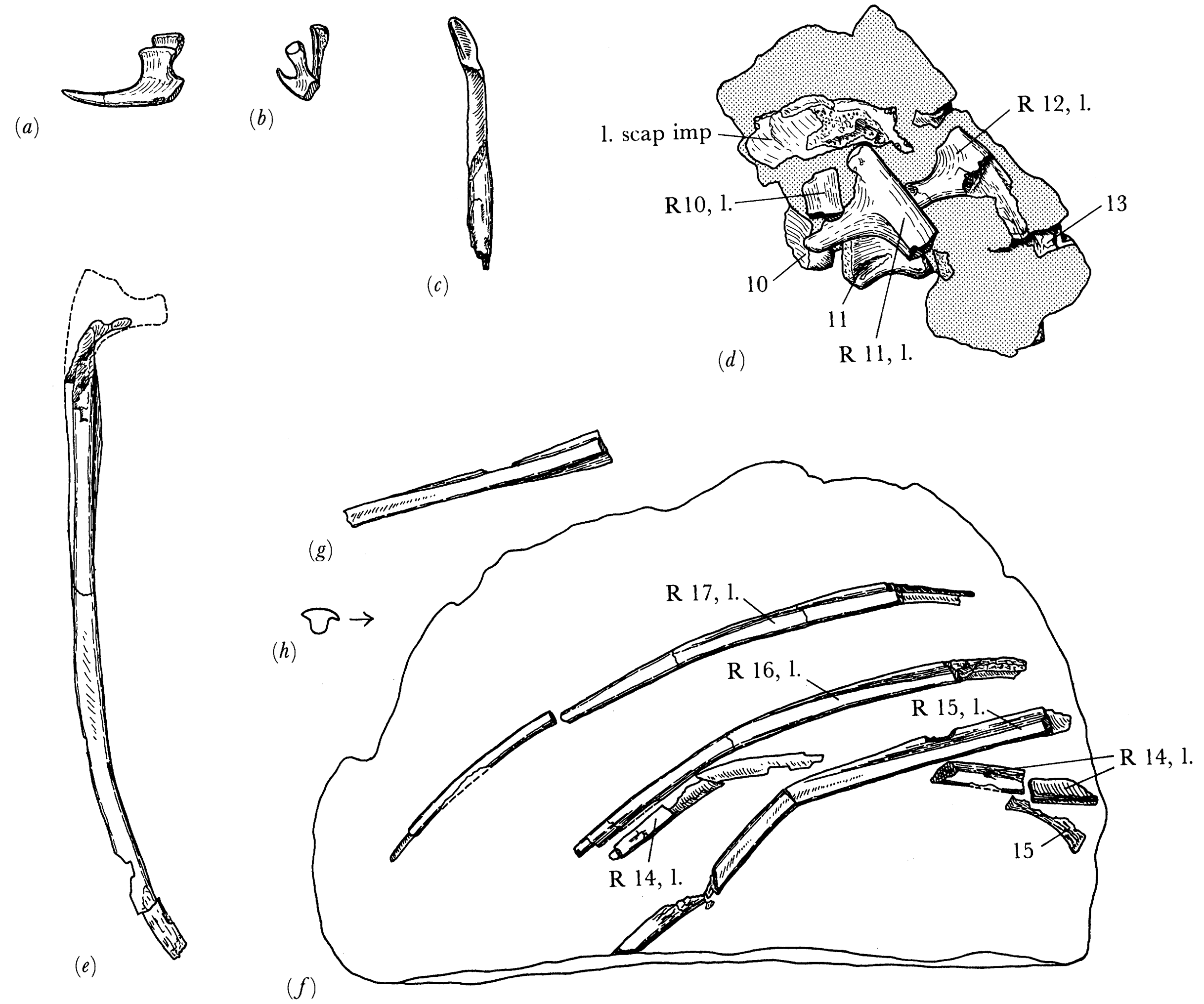

Figure 38. *Sphenosuchus acutus* Htn. (*a*), (*b*) lateral and anterior views of probably 7th cervical rib of right side; (*c*) inner view of distal portion of probably 9th cervical rib of right side; (*d*) outer view of proximal ends of ribs 10–12 of left side; (*e*) inner view of 12th rib of left side, outline of proximal end from piece figured at (*d*); (*f*) piece showing posteromedial views of 14th–17th ribs of left side; (*g*) medial view of part of rib 15 on same piece, to show flanges; (*h*) cross section of proximal end of this rib, anterior side to right. Magn. × 0.75.

and thus cannot be an interclavicle. This bone seems too straight to be a clavicle and there are no facets for such bones on the bone taken to be the interclavicle. The last cervical ribs in Recent crocodiles are usually more blunt at the tips than is this bone, but there is a tendency for there to be a thinner anterior distal expansion. This is quite marked as a thin flange in the ninth cervical ribs of a young *Caiman* skeleton in this Department. The elongated last cervical rib in birds may have an oar-like distal expansion quite like this bone, e.g. *Gavia stellata.* This rib is blunt enough distally to have had a short cartilaginous extension, as in crocodile and bird posterior cervical ribs. The preserved length is 46 mm.

The fairly well preserved proximal ends of two dorsal ribs of the left side are preserved on a small piece which also has the counterpart of the apex of the left scapula (figure 38*d*). The capitulum of the more anterior is only a little way in front of the parapophysis of vertebra 11, hence these ribs are identified as the eleventh and twelfth, and the remaining ribs on the main slab and its associated pieces (figure 1) are numbered to correspond with these two. Rib 11 (left) indents the left scapula blade. Small parts of the shafts of left ribs 10 and 11 have been removed when the left scapula was first prepared, and only the tuberculum of the tenth remains proximally. Distally these ribs can be traced into a vertical ‘cliff’ of matrix which defines the broken anterior edge of the right scapula. There is little doubt that rib 10 emerges behind the scapula, but rib 11 disappears into the matrix. Eleven millimetres further down this edge from rib 10 a slender bone, 4 mm × 2 mm in cross section, was exposed. This proved to be broken, but a sliver continues into the matrix. This is presumably cervical rib 9 of the left side, and its similar thickness to the isolated bone described above supports the identification of the latter. The cross sections of ribs 10 and 11 are noticeably stouter, reinforcing the assumption that there were nine cervical vertebrae. There is no sign of the tenth right rib.

The twelfth rib of the left side (figure 38*d*, *e*) is continuous from its proximal end to its distal termination on the main slab. It measures 122 mm in length and probably little is missing. Crushed segments of ribs identified as the eleventh and twelfth of the right

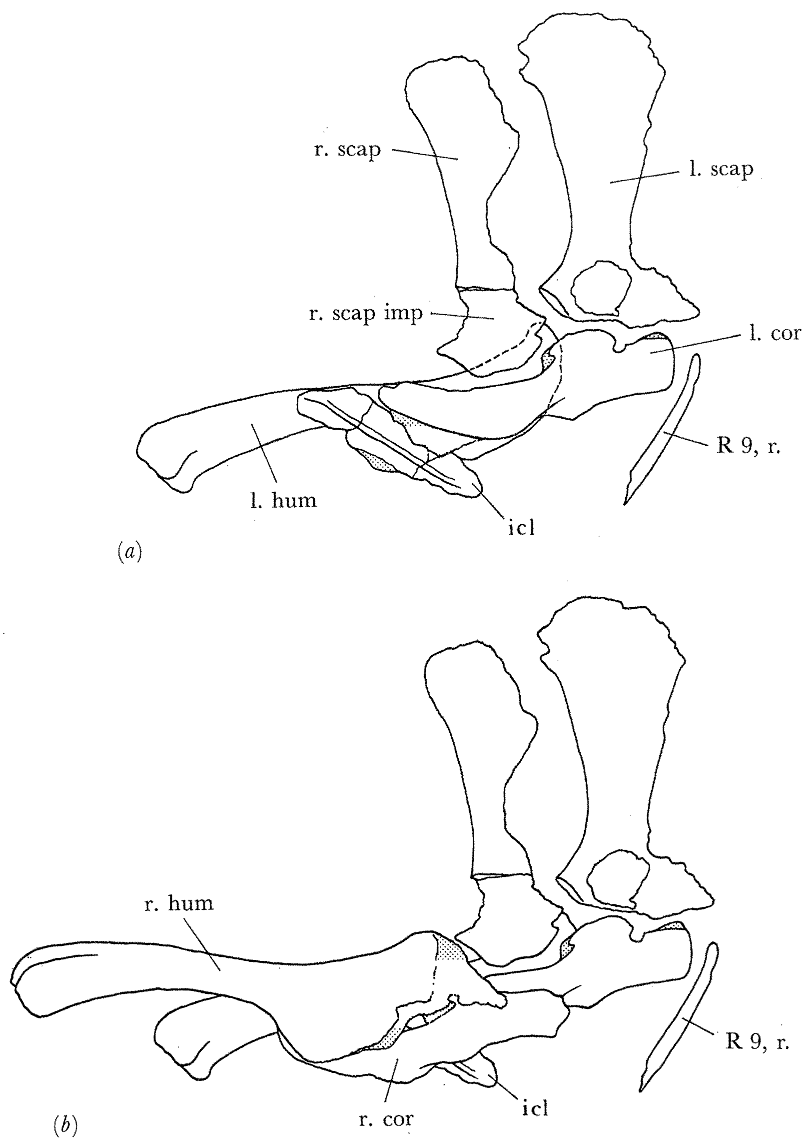

Figure 39. *Sphenosuchus acutus* Htn. (*a*), (*b*) Shoulder girdle and humeri as originally occurring on main slab. The right coracoid and humerus have been added in (*b*). Magn. ×0.5.

side are present on the main slab, together with other rib fragments. Rib 13 of the left side is missing, then follow the shafts of a further four ribs of the left side (figure 1), which presumably are the fourteenth to the seventeenth. The first of these crosses the second obliquely.

Figure 38*d* shows the essential features of the proximal ends of ribs 10–12. The tuberculum of rib 11 is probably incomplete, since the edge between it and the capitulum is damaged, and the other tubercula are more elongated in cross section. The capitulum and tuberculum are closer together in rib 12 than in rib 11, and the tuberculum is less projecting, as befitting the transitional position of these ribs. The difference between them, however, is less than that between the eleventh and twelfth ribs of a modern crocodile.

The dorsal ribs are long and slender, with anterior and posterior flanges proximally, giving a D-shaped cross-section, although the 'straight' limb of the 'D' is in fact arched dorsally (figure 38). The shaft is subcylindrical proximally, becoming more flattened and broader distally as the flanges die out. The development of these flanges cannot be fully traced sequentially; left rib 10 has a sub-triangular cross section as seen at the broken edge in front of the right scapula and there is some indication of a posterior flange as this rib emerges posteriorly. Rib 11, left, has the typical D-shaped cross section as it disappears from view further up the same edge. The more proximal cross section of the same rib on the detachable piece is similar but distorted by compression against the left scapula. The beginning of the anterior flange can be seen on this rib opposite the capitulum. The anterior flanges die out more proximally than the posterior. That on rib 12 arises about 15 mm from the tuberculum, gradually broadens and then dies away some 25 mm more distally. The beginning of the posterior flange cannot be seen on any rib; on the rib just mentioned it dies out 65 mm from the tuberculum, i.e. about halfway down the rib and this relationship evidently holds good for the more posterior ribs.

The three parallel mid-dorsal ribs are seen obliquely, the anterior flanges being hidden. The fifteenth left rib was prepared to show the anterior flange (figure 38*g*).

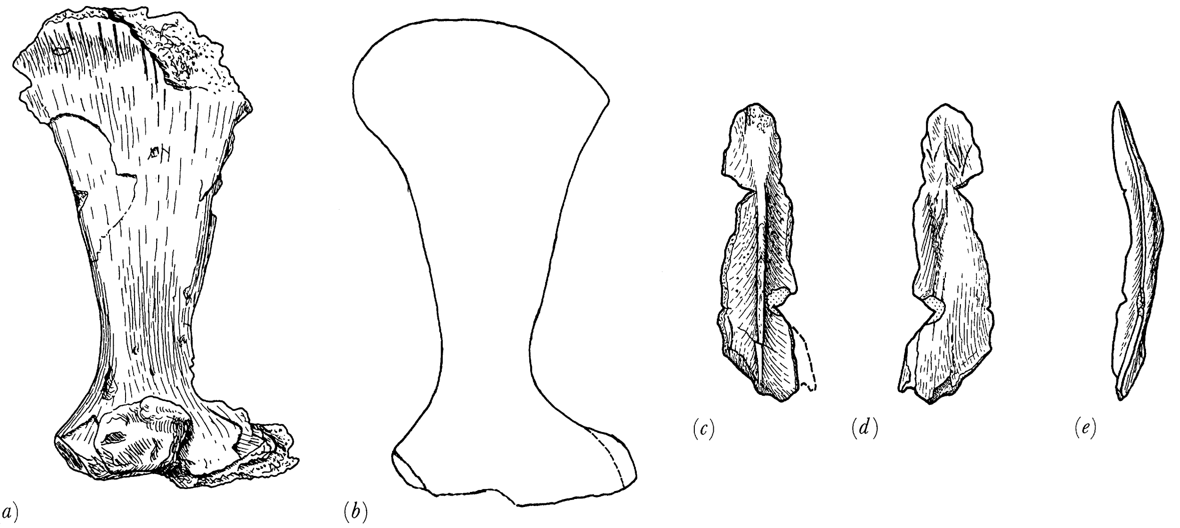

Figure 40. *Sphenosuchus acutus* Htn. (*a*) Medial view of left scapula with probable pathological growth in front of glenoid; (*b*) restored outline of scapula, broken line represents probable anterior limit of bone before crushing; (*c*)–(*e*) dorsal, ventral and right lateral views of interclavicle. Broken line in (*c*) represents small piece in (*d*) which cannot be prepared to show dorsal surface. Magn. × 0.75.

This rib has a shaft more U-shaped in section and measures 6.5 mm across the flanges × 4.5 mm deep. The anterior flange seems to have been bent downwards postmortem. A notch in the posterior flange was exposed during preparation; this may be a tooth-mark, since no bone fragments were found near it. Little can be missing distally from this rib, which measures 115 mm in preserved length.

There are no ossified uncinate processes on the dorsal ribs, and little sign of any cartilaginous origins for them.

Shoulder girdle

This was preserved with the right scapula and coracoid seen in lateral view, a little behind and ventral to the left scapula and coracoid which are seen in medial view (figure 39). The medial margins of the coracoids are nearly parallel, with the interclavicle lying obliquely between them (the identification of this element is discussed below). The right scapula is some 20 mm higher in the matrix at its upper end than the left, but the glenoids are at the same level and the coracoids were close together. The girdle has thus been folded ventrally in such a way that the interclavicle was preserved with its dorsal surface uppermost; at least, the disturbance has been so little that it is hard to see how it could have been turned over. Furthermore, the longitudinal and transverse convexities agree with this orientation. The rear end of the interclavicle lay on the shaft of the left humerus; its oblique termination coincides with the posterior edge of that bone, and it curves down to conform to the shape of the shaft. This termination also coincides with the distal part of the medial ridge leading down from the internal tuberosity of the right humerus. Evidently the ridge acted like a guillotine against the left humerus during the compression of the girdle, cutting off the posterior end of the interclavicle. The latter has unfortunately been lost, but it may well have been equal in length to the preserved part. It appears to have been thin, so that it may have been broken into fragments.

Scapula

The right scapula is very incomplete and poorly preserved, but that of the left side is fairly complete (figure 40*a*). A small detachable piece (figure 38*d*) helps to complete the apex. The blade is triangular in shape and flattened externally. The posterior edge is thick in the central part and thins dorsally, expanding to form a rounded posterior projection which is incompletely preserved. The dorsal border is ill-defined and there was probably a cartilaginous suprascapula. The anterodorsal corner is not fully preserved on either bone. Above the 'neck' the margin develops a very thin anterior shelf on the medial side, 1 or 2 mm wide. There is a shallow longitudinal concavity medially in the neck region, with the usual broad thickening extending dorsally from the glenoid behind it. Haughton's figure (1924) shows this, incorrectly, as a strong ridge.

The glenoid surface is not well preserved on the left scapula and its ventral end is probably missing, together with part of the thick ventral margin in front of it. There is a thin anteroventral expansion, whose anterior margin is crushed and broken so that the outline is uncertain. It is difficult to believe that the scapula projected so far in front of the coracoid, and some of these fragments appear to have 'drifted' forwards into the matrix during the embedding and compression. The lower margin here is fairly straight and there is no reason to think that any of the coracoid is included. Although Haughton states that there was no acromion process, this area cannot be seen and there is no reason to doubt that such a ridge existed.

A rounded mass of bone in front of the left glenoid appears to be a pathological growth. The surface is very irregular, and although continuous with the scapula posteriorly, this lump overgrows the surface anteriorly and dorsally. The medial surface of the right scapula is preserved as an impression at the lower end, part of which was removed in order to take off the left humerus. This surface, which is recorded in the form of

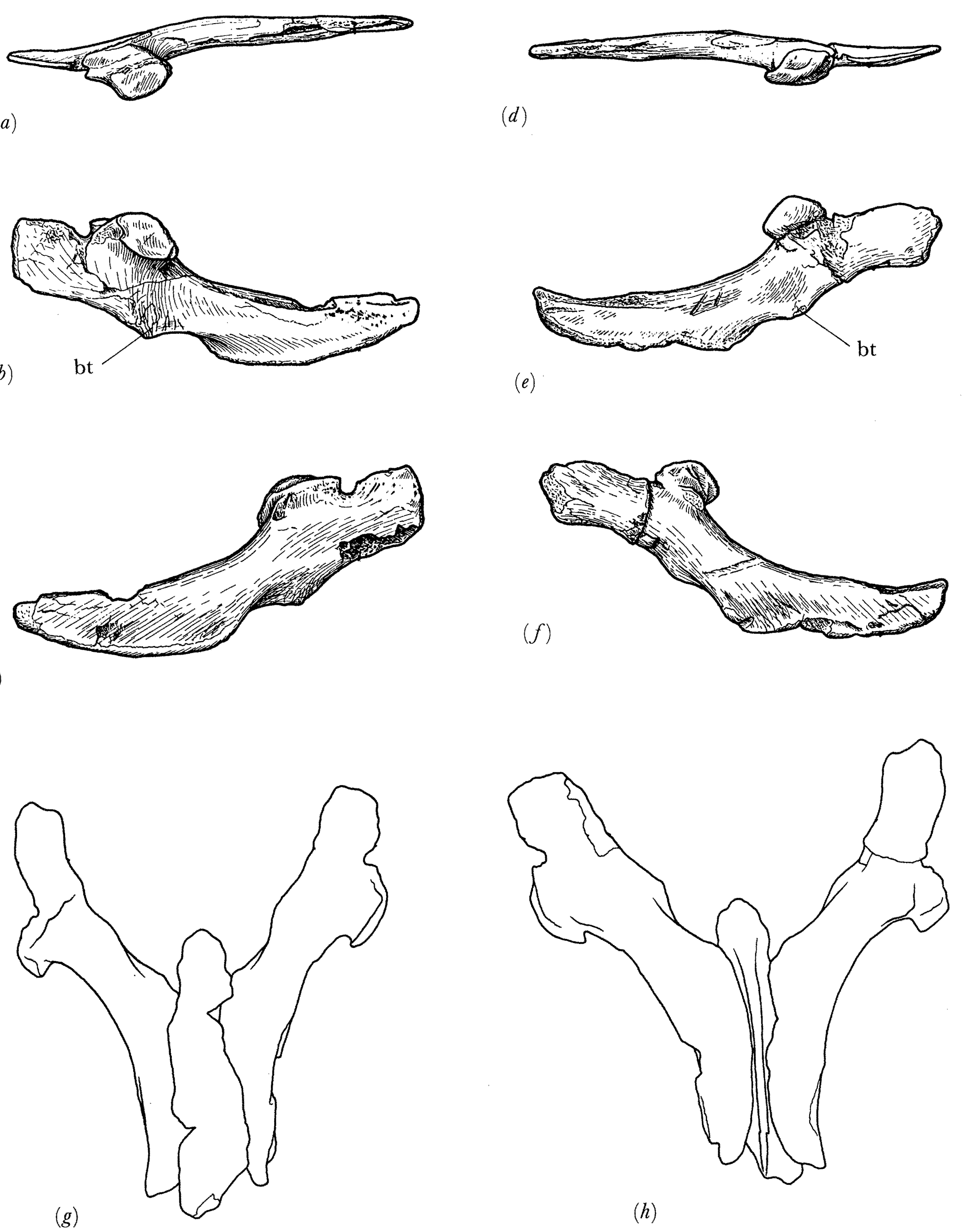

Figure 41. *Sphenosuchus acutus* Htn. (*a*)–(*c*) Proximal, lower and upper views of left coracoid; (*d*)–(*f*) same of right coracoid; (*g*), (*h*) assembly of coracoids and interclavicle in ventral and dorsal views. Magn. ×0.75.

'Vinagel' casts, is smooth and quite normal in contours in the same region as the growth on the left scapula.

Coracoid

Both coracoids (figure 41) are fairly complete, but the glenoid region of the right element has been badly crushed upwards and backwards, and the anterior extension has been shortened by a shear-plane. This bone has a groove on the inner or upper surface caused by pressure against the dorsal ridge on the interclavicle.

The anterior portion of the bone is thin and gently convex externally; internally it is convex dorsoventrally. The dorsal margin is incomplete on both bones, but the coracoid foramen, which is only slightly represented on the right side, was most probably enclosed in bone originally. The bone as a whole is slightly sinuous in dorsal view, curving so that the anterior and posterior ends are parallel. The glenoid is well preserved on the left side, gently convex with a good lip. The projection of the lower margin which has been named the *biceps tubercle* (Walker 1972) † projects ventromedially directly below the glenoid. It is flattened and more pointed because of squeezing on the left side; on the right it is better preserved and ends in slightly roughened, unfinished bone. There is a shallow concavity above and behind it, better preserved on the

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† This is not the same as the 'biceps tubercle' identified by Ostrom (1974) in the theropod *Deinonychus*. The projection or ridge on the coracoid of this dinosaur and certain other fossil reptiles is too posteriorly placed for the origin of the biceps and probably gave rise to a tendinous portion of the coracobrachialis muscle (Walker 1977, pp. 320–321).

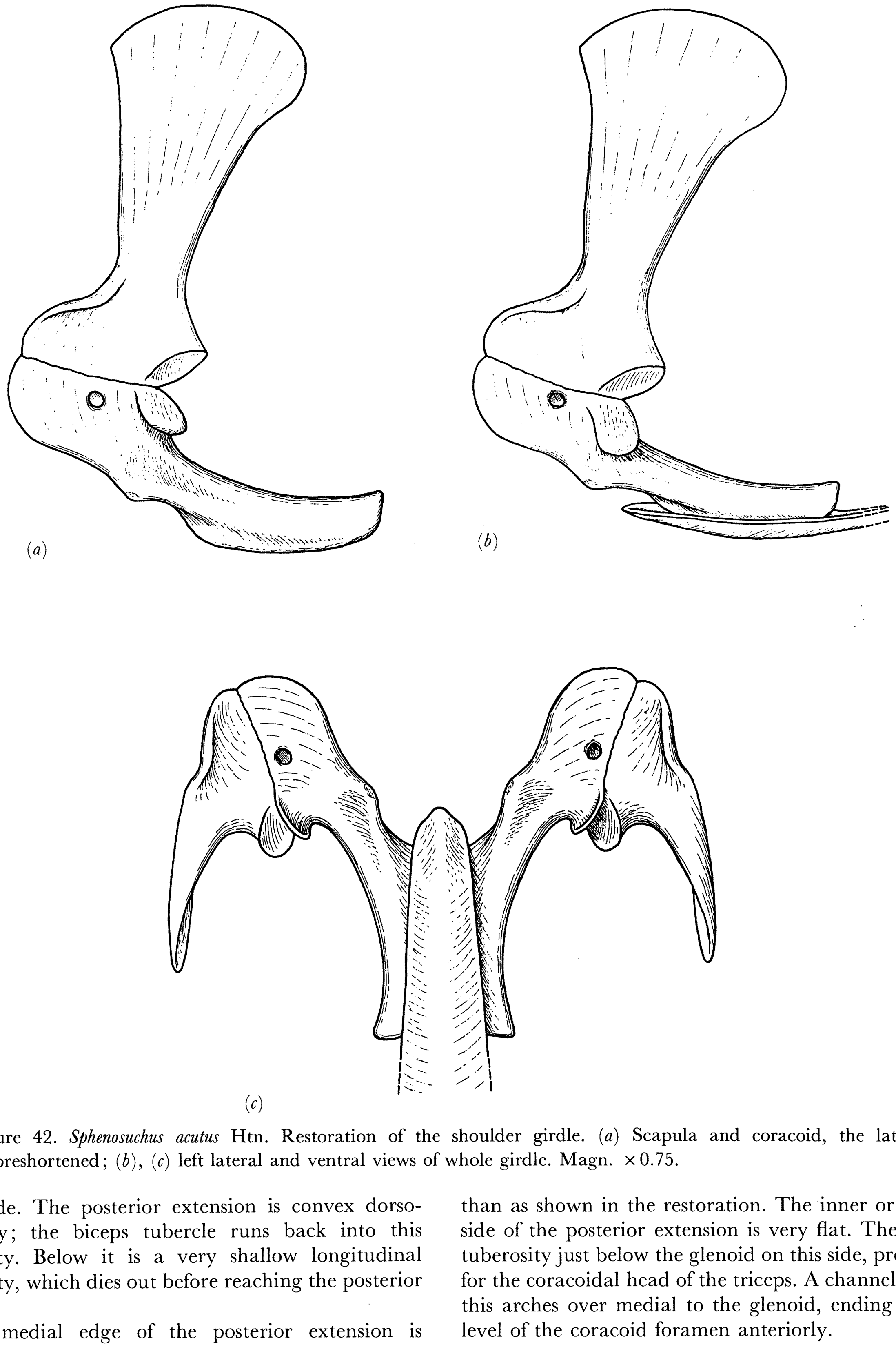


Figure 42. *Sphenosuchus acutus* Htn. Restoration of the shoulder girdle. (*a*) Scapula and coracoid, the latter unforeshortened; (*b*), (*c*) left lateral and ventral views of whole girdle. Magn. ×0.75.

right side. The posterior extension is convex dorsoventrally; the biceps tubercle runs back into this convexity. Below it is a very shallow longitudinal concavity, which dies out before reaching the posterior end.

The medial edge of the posterior extension is somewhat thickened and was evidently covered in cartilage. The posterior end was not pointed, as previous authors have figured it, but bluntly terminated. The posterior half of the upper or lateral margin is incomplete in both bones, so that the full outline is unknown. On the right coracoid there appears to have been a small tubercle on the upper margin halfway along the posterior extension, or alternatively, the posterior termination was broader than as shown in the restoration. The inner or upper side of the posterior extension is very flat. There is a tuberosity just below the glenoid on this side, probably for the coracoidal head of the triceps. A channel above this arches over medial to the glenoid, ending at the level of the coracoid foramen anteriorly.

Interclavicle

The margins of this bone (figure 40*c*–*e*) are very incomplete and both its longitudinal and transverse convexities have been exaggerated by compression against the right coracoid. This has caused the dorsal ridge to be bent over to the right a little at its middle part. The lower surface has also many shear cracks anteriorly. The anterior end was rounded, with a tendency for a blunt point in the mid-line. A small piece that fits on at the rear end shows that the bone was quite wide – 18 mm (doubling from the right side) – and here it seems still to be increasing in width.

Dorsally there is a strong median ridge, flanked by shallow concavities. The ridge broadens and dies out at the anterior end. There is no sign of facets for clavicles. The ridge is also declining at the posterior end and would soon have died out. The upper surface is pitted, particularly in the central region.

Ventrally the surface is smooth with a faint longitudinal ridge anteriorly flanked by shallow concavities, which probably indicate the limits of the origins of the pectoralis muscles. This ridge is replaced behind by a gentle transverse convexity. The posterior end is evidently becoming flattened.

Restoration of the shoulder girdle

As already remarked (see § 2), preparation revealed no trace of a second median ventral ossification in the shoulder girdle. In *Pseudhesperosuchus* too, in which the shoulder girdle is fairly well articulated (Bonaparte 1971), there is only one median ventral element present. The sternum is rarely ossified in reptiles. In thecodontians it was evidently cartilaginous, and is so in present-day crocodiles, although it may be calcified. In any reasonably well-preserved fossil reptilian shoulder girdle, on the other hand, the interclavicle is usually a conspicuous element. The natural assumption would thus be that the median element in *Sphenosuchus* is the interclavicle. It is possible, however, that this bone might be the sternum, and Crush (1984), as a result of correspondence on this point, has identified both an interclavicle and a sternum in *Terrestrisuchus*. It seems to me now, having examined the material, that this is probably mistaken, and that these bones in *Terrestrisuchus* are all the same element, presumably interclavicles. The only specimen identified by Crush as an interclavicle (P.50/1), which appears to be rather narrower than the 'sterna', is probably a smaller and less well ossified (and hence preserved) example than the others. As Crush notes (1984), P.50/1 is 'very damaged and its original shape and length are uncertain'.

Previous workers on *Sphenosuchus* have assumed that the coracoids articulated directly with the interclavicle. Haughton (1924) does not discuss this point directly, but he refers (p. 355), in describing the coracoid, to the 'interclavicular articular surface' of the posterior extension, which shows that he considered this to be the case. Broom does not describe the girdle in detail. His figure (1927, fig. 13) appears to show the medial edge of the posterior extension of the coracoid meeting the interclavicle at the side of the dorsal ridge, but since this is a lateral view and hence foreshortened, it is just possible that he may have visualized the interposition of a cartilaginous sternum, although there is no indication of this in the figure. Bonaparte (1971, p. 72) considered that the lateral border of the interclavicle in *Pseudhesperosuchus* was received into a longitudinal depression on the external surface of the coracoid, near the medial border of the latter. Crush (1984, p. 144) visualized a similar articulation in *Terrestrisuchus*; his account mentions a 'deep trough' on the coracoid into which fitted the edge of the 'sternum'. He considered that a ridge above the trough represents the biceps tubercle. Kermack gave a preliminary account of the same material in 1956 in which he stated that the coracoids 'were firmly articulated' with the 'large interclavicle' (the shoulder bones in fact occur in a disarticulated state). However, a specimen of *Terrestrisuchus* from a different locality (a fissure in Cromhall (or Slickstones) Quarry, Gloucestershire) collected and prepared by Mr R. Croucher of the Palaeontology Department of the British Museum (Natural History) (B.M.N.H. R10002), shows a large single median ventral element articulated with the coracoids in the manner postulated by Crush (1984).

The medial edges of the coracoids of *Sphenosuchus* do in fact articulate quite convincingly with the depressions on either side of the median dorsal ridge on the interclavicle, in spite of the distortion of the latter (figure 41*h*). The ridge also corresponds in length to these medial edges. However, there are difficulties in taking this apparent articulation at its face value. An articulation between coracoids (or procoracoids) and interclavicle is very rare in reptiles, and apparently is known to occur only in some dicynodonts (Watson 1960; King 1981). Kemp (1982, 1985) speaks of such an articulation in pelycosaurs, but this is contrary to the clear statements of Romer (1922, p. 551) and Romer & Price (1940, p. 114). These authors make it clear that there was a short vertical gap between the procoracoids and the interclavicle. The situation in thecodontians (Cruickshank 1972; Ewer 1965; von Huene 1942; McGregor 1906; Walker 1961) was evidently like that in most modern lizards or in *Sphenodon*, with the coracoids (or their cartilaginous epicoracoid continuations) meeting or perhaps overlapping a little in the mid-line, above but not touching the anterior part of the interclavicle. Posteriorly the coracoids articulated, probably by means of grooves, with the cartilaginous sternum, to the lower surface of which was attached the posterior part of the interclavicle. In modern crocodiles, on the other hand, the coracoids articulate as usual by epicoracoid cartilages with grooves in the side of the sternum, but the latter completely separates them. The grooves diverge posteriorly at *ca.* 45°, contrary to the impression given by many figures in the literature, and come close to each other anteriorly, terminating above the sides of the interclavicle. The interclavicle lies below the sternal cartilage as usual, but projects freely for a considerable distance in front of it. There is thus no articulation between coracoids and interclavicle in thecodontians or typical crocodiles.

One might take the opposite view and argue that, if the coracoids articulated directly with the median bone, then the latter is an ossified sternum. However, against this is the lack of a second median element in *Sphenosuchus* and *Pseudhesperosuchus* (because it seems unlikely that the interclavicle would have atrophied completely). In *Terrestrisuchus* also, in articulated or not greatly disarticulated girdles, only one median element is found. It is also difficult to see the necessity for such a strong median dorsal ridge on the inter-

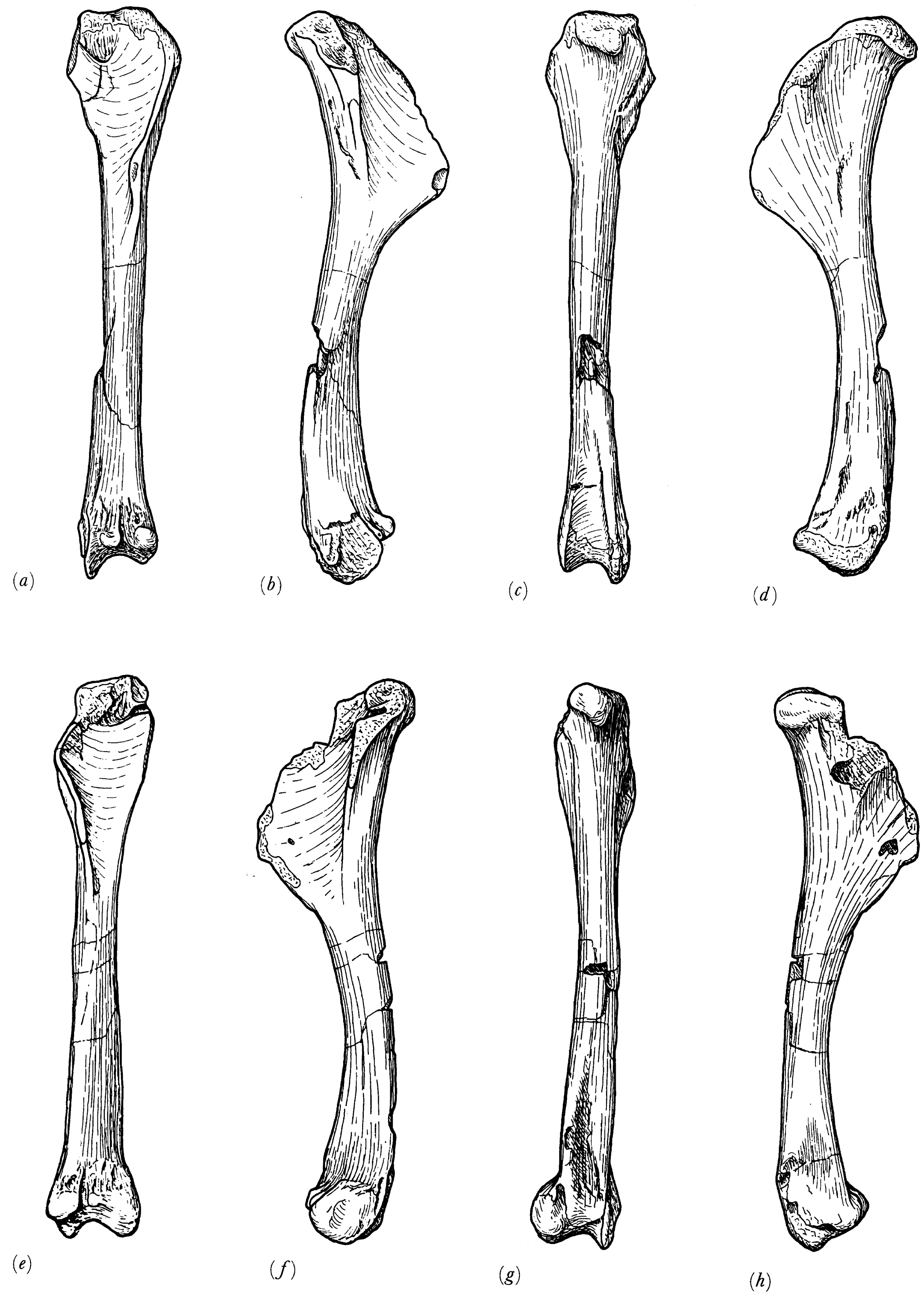


Figure 43. *Sphenosuchus acutus* Htn. (*a*)–(*d*) Anterior, medial, posterior and lateral views of left humerus; (*e*)–(*h*) same of right humerus. Magn. ×0.75.

clavicle of *Sphenosuchus* unless this served as a brace for the medial edges of the coracoids. As far as I am aware, this feature is unique.

The alternative is to assume that the appearance of an articulation is spurious, and that the coracoids were separated by a cartilaginous sternum as in typical crocodiles, the ridge on the interclavicle fitting into a groove on the undersurface of the sternum. Against this is the situation in *Pseudhesperosuchus*. The coracoids are not quite correctly articulated in the specimen (*pace* Crush 1984) because the longitudinal depressions which, according to Bonaparte, received the lateral edges of the interclavicle, are exposed anteriorly (1971, fig. 28B). Nevertheless, as preserved, the coracoids nearly meet above the interclavicle and there is little room for cartilage between them. Unfortunately, the folding of the ventral part of the girdle in *Sphenosuchus* has obscured the original relationships.

To sum up, it is considered most likely that the apparent articulation of coracoids with interclavicle is real. However, the situation is slightly different from that in *Pseudhesperosuchus*, *Hesperosuchus* (Colbert 1952, fig. 26) and *Terrestrisuchus*. In these animals the edge of the interclavicle was received into a 'trough' in the coracoid, whereas in *Sphenosuchus* the reverse was the case, the coracoid resting in a depression on the interclavicle and abutting (by means of a coating of cartilage or 'epicoracoid') against the dorsal ridge on the latter. These differences are really more a question of which part of the contact is emphasized, because in the three genera cited the coracoid also overlapped the interclavicle dorsally and in *Sphenosuchus* there is a very shallow longitudinal depression on the coracoid which received at least part of the edge of the interclavicle.

In the restoration (figure 42) the sternum would appear to have been rather narrow, situated as it was entirely behind the coracoids. However, the posterior terminations of the coracoids could well have been somewhat broader than as restored, allowing for a broader sternum. The thin posterior end of the interclavicle is assumed to have been applied to the undersurface of this cartilaginous sternum; judging by the large interclavicle of *Terrestrisuchus*, this posterior end could have been as long as the part preserved. The anterior part of the coracoid would have sloped inwards at *ca.* 45°. The glenoid faces to a certain extent laterally and also considerably downwards, more so than in a Recent crocodile, apparently.

Humerus

The left humerus is the more complete of the two proximally, the right distally (figure 43). The left humerus is deeply notched a little below the mid-point, and part of the shaft has been forced inwards. This has probably been caused by compression against the rear end of the interclavicle and the shaft of the right humerus. The medial margin of the bone has also been forced backwards, accentuating the trochlear groove on the posterior surface and pushing the medial condyle a little distally. Some small scars just above the notch could be tooth marks. The bone was seen to be hollow, the cavity filled with matrix, the walls being some 2 mm thick.

The head of the bone curves backwards to a large, rounded, ball-like articular surface. The ridge leading to the deltopectoral crest extends anterolaterally and is at first thick-edged, expanding to a tuberosity set on the lateral side of the edge. From this point the ridge thins and swings abruptly to run anteromedially to the summit of the crest, which is thickened. The profile of this section is not concave, as in the crocodile, but was originally probably slightly convex. The change in direction at the tuberosity appears to correspond to the right-angled 'shoulder' at the lateral border of the head in the modern crocodilian humerus, but in the fossil it is more distally placed.

There was a strong internal tuberosity, broken off in both bones, which tapers distally to a sharp ridge. Lateral to the tuberosity on the anterior surface is a deep ligament pit which bears longitudinal striations.

The distal end is damaged in both humeri. The left humerus has lost part of its medial condyle, and the shaft of the right humerus has been crushed from side to side just proximal to the condyles. The medial condyle is more prominent than the lateral. There is a marked trochlear groove distally between the condyles and this runs a considerable way up the posterior surface. Anteriorly a deep ligamental groove separates the condyles and there are longitudinal striations and pits proximal to the condyles on this surface.

The rather prosauropod-like curvatures of the distal half of the bone, especially the posteromedial edge, have certainly been exaggerated by crushing on the left humerus, and probably also on the right humerus, although they are nearly symmetrical.

Tibia

The tibia (figure 44) is a curiously curved, slender bone. The resemblance to the tibiae of *Hesperosuchus* (Colbert 1952, and personal observations), *Saltoposuchus* (von Huene 1921, and personal observations) and *Pseudhesperosuchus* (Bonaparte 1971), demonstrates that these curvatures, although no doubt somewhat exaggerated, are largely original.

The proximal end is crushed on the lateral side, so that the proximal surface slopes too steeply laterally and the cnemial crest is probably exaggerated. The proximal surface is very irregular and evidently possessed a cartilaginous capping. The shaft is hollow, the cavity being filled with matrix and crystalline calcite, and has walls 2 mm thick. The shaft curves anteriorly and also medially approaching the distal end.

The distal end has two articular regions set at a little less than 90°. On the medial side an anteroposteriorly elongated broken surface indicates a projection which, by analogy with *Saltoposuchus* and *Hesperosuchus*, formerly extended distally well beyond the lateral facet. The latter is a flat, smooth surface with a slight lateral lip. It faces backwards and downwards at *ca.* 45°. This facet evidently received the dorsomedial surface of the dorsolateral process of the astragalus, precluding movement between them. There is a concave area posteriorly between this facet and the medial portion of the distal end.

Fibula

This is only represented by the distal portion (figure 44*h–j*). The shaft is hollow, the lumen being filled with crystalline calcite; the walls are 1 mm thick. The inner side of the shaft is flattened. The distal end as preserved is elongated and very slightly concave anteroposteriorly. However, the scar on the medial surface shows that, as expected, the bone originally expanded medially to contact the distal end of the dorsolateral process of the astragalus. Nevertheless, it does seem that the distal end was narrower than in a modern crocodilian fibula, in which the breadth exceeds the length.

Metatarsals

Three metatarsals showing their upper surfaces (figure 45*a*) are preserved lying closely side-by-side. The tilt of the broken proximal end (and its impression) of the longest of these shows that it is of the left foot, thus these are metatarsals I–III. Lying across these

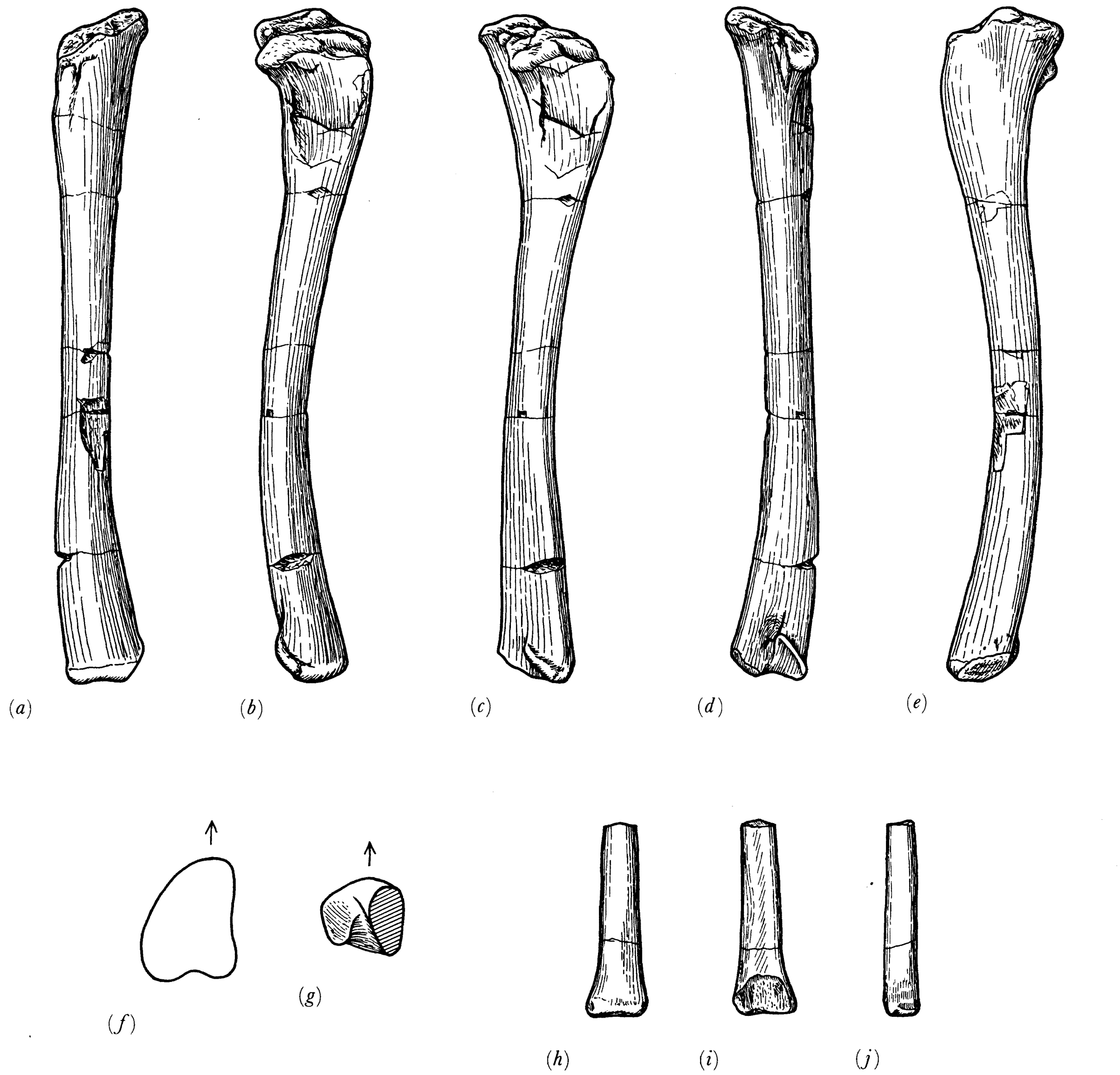


Figure 44. ***Sphenosuchus acutus*** Htn. (*a*)–(*e*) Anterior, anterolateral, lateral, posterior and medial views of right tibia; (*f*), (*g*) outline of proximal end and distal view of same, anterior side up; (*h*)–(*j*) lateral, medial and posterior views of distal portion of right fibula. Magn. × 0.75.

obliquely is another long metatarsal showing its lower surface. From its proximal tilt this is also of the left foot and is thus metatarsal IV. The distal end of this metatarsal just touches a complete detached metatarsal, 63 mm long, also inverted, which from its proximal tilt is of the right foot. The distal third came off during preparation; comparison with the left metatarsals allowed no doubt that this is the antimere of metatarsal III. The cast from the impressions of the bases of the left metatarsals (figure 45*b*) also shows that the third is practically complete at 61 mm. The impression of the distal end of a bone lateral to this metatarsal shows part of the condyles and might be metatarsal V, but it seems rather substantial for this element and could be the end of a phalanx or of metatarsal II or IV of the right foot. Assuming that metatarsals I–III of the left foot ended proximally in line with each other allows one to estimate the lengths of I and II (see table 1).

Metatarsal I is slender in the shaft, with a fine lumen. It expands considerably distally, especially in a dorsoventral direction, but this end is small compared with those of the adjacent metatarsals. Metatarsals II and III must originally have diverged distally, since their present close contact does not allow room for the collateral ligament of II; metatarsal I may also have diverged, or it may have been attached to the medial side of metatarsal II, as in *Hallopus* (Walker 1970). The distal articular surface of I is a single surface, seemingly not extending round to the lateral side but curving medially in roughly a quarter circle. It is also strongly convex dorsoventrally. The distal end measures 4 mm in breadth and 6 mm in depth. There is a shallow medial ligament-pit placed low down. The shaft is 4 mm deep at the break. This metatarsal is thus reduced and it seems that the first phalanx was inclined medially relative to the axis of the metatarsal.

The remaining metatarsals are similar in having only shallow dorsal depressions behind the distal condyles which are themselves not very pronounced

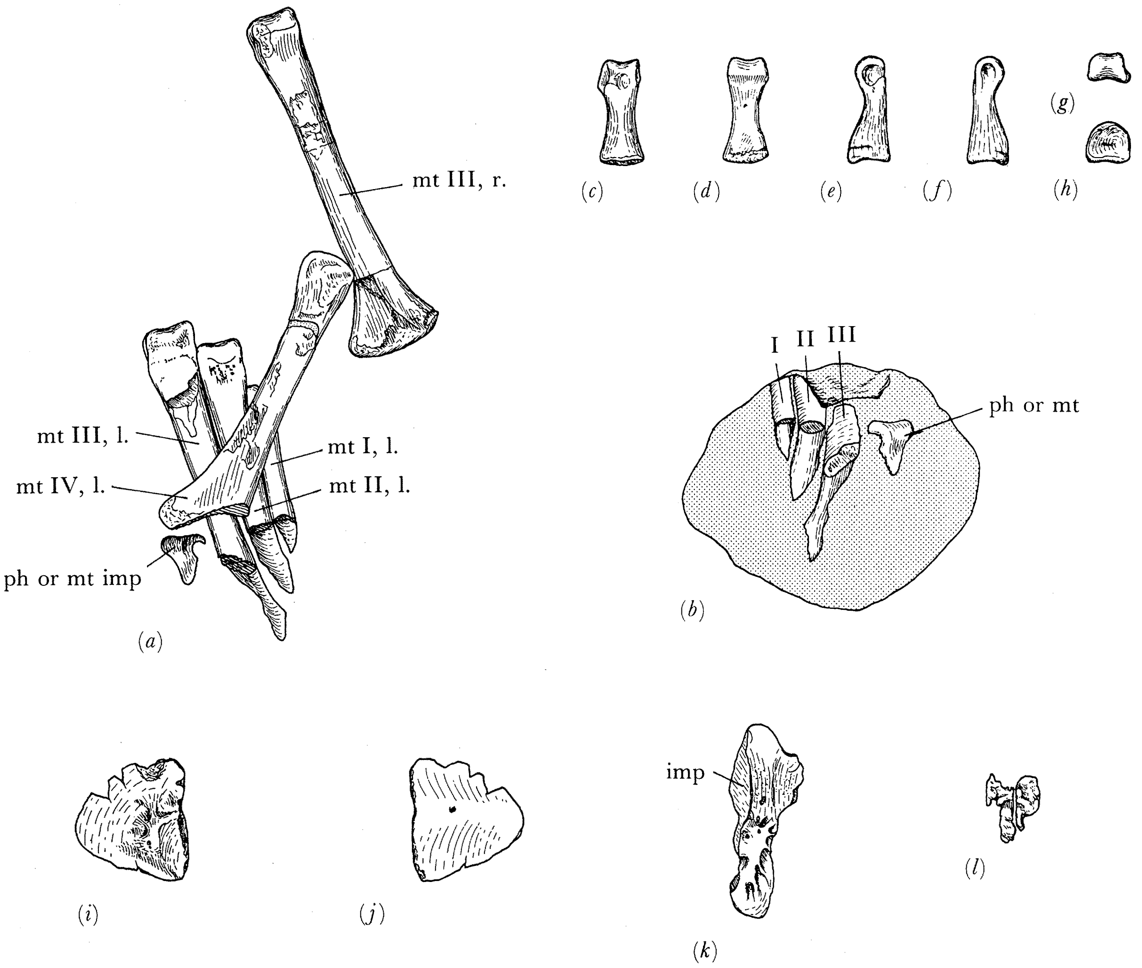


Figure 45. *Sphenosuchus acutus* Htn. (*a*) Group of metatarsals on main slab; (*b*) cast of proximal ends of left metatarsals from same group, giving lower surfaces; (*c*)–(*h*) dorsal, ventral, left side, right side, distal and proximal views of isolated phalanx from main slab; (*i*), (*j*) dorsal and ventral views of probably first cervical dorsal scute of left side; (*k*) dorsal view of posterior cervical dorsal scute; (*l*) possible ventral scute or pair of scutes. (*a*)–(*h*): Magn. ×0.75; (*i*)–(*l*): magn. ×1.

except on the ventral side. Metatarsal II has a very shallow medial ligament-pit. The distal breadth is 7.5 mm, the depth 7 mm. The shaft is 4.5 mm wide at the break. Metatarsals II and III, left, and III, right, have crystalline calcite within a good-sized lumen.

The shaft of metatarsal III is long and parallel sided. The proximal end is nearly symmetrical, tilted at *ca.* 30° in the right-side bone, but this has been crushed; in the antimere the tilt is *ca.* 45°. Distally the ventral condyles are abraded in the right-side element. The medial ligament-pit is shallower than the lateral. The distal breadth is 9 mm, the depth 7 mm. The shaft is 5.5 mm wide and 3.5 mm deep at a minimum. The proximal diameter is 16 mm.

Metatarsal IV is rather damaged in the shaft, crushed proximally, and the distal end has lost the lower surface of the lateral condyle. There is no 'saddle' in the distal profile. The medial ligament-pit is shallow. The distal breadth is 7.5 mm, the depth *ca.* 7 mm. The tilt appears to be 45°, but the distal end has been displaced at a break and the condyles are seen obliquely.

An isolated *phalanx*, 18.5 mm in length, from the main slab, is well preserved (figure 45*c–h*) but could be from either the hand or the foot.

Dorsal scutes

A thin, sub-triangular bone (figure 45*i,j*) which was very conspicuous at the rear of the right lateral temporal fenestra is regarded as one half of the first pair of cervical scutes. Curiously, no previous author has mentioned this bone. It was situated just below the rear end of the squamosal, a short distance lateral to the posterior edge of the right quadrate, the smooth lower surface being exposed. It will be described as if it were the left member of the pair, although it may in fact have been from the opposite side.

One edge is almost straight, irregular in detail, and slightly thickened. This is evidently a sutural or possibly a hinge-like contact (Chatterjee, 1978) for the opposing scute, and is thus medial. The anterolateral and posterolateral edges are thin, the former convex in outline, the latter almost straight. The scute as a whole is gently arched from side to side. The upper surface has a weak ornament of pits and ridges centred on a low boss, the highest part of which is one third the distance from the medial and posterior edges. The lower surface is smooth, with a low transverse swelling just in front of the middle of the scute. In front of this the surface is flat; behind it it is shallowly concave.

The position of the boss suggests that this is a left side scute, since this feature is usually situated posteriorly. The ventral concavity would then be correctly positioned to overlap the next succeeding scute.

There is little doubt about the correct identification of this element as a scute, although it may not in fact have belonged to the first pair. The rear edge, however, is not set at right angles to the medial edge, as it commonly is in paramedian dorsal scutes. The first pair of cervical scutes may be sub-triangular, as in the probable protosuchian *Dyoplax* (Fraas 1867, and personal observations) with curved anterolateral margins, but the posterior edges are transverse. However, triangular cervical scutes occur in some phytosaurs, and Chatterjee has figured a fifth cervical scute (1978, fig. 9b) in *Parasuchus* in which the rear edge is oblique. This scute, however, is longer than broad. Camp (1930) figured as the third cervical of *Rutiodon adamanensis* a triangular scute in which length and breadth are equal. The rear border is somewhat oblique. The scutes in *Rutiodon* have straight medial edges which are irregular in detail, are thickened along the mid-line, and articulate loosely by suture. In *Parasuchus* also the scutes hinge together. Triangular dorsal scutes with oblique posterior margins also occur in *Teleosaurus* (Eudes-Deslongchamps 1869). The scutes of the first pair in the sphenosuchid *Dibothrosuchus* (Wu 1986) are similar in shape to the bone in question. These dorsal scutes also appear to be sutured together in pairs.

The size of this bone rules it out as being a palpebral (or supraorbital) bone. The sutural edge would have to fit against the prefrontal and lachrymal, on which there is no obvious contact surface, and in such a position the bone projects much too far laterally (beyond the outer edge of the jugal) to fit any likely sized upper eye-lid. It is also too far anterior when the side view is considered. Palpebral bones in modern crocodilians usually do not project beyond the general curve of the skull roof, except in *Paleosuchus*. In *P. palpebrosus* the very large palpebral is triangular and projects laterally (Kälin 1933, pl. 14). However, this bone takes up most of the upper eye-lid and folds down to cover the eye completely when the latter is closed (Neill 1971). There is thus no real comparison with the element under consideration. Another possibility, that the *Sphenosuchus* bone might be the anterior (or posterior) member of a pair of supraorbitals, as in protosuchian or notosuchian crocodiles (Walker 1968; Nash 1975; Crompton & Smith 1980; de Gasparini 1971), which met along the sutural edge, meets with the same objection of lateral projection. Furthermore, this bone in *Sphenosuchus* is sculptured, whereas the skull roof is practically devoid of ornament, and it has a transverse convexity on the lower surface, making it an unlikely shape for a supraorbital or palpebral bone.

An incomplete posterior cervical scute (figure 45*k*) occurs between the neural spines of the seventh and eighth cervical vertebrae. This scute is presumably the right-hand member of the pair, but it is hardly possible to be certain. Both edges are incomplete, the presumed medial side being partly represented by an impression. The length seems to be complete at 25 mm. The anterior part of the upper surface is smooth and gently convex anteroposteriorly. Then succeeds a concave portion, followed by a more pronounced elongated boss, surrounded by pits and ridges which show a tendency to radiate, especially posteriorly. The anterior part also forms a weak longitudinal ridge. A narrow canal runs obliquely upward and backward through the scute about halfway along the broken medial edge.

This scute appears to have been narrow, but this may be misleading. The anterior end could have formed a projection as in dorsal scutes of *Saltoposuchus* (von Huene 1921) and *Terrestrisuchus* (Crush 1984). At any rate it is clear that *Sphenosuchus* possessed a paired series of paramedian dorsal scutes.

Ventral scute?

A possible ventral scute or perhaps a pair of scutes (figure 45*l*) was found when a thin piece of matrix was flaked off dorsal to the right humerus and in front of a group of gastralia. Further chiselling revealed no additional scutes, but because of the preservation of only two dorsal scutes their absence is not surprising. At first regarded as a ventral scute (Walker 1970, p. 349), later preparation showed that the bone consisted of two parts closely parallel to each other, but joined by a thin bridge of bone (since broken off) near the end which it is convenient to call 'posterior'. The right-hand element measures 7 mm × 3 mm, the left is 8.5 mm × 3.5 mm. Both seem to have been rectangular, thin, with irregular sculpture on both surfaces. These bones resemble small, rectangular scutes such as occur, for example, in *Pedeticosaurus* (van Hoepen 1915), where they are a little less than half as long as the dorsal scutes, which is about the proportion seen here. The proportion of length to breadth would agree better with *Pedeticosaurus* scutes (a little longer than broad) if the specimen were one decayed scute rather than two. However, the occurrence of sculpture on both 'upper' and 'lower' surfaces is peculiar and the identification as scutes, and hence the occurrence of ventral armour in *Sphenosuchus*, must be regarded as uncertain.

Abdominal ribs

Several slender bones, *ca.* 1 mm in thickness, occur in the region between the right humerus, the distal ends of the ribs, and the presumed proximal ends of the left tibia and fibula (figure 1). Some of these are straight, some curved, and one or two show a slightly expanded end. Most are broken. These are almost certainly abdominal ribs but show no definite arrangement.

5. ANATOMICAL INTERPRETATIONS AND COMPARISONS

(*a*) *Cranial nerves*

The cranial nerves have been mentioned at various places in the description of the bones of the skull, but it is convenient to review them briefly at this point and to discuss the evidence for the identification of some of the foramina.

The *olfactory nerves* have left no trace on the bones;

fine grooves on the undersurfaces of the frontals in front of the depressions for the olfactory bulbs are more likely to have been vascular in nature.

The identifications of the *oculomotor*, *optic* and *trochlear* nerve foramina are mutually interdependent. The laterosphenoids evidently met the rear end of the cartilaginous interorbital septum some way below the olfactory tracts, nearly forming a bridge in the dried skull. A critical question is whether the optic nerves emerged above or below this bridge. In Recent crocodiles the laterosphenoids may meet, or nearly meet, both above and below the median optic nerve foramen. However, the lower contact, which seems a constant factor in well-ossified skulls, also meets an upward extension from the median basisphenoid rostrum ('dorsal presphenoid' of Müller (1967)) forming a firm vertical brace. There is no reason to think that such a structure was present in *Sphenosuchus*, and as it also appears to be absent from the skull of the primitive Liassic crocodile *Pelagosaurus*, it may well be a relatively advanced crocodilian feature, perhaps one of the complex of characters which contributes to the rigidity of the crocodilian skull. The position of the optic nerve foramen in modern crocodilian skulls is variable: in *Crocodylus* and *Gavialis* it is closer to the olfactory tract aperture than to the metoptic foramen (this term is used here for the opening in crocodilian skulls between laterosphenoid and basisphenoid at the side of the pituitary fossa, as it seems to correspond, at least in part, to the embryonic metoptic fenestra), whereas in *Osteolaemus* the situation is reversed: the lower bridge is quite short, and the laterosphenoids nearly meet over a long area above the optic foramen. In present-day crocodile and most bird skulls the trochlear foramen is close to (posterodorsal or posterior to) the optic foramen and (in crocodiles) is in front of the region where the groove or canal for the ophthalmic branch of the trigeminal turns upwards; IV also emerges underneath, or close to, the anterior course of V_1, which is often shown by a groove. The oculomotor nerve, on the other hand, emerges more or less directly ventromedial to the turning-point of V_1 and is always posteroventral to IV. In both groups III emerges behind II, with a bony bridge between them which is of variable length in crocodiles but short in birds. Either III or IV or both may be confluent with the optic foramen in birds, this being also very dependent upon age. The grouping of II, III, IV and VI is very similar, in fact, in the bird and crocodile skull, though a foramen for the ethmoidal artery, above the optic foramen, is wrongly identified as the trochlear foramen in some accounts of the bird skull. The same general relationship between II, III and IV is also found in *Sphenodon* and *Varanus* (Säve-Söderbergh 1947, figs 1 and 4).

Comparing the situation in *Sphenosuchus* with the foregoing, it is clear that the foramen in the right laterosphenoid which runs down to the lower edge as a closed slit (figure 27*e*) is the trochlear foramen (IV), while the small section of finished edge ventromedial to this is part of the optic foramen (II); the embayment below the turning-point of V_1 is in the correct position for the oculomotor foramen (III), but since the edge is incomplete it can only be taken as indicating the approximate position of this foramen. The only other possibility is that the 'foramen with the slit' might be for III, in view of the fact that in *Crocodylus*, *Alligator* and *Gavialis* this nerve emerges through a foramen or notch at the top of the metoptic foramen (in *Osteolaemus* this notch is barely noticeable). However, if this were so, the trochlear nerve in *Sphenosuchus* must have emerged through the upper foramen in the laterosphenoid (figure 6*e*), which is in an improbably high position for this nerve. Conversely, the 'foramen with a slit' is too small for the oculomotor, which is the largest of the three eye-muscle nerves. Furthermore, on the inner surface of the right laterosphenoid a shallow groove (figure 28*b*) runs *downwards* and forwards into the 'foramen with a slit', above the course of V_1 as shown by the groove on the outer surface. This agrees with the identification as the trochlear foramen, since the latter nerve appears (after crossing over the brain) high up between the optic lobe and the cerebellum and runs down and forwards, whereas the oculomotor nerve arises low down on the mid-brain and is below the ophthalmic branch of the trigeminal (Romer 1956; 1962). Thus there is little doubt of the correct identification of these nerve foramina.

The optic foramen is thus set relatively lower down than in typical crocodiles, a condition which is no doubt connected with the relatively higher skull and more laterally facing orbit of *Sphenosuchus*. The estimated breadth of the confluent optic nerve foramina (8 mm) is of the right order of size to compare with this foramen in modern crocodile skulls. The tab of bone between the notches for II and III would thus correspond to the process which meets the rostrum of the basisphenoid in the modern crocodilian skull.

The identification of the *trigeminal foramen* presents no difficulty, since it notches the anterior border of the prootic. The upper half of the foramen, however, above the constriction, probably served for the emergence of the middle cerebral vein (see below). The Gasserian ganglion would have been located immediately outside the lower half, or trigeminal foramen proper (Fischer 1852; Hopson 1979). The course of the *ophthalmic branch* of the trigeminal is clearly marked by the groove which runs along the lower margin of the laterosphenoid (figures 21, 23 and 27*e*), in line with the lower half of the foramen. The resemblance to the crocodile is striking, particularly to *Osteolaemus* which lacks the usual bridge over this ramus. According to Fischer (1852), the ophthalmic ganglion in *C. porosus* is formed while the nerve is still partly within its special canal in the laterosphenoid; in *Sphenosuchus* it thus probably lay in the above-mentioned groove, some distance in front of the trigeminal foramen. The faint groove which runs up the lateral buttress of the laterosphenoid in *Sphenosuchus*, immediately above the trochlear foramen, is probably for the *ramus frontalis* of the ophthalmicus, as figured by Säve-Söderbergh (1947) for *Varanus* and *Sphenodon*; a groove in this position is particularly well marked in adult *Osteolaemus*.

The *ramus nasalis* in modern reptiles continues forwards above the optic nerve (Watkinson 1906;

Säve-Söderbergh 1947) to enter the nasal capsule. Information on the precise anatomical relationships of the anterior course of this nerve (and associated blood vessels), particularly to the skull bones, is difficult to obtain for adult crocodiles; embryonic conditions have been described by Shiino (1914) but are not very helpful. Meek (1911) shows the nerve passing lateral to the olfactory bulb and medial to the descending process of the prefrontal in *C. porosus*, and a similar lateral or ventrolateral relationship obtains in other modern reptiles (Bellairs & Kamal 1981). In *Sphenosuchus* there were evidently two channels entering the bony nasal cavity from the upper part of the orbit, as evidenced by the various notches and small processes from the adjoining regions of the prefrontal and frontal (figure 6). The small ventrolateral process from the crista cranii of the frontal and the little upward process from the prefrontal partly separate a more lateral foramen from a more medial and posterior notch which is considered to have transmitted the ramus nasalis of the ophthalmic nerve. This probably ran forwards very close to the olfactory bulb, slightly grooving the lower edge of the crista, and passing between its two small projecting tabs. It was suggested (Walker 1972) that the more lateral foramen may have permitted the passage of the duct from a salt-excreting gland located on the skull roof. The possible existence of such a gland is considered further below. Also to be taken into account in the elucidation of these structures is the likely presence of a nasal or ethmoidal artery and vein entering and leaving the capsule in this region.

The *abducens nerves* pierced the dorsum sellae (figure 30*c*) in the usual way and emerged at small, forward-facing foramina just above and a little behind the pituitary fossa, at the back of the sinus between the basisphenoid and laterosphenoids (figures 21*f* and 23*d*). Owing to the pneumatization, their canals are almost reduced to bony tubes.

The foramen for the *facial nerve* (figures 21–24) pierces the prootic and its main or *hyomandibular ramus* led backwards over the fenestra ovalis in a groove. As already noted, the postfenestral (pneumatic) depression lay medial to this nerve. Its more posterior course leaves no trace on the bones, but evidence of the *chorda tympani* branch is seen in the lower jaw. A groove, virtually a foramen at its posterior end, commences in the notch between the two posterior processes of the prearticular and runs forwards along the dorsomedial angle of the longitudinal channel in this bone (figure 33*h*, *i*). This groove was certainly for the passage of the chorda tympani nerve, which evidently lay alongside Meckel's cartilage as far as the base of the adductor fossa. The anterior emergence of the nerve in the floor of the fossa cannot be exposed because of the proximity of other bones.

The posterior position of entry of the nerve into the lower jaw poses a problem because of damage to the area adjacent to the foramen aërum. Bender (1906) states that, in the alligator, the chorda tympani enters through a special foramen in the retroarticular process and then runs through the articular to the medial side of Meckel's cartilage. A very small foramen, presumably for this nerve, is often distinguishable in modern crocodilian jaws just medial to and in front of the foramen aërum, or just below the glenoid on the medial surface. The anterior emergence of the nerve is difficult to find in the dried skull, as there are several very small foramina, and it would require a dissection of the bone to identify it. There does not seem to be a medial subcutaneous groove, as in birds, however.

In birds the foramen for the chorda tympani is usually separate from and a little anterior to, the foramen pneumaticum but may be just within its mouth. In many cases the nerve emerges on the medial surface just below the glenoid and runs anteroventrally for a few millimetres subcutaneously in a groove before re-entering the bone, finally emerging more anteriorly.

There is evidence for the course of the chorda tympani in the thecodontian *Stagonolepis*, although this was overlooked in the original description (Walker 1961). A small foramen enters the articular behind the medial side of the posterior rim of the glenoid in this form, piercing the bone in an anteroventral direction and emerging below the glenoid on the medial surface at the posterior end of a groove 9 mm long. The latter can be seen on the figure of the jaw, below the letters 'ar' (Walker 1961, fig. 6c). Whether the groove was completely concealed by the prearticular, as I have shown it, is difficult to determine because of the preservation, but a notch in the margin of the prearticular suggests that it had a short exposure.

Thus in *Sphenosuchus* the nerve may have entered through the foramen aërum and emerged from the large foramen in the anteroventral concavity (figure 34), although this seems to have been mainly pneumatic, thence running down and forward superficially, to the notch in the prearticular. Alternatively it passed by a separate small foramen in front of the foramen aërum, through the medial edge of the articular where the bone is broken away, and then ran down as before.

The *palatine ramus* of the facial nerve branched off immediately outside the facial foramen, passing over a slight notch in its anterior rim. Its proximal course is indicted by a narrow groove (figure 21*f*) which skirts the lateral or posterior edges of the two pneumatic foramina in the anterior wall of the cochlear recess, and runs down to the 'shoulder' or notch in the edge of the basisphenoid at the lower end of the basisphenoid plate (figure 23*b*, *d*). Here the palatine nerve joined the internal carotid artery and probably dipped with it into the channel at the base of the postcarotid recess. Its further course (or perhaps that of the palatine artery) is indicated by a groove which descends almost vertically along the outer side of the root of each basipterygoid process (figure 21), curving round posteriorly and medially below on to the inner surface (figure 27*b*) as in *Sphenodon* (Säve-Söderbergh 1947). The direction of the groove in *Sphenosuchus* indicates that the nerve or artery left the internal carotid a little in front of the lowest point reached by the latter in its sigmoid course along the braincase. The further course of the palatine nerves cannot be traced directly, but there is little doubt that they ran forwards between the basipterygoid processes, just below the interbasipterygoid lamina, accompanied by the palatine arteries, to emerge anteriorly at the base of the rostrum. The route of the palatine nerve described above is essentially that found in the modern crocodilian skull, but since to demonstrate this would involve a detailed consideration of the homologies of the various parts of the basisphenoid and its air passages, it is deferred for now. The Lower Jurassic crocodile *Pelagosaurus* is even more like *Sphenosuchus* in the braincase; here the courses of the palatine nerves or arteries are clearly marked by a pair of grooves passing forwards between the basipterygoid processes.

It is possible that the groove which runs just below the upper margin of the basipterygoid process in *Sphenosuchus* and passes over the facet (figure 25*e*) may also have carried a nerve or artery or both. The medial cranial sympathetic trunk does not seem to have been described in crocodiles, but in lizards (see Willard 1915; Adams 1942; Oelrich 1956) and probably in *Sphenodon* (Säve-Söderbergh 1947, fig. 8) this nerve is intimately associated with the palatine nerve and runs below the basipterygoid process. In birds, however, the sphenopalatine nerve (a branch of the medial cranial sympathetic) accompanies the sphenomaxillary artery (a branch of the internal carotid), and these are distinct from the palatine nerve and artery (Wingstrand 1951; Baumel 1975*a*, *b*). There may be up to four foramina for these structures on each side, piercing the sphenoid complex behind the basipterygoid processes. Relationships of these nerves and vessels to the process are rarely clearly described in the literature, but putting together personal observations on bird skulls with what statements are available (Crompton 1953; H. J. Müller 1963; Toerien 1971), there is little doubt that the former pair pass over, the latter under, the process, when this is present. Thus the upper groove in *Sphenosuchus* may indicate the passage of a sphenopalatine nerve and accompanying artery.

The three foramina for the divisions of the *auditory nerve* are closely comparable to those in the modern crocodilian skull. The deployment of the nerves to the various portions of the labyrinth has been excellently figured in the classic work of Retzius on the alligator (1884) and, although he does not deal with their relations to the foramina, it is not difficult to determine these by collating his figures with observations on crocodilian skulls, which differ from each other only in very minor details as far as these foramina are concerned. According to Retzius, the ramus anterior of the acusticus supplies the anterior and external ampullae and the macula utriculi by a branch which evidently passes through the anterior foramen. The anterior ramus also sends a branch to the anterior part of the macula sacculi via the middle foramen. The ramus posterior passes through the posterior foramen and innervates the posterior part of the macula sacculi, the posterior ampulla and the macula neglecta, the papilla basilaris and the macula lagenae. Most workers on the archosaur braincase have assumed that the posterior foramen transmits only the posterior acusticus; Glatt (1975), however, gives a different proximal arrangement of the nerves in *Caiman crocodilus*. According to him, the anterior acusticus also supplies the posterior part of the macula sacculi, the posterior ampulla and the macula neglecta by means of a ganglion bridge which passes through the posterior foramen. (This ganglion bridge is, rather confusingly, allocated to the posterior ganglion). On this view, the posterior nerve supplies only the cochlea and lagena.

In *Sphenosuchus*, as in the crocodile, two foramina are found entering the floor of the auditory capsule anteriorly (figure 22*d*). Their relative sizes, and the positions in which they occur with respect to the various depressions and cavities of the vestibule leave no doubt as to their identification: the larger, more anterior of the two is for the branch of the anterior acusticus which supplied the anterior and external ampullae and the macula utriculi, while the foramen close behind it transmitted the nerve to the anterior part of the macula sacculi. It is noteworthy that in *Sphenosuchus* this foramen is much smaller than the one in front of it, whereas in Recent crocodiles the disparity is usually not very great. Whether or not the third or posterior foramen in *Sphenosuchus* (figures 22 and 24) transmitted part of the anterior nerve does not really concern the present discussion, because the sense organs supplied through this foramen are the same in each case. Thus one can assume three rami within the capsule: one to the cochlea and lagena, one to the posterior part of the macula sacculi, and one to the posterior ampulla (including a small distal twig to the macula neglecta). The first and last of these are indicated by respectively, the channel running down the prootic from the posterior foramen, which evidently supplied the cochlear ganglion, and the groove on the opisthotic passing back along the threshold of the vestibule. This groove extends too far posteriorly to have housed a ganglion bridge like that figured by Glatt (1975). The posterior groove, and the apparent reduction of the anterior saccular nerve in *Sphenosuchus*, show an advance on the usual crocodilian condition and suggest an approach to the situation in birds. There is no definite indication of the posterior saccular nerve in *Sphenosuchus*, but this is not surprising since the crocodilian otic capsule likewise lacks any internal trace of this nerve on the bones.

The *glossopharyngeal*, *vagus* and *accessorius nerves* certainly emerged through the metotic foramen. In typical crocodiles these nerves enter the metotic foramen internally but are diverted backwards by the ossification of the subcapsular process which closes off the lower part of the primitive cranio-quadrate passage, consequently they emerge on the occipital surface of the skull. In *Sphenosuchus* some development of a subcapsular process had occurred, as witnessed by the laterally projecting floor to the recessus scalae tympani, but not sufficiently to cause any enclosure or diversion of the relevant nerves. The metotic foramen is partially subdivided by a central thickening of the opisthotic ledge. The ventral portion of the opening (figure 22) no doubt served for the medial extension of the perilymphatic sac, as the perilymphatic duct, from the recessus into the cranial cavity, and on this account probably also transmitted the *glossopharyngeal nerve* which is usually closely associated with the duct (Romer 1956; Baird 1970). The nerve would thus have travelled obliquely backwards across the floor of the recessus, passing close behind the little upward flange

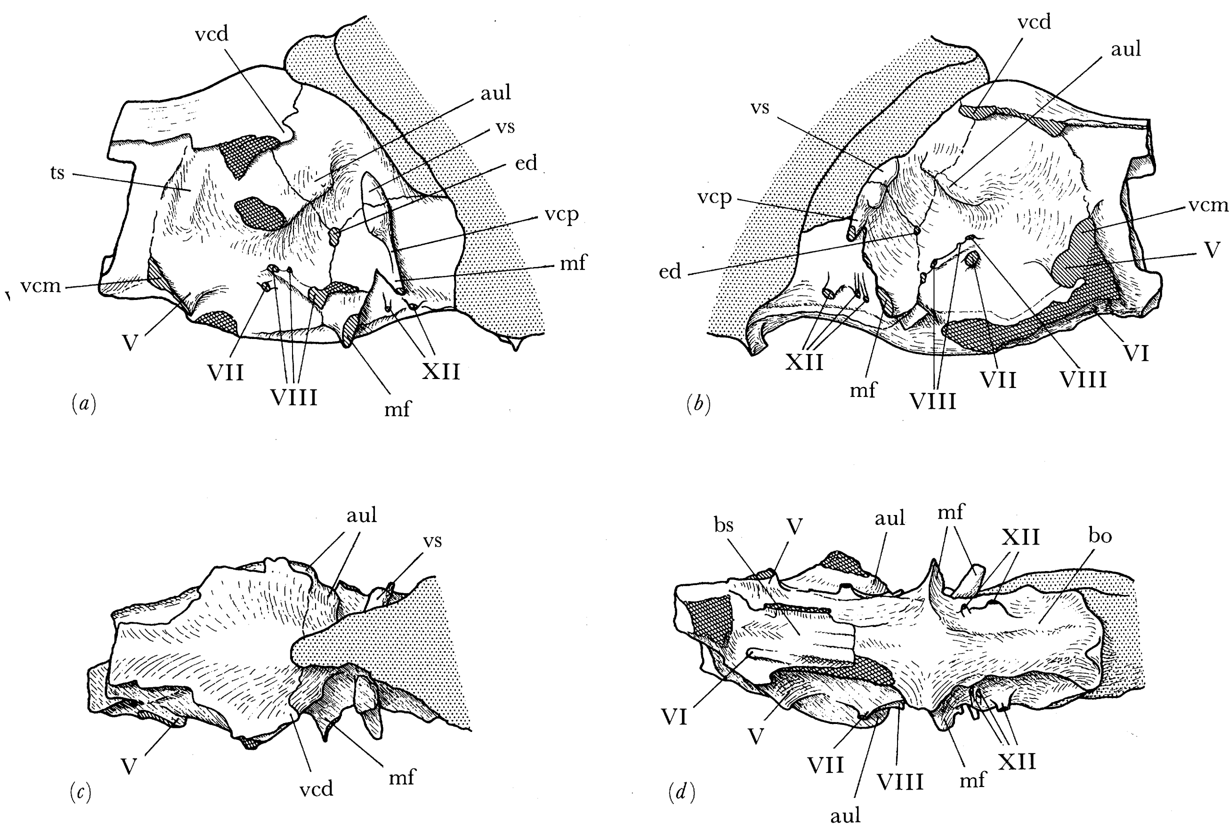


Figure 46. *Sphenosuchus acutus* Htn. Endocranial cast. (*a*) left side; (*b*) right side; (*c*) dorsal; (*d*) ventral views. Foramina hatched, defects in cranial wall cross-hatched. Magn. × 1.5.

from the outer edge of the exoccipital which indicates the course of the stapedial artery, and running medial to (or behind) that vessel. The *vagus* and *accessorius* nerves would have emerged from the posterior or dorsal part of the metotic foramen (figure 24). These nerves no doubt passed out across the floor of the recessus.

In living crocodiles the glossopharyngeal and vagus nerves (including in the latter the accessorius) form ganglia immediately outside the skull in, or close to, the large external 'vagus' foramen, from which all three nerves emerge. These ganglia, with the superior cervical ganglion, form either a single mass or separate but closely-associated ganglia (Fischer 1852; Shiino 1914; Bellairs & Shute 1953). It seems probable that in *Sphenosuchus* the ganglia of the IXth and Xth nerves, and the superior cervical ganglion, lay close to and just outside the ridge which curves down and forwards from the paroccipital process to the exoccipital, just behind and lateral to the little flange on the latter.

The lateral cranial sympathetic trunk, a large nerve in modern crocodiles, starts from the superior cervical ganglion (Bellairs & Shute 1953) and enters the 'vagus' foramen. Its course in the modern crocodilian skull may have significance in relation to the problem of the unusual position of the stapedial artery in these forms, which is discussed below. The nerve, however, has left no trace in the case of *Sphenosuchus*.

A smaller anterior and a larger posterior foramen emerge from the exoccipital on each side (figures 22*c* and 24*b*). In crocodile and bird skulls there are commonly two such disparate foramina which transmit branches of the *hypoglossal nerve*, but there may be two small anterior foramina instead of one. Internally in *Sphenosuchus* the right side shows two small anterior foramina (figure 30*d*), the left only one. Thus there were evidently three hypoglossal roots in this specimen, at least on the right side, the anterior two of which emerged through a common external foramen, or joined within the braincase wall.

(*b*) ***Brain and endocranial cast*** (***figures* 28*b* and 46**)

The endocranial cast was made by pouring silicone rubber into the cranial cavity through the foramen magnum, the various gaps and cranial nerve foramina having been first stopped up with plasticine. The bridge of matrix between the otic pyramids which had been left to support the more fragile left side, and which appears on figure 30*b–d*, was first removed. Because of fragility and loss of bone it was impossible to clean very far between the laterosphenoids, so that the cast extends only a little way in front of the trigeminal foramen. Part of the supraoccipital is missing, hence the dorsal profile of the posterior portion is seen only on the left side. The left otic capsule, as was expected, broke when extracting the cast, but was repaired with virtually no loss. The temporary removal of most of the left capsule enabled a clearer view of the lower part of the inner surface of the right capsule to be obtained, and the opportunity was taken to photograph this. It could also be seen more clearly, on the left side, how the basioccipital rises up as a strong, blunt pyramid at the lower end of the cochlear recess, with the prootic having a very strong contact with the sloping anterior surface, the opisthotic being less massive than the prootic. The exoccipital also has a very strong contact with the basioccipital, and is very wide: 7.5 mm at the small flange for the stapedial artery.

In addition to the endocranial cast, a rubber latex cast was made of part of the nasal cavity when disarticulation of this region occurred during preparation. This cast also shows the upper parts of the olfactory bulbs, the impressions of which are also seen in figures 5*c*, *e* and 6*b*. The olfactory bulbs were elongated and somewhat compressed, although allowance must be made for the *post mortem* squeezing of the skull. The cast shows that they were deeper than wide. Fine grooves on the undersurfaces of the frontals leading away from in front of the impressions are more likely to have been vascular than to indicate the olfactory nerves; in *Crocodylus porosus*, Meek (1911) shows the nerves coming off in a more ventral position, also Wettstein (1937–54) in *Alligator*. The impressions of the upper surfaces of the bulbs are located between the posterior orbital processes of the prefrontals.

The bulb impressions taper only slightly to a short, but relatively wide olfactory tract region between the deep crista cranii frontales (figure 6*e*), swelling out again to the region of the cerebral hemispheres between the laterosphenoids. Little more can be said of these than has been given in the description of the bones; a natural cast of the region of the left cerebral hemisphere is seen where the bone has been lost (figure 17*a*, *b*). This region is very similar in form to that of a modern crocodile. It seems doubtful that the shallow posterior concavity seen on the right laterosphenoid could represent the optic lobe; it seems too low down for this structure and its significance is unknown. In the bird skull a similarly placed, but stronger and more oblique ridge, separates the cavities for the cerebral hemisphere and the optic lobe; the latter, of course, is much lower down than in the crocodilian brain.

In the study of the endocranial cast proper, comparison has been made with sagittally sectioned skulls of *Crocodylus acutus* and *Gavialis*, and endocranial casts made from these, as well as with figures of the endocranial cast of *Caiman crocodilus* given by Hopson (1979). In general, the brain seems to have been very similar to that of a modern crocodile, differing chiefly on account of the longer prootics and laterosphenoids. The cranial cavity is, however, relatively deeper, especially in the posterior half, and the upward and downward flexures in front of the foramen magnum are more marked.

The endocranial cast is considerably taller than wide, its maximum dimensions being 23 mm high × 15 mm transversely, in the region of the auricular lobes, allowance being made for a defect in the cranial wall. Some *post mortem* compression of the cavity has taken place, but is unlikely to have been great as the braincase is strongly built. The sutures and nerve foramina need little further description, so that only features which are not obvious from the figures will be mentioned. In view of Hopson's remarks (1979) about the strong influence of the longitudinal venous sinus and thick dura mater on the form of the endocranial cast in *Caiman crocodilus*, especially in the mid- and hind-brain regions, it is clearly necessary to be cautious in interpreting the cast in terms of brain structures.

The sides of the cast are strongly pinched in by the otic bullae (cf. figure 30*c*); above this region the cast is very narrow at the upward flexure, but broadens out rapidly at the region of the auricular lobes and above this at a pair of small backward projections which indicate the entry of veins (venae capitis dorsales) on the supraoccipital (or epiotic)/parietal sutures. These projections appear to correspond to those labelled 'vc' by Hopson on the *Caiman* cast (1979, figs 1 and 2). The median ridge above the otic depressions probably indicates the longitudinal dorsal venous sinus. The domelike expansion below the parietals perhaps indicates an expansion of this sinus, the broad ridge which continues the dome forwards probably marking its forward extension.

There is some doubt as to whether the auricular (or floccular) lobes of the cerebellum are represented on the cast. Hopson (1979) describes a 'thick pocket of the dura which lies in a broad depression in the anterolateral wall' of the otic bulla in *Caiman* (presumably 'anteromedial' is meant). This depression receives small vessels from the 'recessus lateralis' of the longitudinal sinus which break up into small twigs penetrating the bone. These twigs are represented by tiny processes (not figured) on the *Caiman* cast. The description suggests a comparison with the projections which I have labelled 'auricular lobe' on figure 46, from the posterior ends of which arise small processes representing foramina entering the bone. However, the comparison is uncertain. The projections on the cast of *Sphenosuchus* are large, lateral swellings, bulging out below the processes which indicate the venae capitis dorsales and are situated well behind the trigeminal foramina. They terminate posteroventrally as lobate areas which entered depressions within ridges which represent the arcs of the anterior vertical semicircular canals and the superior sinuses of the utriculi. In Hopson's figure, and in my endocranial casts of *Gavialis* and *Crocodylus*, the depressions which he mentions are scarcely detectable; the 'recessus lateralis' (Hochstetter 1906), or transverse sinus (Dendy 1909, p. 423), is represented, as Hopson says, by a broad swelling which runs down and a little forward to the trigeminal foramen. There is a faint indication of the transverse sinus in *Sphenosuchus* in the form of a broad shallow depression curving down the anterior end of the prootic to the trigeminal foramen. This appears as a low ridge on the cast (figure 46*a*). Because in *Sphenosuchus* there is reason to think that the transverse sinus discharged via the upper part of the trigeminal foramen as the middle cerebral vein, whereas this vein appears and is later lost in the embryo crocodile (Hochstetter 1906), the vascular arrangements were not identical and hence a different interpretation of the cast in this area is permissible. It is considered, therefore, that the marked projections on the *Sphenosuchus* cast do indicate a substantial development of the auricular lobes of the cerebellum. The cerebellum itself would presumably have tapered back between the otic bullae.

The transverse sinus occurs at the junction of the optic lobes and cerebellum, hence the optic lobes in *Sphenosuchus* must have lain within the posterior parts of the laterosphenoids. As already mentioned, no certain trace of these structures can be made out.

Other features of the cast can be dealt with briefly. The groove in which lie the three foramina for the auditory nerve branches is represented by a ridge below the anteroventral part of the otic bulla depression. On the left side anteroposterior compression of the capsule has opened a cleft along the loop-closure suture; there is thus a projection on the cast here, connection to the posterior auditory foramen, which has been a little enlarged. The metotic foramen is partially closed on each side, hence it appears as a discontinuous ridge. The presumed vascular sinus on the posterior cerebral vein is well shown as a projection on both sides; the ridge running down from it into the upper end of the metotic foramen probably indicates the course of the vein itself. On the right side the small projection representing the diverticulum of the longitudinal sinus ('vcp' of Hopson (1979, figs 1, 2)) is hidden by these ridges, hence does not appear on figure 46*b*. This projection is not preserved on the opposite side.

(*c*) ***Pneumatization*** (***figures* 28 *and* 59–62**)

The skull of *Sphenosuchus* is permeated by many cavities not usually found in reptilian skulls. Although some of these may have had additional functions, the basic reason for the existence of these cavities is believed to be that they housed pneumatic diverticula. The main evidence for this conclusion is as follows.

1. Many of them lie between the side wall of the braincase and the pterygoquadrate arch, so that they can be regarded as branches of the middle ear cavity.

2. Others can reasonably be assumed to have had communication with the throat or nasal cavity, or with the middle ear, by less direct routes (e.g. cavity in the articular).

3. Nearly all can be shown to have homologues in the modern bird or crocodilian skull or both, where they are known to be pneumatic.

4. The large size of these cavities, which in some cases is too great to have accommodated only the nerves and blood vessels normally found in such regions (e.g. the pre- and postcarotid recesses).

5. The position of many of the cavities makes it unlikely that they housed other structures such as muscles (e.g. the rostral cavity).

The pneumatic spaces found in the *Sphenosuchus* skull may be listed briefly here for convenience (paired unless otherwise stated).

1. Within the rostrum, below and in front of the pituitary fossa: the rostral recess (median).
2. The precarotid recess (median).
3. The cavities within the basipterygoid processes.
4. The postcarotid recess (median).
5. The basioccipital recesses.
6. The sub-basisphenoid recess (median).
7. The depressed areas at the sides of the prootics, in front of and lateral to the prootic parts of the cochlear prominences (prootic recesses).
8. The facia antra.
9. The mastoid antra.
10. The two cavities along the palatine branch of nerve VII (the precochlear cavities).
11. The temporal canal (p. 8), with its anterior entrance, the anterior temporal foramen, and an entrance behind the quadrate, the postquadrate foramen.
12. The shallow depression (postfenestral depression) behind the fenestra ovalis and fenestra pseudorotunda, crossing the prootic/opisthotic suture.
13. The pit in the posterior surface of the quadrate.
14. The cavity within the medial side of the articular.

Other cavities which may possibly have been pneumatic are:

15. The antorbital fenestra and its surrounding fossa.
16. The dorsal channel in the maxilla–jugal.
17. The cavity entering the ectopterygoid.
18. The cavity entering the pterygoid.
19. The large cavity between premaxilla and maxilla, opening to the palate.

(*i*) *Comparison with crocodiles*

The pneumatic or eustachian spaces in the crocodilian skull, both fossil and Recent species, have been studied by many workers, including Owen (1850), Eudes-Deslongchamps (1864), Miall (1878), van Beneden (1882), Chapman (1894), Colbert (1946), Müller (1967), Iordansky (1973), Hecht & Tarsitano (1983) and Tarsitano (1985). The earliest accurate account, and still in many ways the clearest, is that by Owen (1850). The nomenclature he introduced for the main passages in the modern crocodilian skull has been very widely used and it does not seem necessary to use new and more cumbersome terms, as has been done by Busbey & Gow (1984) and Tarsitano (1985). Accordingly 'median eustachian' and 'lateral eustachian' will be used for the median and lateral ventral apertures and canals respectively. The dorsal transverse air passage through the supraoccipital, the entrance to which is primitively ringed completely round by prootic, was termed the 'antrum mastoideum' by Hasse (1873, p. 690), and this usage has been widely followed (see, for example, Wettstein 1937–54; Müller 1967). More recent workers have introduced different names for it, for example Iordansky (1973: 'transverse canal'), Busbey & Gow (1984: 'dorsal transverse pneumatic sinus'). Tarsitano (1985) calls it the 'intertympanic sinus', a usage particularly liable to confusion, as 'intertympanic' has also been used for the median ventral aperture and canal (Wettstein 1937–54; Müller 1967) deriving from van Beneden (1882: 'trou intertympanique'). The only objection to the term 'antrum mastoideum' or, informally, 'mastoid antrum', might be that confusion could arise with a similar term for part of the mammalian middle ear, but this possibility is believed to be remote and Hasse's usage will therefore be followed here.

The discussion which follows is mainly intended to establish homologies between the pneumatic cavities in the skull and jaw of *Sphenosuchus* and those of modern crocodiles, insofar as these exist, but remarks on some fossil forms are also included. It should be noted that in order to establish homology the cavities in each case should be surrounded by the same bones, and not merely lie approximately in the same position in the skull.

A brief description of the main pneumatic cavities in the modern crocodilian skull will first be given to provide a basis for comparisons. It is convenient to introduce (with two additions) the abbreviations used by Colbert (1946), to avoid repetition of long descriptive phrases. A large median eustachian canal (*Me*) enters below on the basioccipital/basisphenoid suture, and after ascending for a short distance, divides into an anterior median branch which runs into the basisphenoid (*Mea*) and a posterior median one into the basioccipital (*Mep*). The *Mea* divides within the basisphenoid into a pair of canals which emerge laterally and pass up the flanks of the bone on to the prootics. Here each passes in the narrow channel between the cochlear prominence and the flange below and behind the trigeminal foramen (or crista prootica). This lateral branch may be abbreviated to *Meal* (plural *Meall*). The *Meal* enters the tympanic cavity high up, in front of the fenestra ovalis. It is walled in laterally mainly by the pterygoid and quadrate. An important point is that the *Meal* crosses *lateral* to the internal carotid artery as the latter arches downwards in its bony canal through the basisphenoid. The cast of the eustachian system of *Crocodylus acutus* figured by Colbert (1946) is peculiar, and must have been defective in some way, because it shows the internal carotid running forwards entirely above the *Meal*, whereas the latter should cross it at right angles. A skull of *C. acutus* in this Department shows the normal arrangement. Colbert is also incorrect in stating that the *Meal* enters the rhomboidal sinus. Iordansky (1973) repeats this error, and also (incorrectly) shows the rhomboidal sinus lying in the basisphenoid.

The *Mep* likewise divides into right and left branches (*Mepll*) which emerge on the sides of the basioccipital near its junction with the exoccipitals. Here the *Mepl* joins with the lateral (or true) eustachian tube (*Le*) to form a small expansion at the base of the tympanic cavity, called by Owen the rhomboidal sinus (*Rs*). This lies just behind the lower end of the cochlear recess and below the upward arch of the internal carotid artery. Tarsitano's account of this region (1985) is difficult to follow and he seems to regard the *Rs* as extending considerably further dorsally than in Owen's original definition.

The paired *Le* tubes enter the skull by smaller foramina on either side of the *Me*, passing up along the contact between basioccipital and basisphenoid. In the lower half of its course the *Le* lies largely in the basisphenoid; in the upper half its medial side lies in a groove in the basioccipital. It enters the *Rs* lateral to and a little in front of the *Mepl*.

The two tympanic cavities communicate with each other by the mastoid antrum (*ma*) which passes across the skull from side to side through the supraoccipital/epiotic. Pneumatization from the tympanic cavity also enters the articular bone in the lower jaw via a canal in the quadrate and the foramen aërum situated posteromedial to the cotylus.

Some soft-part anatomical structures should also be mentioned as they provide landmarks which help in determining homologies. The internal carotid artery enters the skull almost vertically from below through a foramen in the projecting ridge of exoccipital (probably part of the ossified subcapsular process) which runs down the basioccipital. It arches over dorsally through the bone, emerging within the tympanic cavity as a projecting tube behind the cochlear prominence. It descends and passes forwards close outside the lower half of the cochlear recess in a membranous tube in the region where the prootic and opisthotic diverge to expose the membranous lateral wall of the cochlea (lagenar region). It then enters the posterior outer corner of the basisphenoid close to the prootic and runs down through the bone, finally curving up and forward again to enter the back of the pituitary fossa. Thus it describes a 'römischen **S**' along the side of the braincase as described by Rathke (1866, p. 228).

There is no palatine artery branching from the internal carotid in modern crocodiles: it has been replaced by branches from more laterally placed vessels (Shindo 1914).

The palatine branch of the facial nerve follows the *Meal*; in a large *Osteolaemus* skull in this Department its course is well marked by a groove which runs down the channel in the side of the prootic. Below this the groove lies in the side of the basisphenoid, crossing the slight bulge made by the carotid canal. In *Osteolaemus* the *Meall* form a fairly substantial sinus passing through the basisphenoid from side to side. The palatine nerve runs to about half-way down the anterior wall of this sinus and then enters the bone, continuing downwards at first and then turning sharply forwards to emerge at the base of the rostrum at the junction with the pterygoid, close to the mid-line. Romer's statement (1956, pp. 143–144) that the internal carotid is accompanied for part of its course in its canal by the palatine nerve is thus incorrect.

Before turning to questions of homology it is necessary to establish the courses of the above vessel and nerve in *Sphenosuchus*. As regards the internal carotid artery, the detailed evidence will be given later but there is good reason to think that it was very similar to the pattern seen in modern crocodiles (figure 49). Anteriorly, however, the arteries were not completely enclosed but, after crossing the notches or shoulders at the lower end of the basisphenoid plate (figures 22*a* and 23), they dipped down into the channels at the base of the postcarotid recess and then ran up the sides of the carotid pillar into the pituitary fossa. Presumably a palatine artery was given off at or close to the lowest point, accompanying the palatine branch of the facial nerve round the back of the posterior 'strut' of the basipterygoid process. The groove here may in fact represent the artery, rather than the nerve. Whether or not a ramus of the artery and a nerve passed forwards *over* the basipterygoid facet does not concern the present discussion. The course of the palatine division of VII is clear: see §§4 and 5*a*.

The basioccipital recesses of *Sphenosuchus* (item 5 of the list on p. 75) are homologous with the *Mepll* of the crocodilian skull. The triangular entrance to these is entirely bordered by basioccipital, so that it may be regarded as a very abbreviated *Mep*. The *Mepll* in *Sphenosuchus*, however, do not emerge at the sides of the basioccipital, although they come close internally to the depressions on the lateral surfaces at the tops of the *Lee* grooves. A true *Rs* is thus not formed.

At first sight, one might think that the crocodilian *Meall* might correspond to the large sinus (postcarotid recess (4)) in *Sphenosuchus* which passes through the basisphenoid from side to side, particularly because in *Osteolaemus* the *Meall* form a good-sized transverse passage through this bone. This comparison, in fact, was the basis for citation of the postcarotid recess of *Sphenosuchus* as a crocodilian feature (Walker 1970, p. 349, item (g)). However, the comparison cannot be sustained, because the internal carotid tube passes *above* the transverse passage in *Osteolaemus*, but curved *below* it in *Sphenosuchus*. Furthermore, the palatine nerve runs down the front wall of the passage in crocodiles, but in *Sphenosuchus* it would have accompanied the internal carotid along the posteroventral side of the postcarotid recess (figure 49), leaving it ventrally to curve round the back of the basipterygoid process.

The anatomical relationships cited above in fact suggest that the equivalent of the transverse sinus of *Osteolaemus* is the large concavity *below* the braincase in *Sphenosuchus* which lies in front of the tubera and their connecting ridge, and behind the concave rear surfaces of the basipterygoid processes, facing posteroventrally. That this was at least partly pneumatic is also shown by the necessity for pneumatization to enter the basioccipital to gain access to the basioccipital recesses or *Mepll*. This concavity, or sub-basisphenoid recess (6), is equivalent to the *Me* plus the *Mea*. The concave sides of the basisphenoid below and behind the postcarotid recess, the sides of the recess itself, and the prootic recesses (7), are the equivalents of the *Meall*. Although much wider, more open channels than in modern crocodiles, they have the same anatomical relationships as in the latter, crossing outside the internal carotid arteries more or less at right angles and then running upwards and slightly backwards on to the prootics, following the routes of the palatine branches of the facial nerves. The course of this nerve ventrally and medially on the anterior side of the sub-basisphenoid recess is similar to its course on the anterior wall of the transverse sinus in the basisphenoid of *Osteolaemus* and, taken with the position of the internal carotid, suggests a homology or partial homology between these cavities. As will be seen below, this conclusion is confirmed by the embryological evidence.

The lateral eustachian tubes (*Lee*) in *Sphenosuchus* were evidently in a similar position to those of Recent crocodiles. On the right side of the skull a fine groove representing the *Le* runs up the side of the basioccipital, in the channel between the descending tongue of exoccipital and the squamous overlap of the basisphenoid. It terminates just behind the lower end of the cochlear recess, in the position of the crocodilian *Rs*. There is a small depression here in *Sphenosuchus* although, as previously noted, the equivalent of the *Mepl* does not break through to this region. The *Le* may originally have been walled in laterally by the thin posterior parts of the basisphenoid, as in the crocodile; these areas in *Sphenosuchus* are too imperfect to settle this question. However, such enclosure is unlikely, since these thin 'wings' in the modern crocodile are probably derived from the anterior part of the basisphenoid of a *Sphenosuchus*-like ancestor, and owe their present position to the fore-and-aft compression of the braincase and the enclosure of the anterior part of the eustachian system.

Study of the early Jurassic crocodile *Pelagosaurus* confirms the correctness of the homologies for *Sphenosuchus* suggested above. Two specimens of *Pelagosaurus typus* are particularly valuable in this respect, one an almost complete skull, the other less complete but disarticulated. These specimens from the Upper Lias of Normandy, figured by Eudes-Deslongchamps (1864), are in the collection of the British Museum (B.M.N.H. 32599 and 32600). Practically all details of the air passages, cranial nerves, etc. can be determined from these two specimens in combination. Like that of *Sphenosuchus*, but in contrast to modern crocodiles, the braincase of *Pelagosaurus* is elongated (figure 47*d–f*). The basisphenoid has a large ventral exposure, is long and ventrally keeled, the keel joining with a transverse ridge at the back of the bone. The *Me* opens directly backwards behind this ridge. Just within the entrance the *Mep* opens upwards into the basioccipital (figure 47*e*). The resemblance to *Sphenosuchus* is very marked, since the *Mep* divides immediately into a pair of elongated cavities separated by a longitudinal bar. In addition, the apertures converge anteriorly and the bar tapers forwards. Each of these cavities or *Mepll* extends back as a pocket within the basioccipital, although they are relatively smaller than in *Sphenosuchus*. Unlike the latter, but like the modern crocodile, the *Mepl* in *Pelagosaurus* communicates dorsolaterally with the *Le* at a rhomboidal sinus situated behind the lower end of the cochlear recess. In B.M.N.H. 32600 the cochlear recess grooves the rear edge of the right prootic.

The *Mea* in *Pelagosaurus* runs forward into the basisphenoid and expands into a large cavity. This passes across from side to side and is partly enclosed by the pterygoids laterally and possibly by the quadrates more dorsally. In front of it there is a pair of ventrolaterally facing, flat and slightly roughened surfaces for the pterygoids. These appear to represent the basipterygoid facets, and between them a pair of fine grooves runs forwards. These grooves are concealed by the pterygoids below (in the complete skull) and run forwards into the pterygoids. Evidently the grooves indicate the courses of the palatine branches of the facial nerves (VII) and perhaps the palatine arteries. On either side the basisphenoid contracts behind the basipterygoid facet and forms a broad,

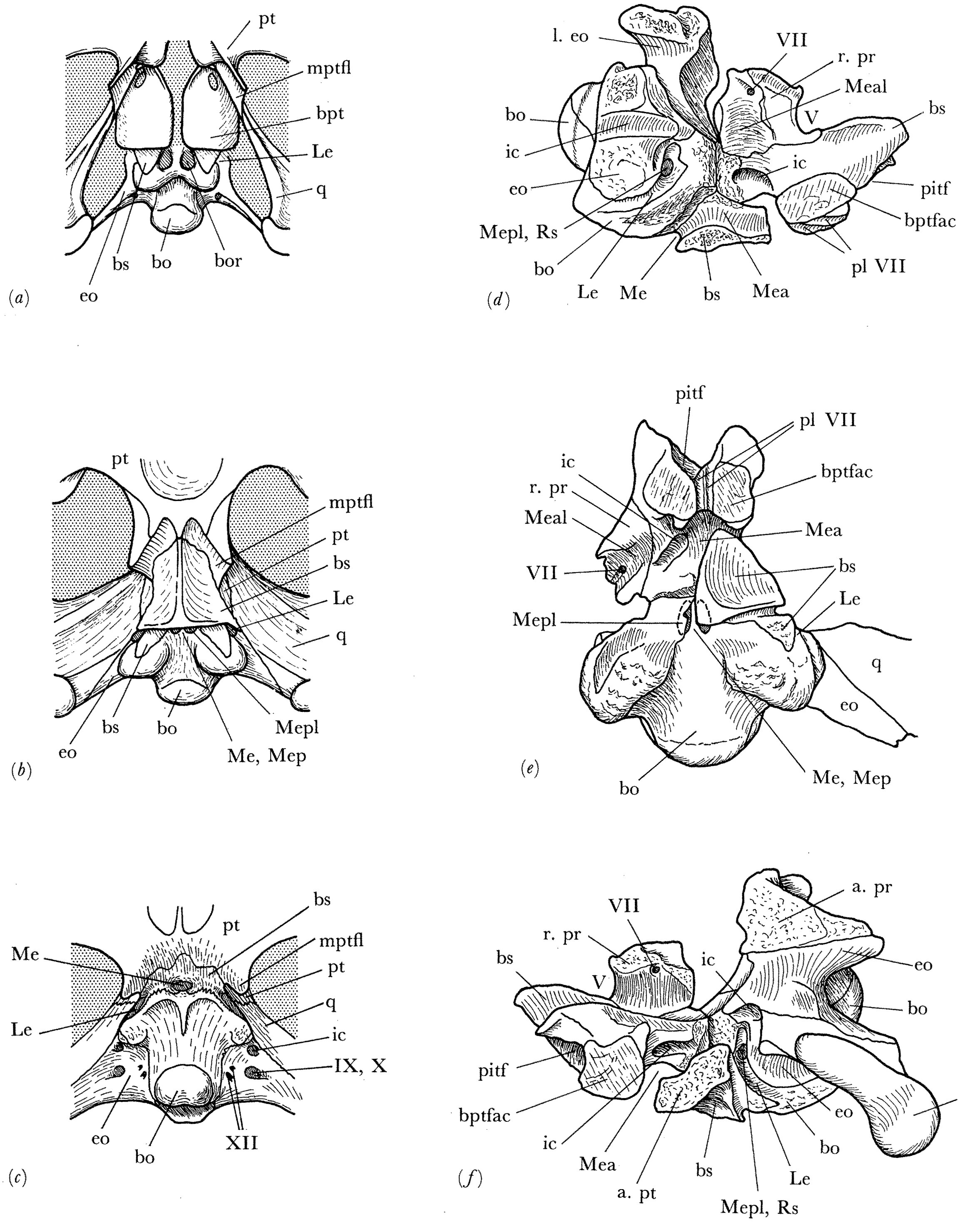


Figure 47. (*a*)–(*c*): Degrees of enclosure of the eustachian system. Ventral views of the basicranial regions of (*a*) *Sphenosuchus*, magn. ×0.75; (*b*) *Pelagosaurus* (B.M.N.H. 32599), magn. ×0.9; (*c*) *Alligator*, magn. ×0.9. (*d*)–(*f*): Braincase of *Pelagosaurus* (B.M.N.H. 32600) in right side, ventral and left side views. The ventral parts of the basisphenoid were presumably originally continuous. Magn. ×1.5.

shallow depression which continues round on to the prootic, passing up between the cochlear prominence and the crista prootica (figure 47*d*,*f*). Because of the elongation of the prootic these two ridges are widely separated in *Pelagosaurus*. The internal carotid arteries have the usual crocodilian posterior course, but are not entirely enclosed in front, passing in grooves in the roof of the *Mea* and then running forwards in tunnels between the basipterygoid facets into the back of the pituitary fossa. The broad channels on the sides of the basisphenoid and prootics thus represent the *Meall*, which passed outside the internal carotids and so had the same relationships to them as in the present-day crocodilian skull.

The lateral eustachian tubes (*Lee*) are represented by grooves on the sides of the basioccipital, between the exoccipital overlaps and the paired tongue-like processes of the basisphenoid which project backwards from behind the transverse ridge already mentioned. The grooves run downwards and backwards and are almost entirely on the basioccipital, the basisphenoid tongue contributing only slightly at the lower end. The *Le* seems to have been exposed almost all the way up to the *Rs*, the dorsal end perhaps being concealed by the posterodorsal tip of the basisphenoid.

The paired grooves in *Pelagosaurus*, which run across the bases of the posterior tongues of the basisphenoid immediately behind the transverse ridge, do not appear to be part of the eustachian system, but probably mark the line of junction between the originally anterior and posterior ventral parts of the basisphenoid (see below).

Pelagosaurus thus confirms the homologies already suggested for *Sphenosuchus*, and stands morphologically intermediate between the latter and the modern crocodilian skull. As in *Sphenosuchus*, the *Mea* (equivalent of the sub-basisphenoid recess) is large and passes via broad *Meall* on the prootics to the anterior parts of the tympanic cavities. The *Meall* cross over the internal carotid arteries. The palatine ramus of VII ran down the *Meal* and turned forwards close to the mid-line, also crossing over the internal carotid. The *Mep* opens upwards into the basioccipital and immediately divides into two elongated *Mepll*. The *Me* is large and opens mainly backwards. The *Lee* are exposed grooves on the sides of the basioccipital running down and back between the exoccipitals and the tongues from the basisphenoid. On the other hand, *Pelagosaurus* resembles the typical crocodile in that the *Me* and *Mea* are enclosed in bone and the *Mepl* emerges laterally to join the *Le* in a rhomboidal sinus. The quadrate and pterygoid are, of course, fused to the braincase in *Pelagosaurus*.

Comparison of *Pelagosaurus* with *Sphenosuchus* suggests that in phylogenetic history the enlarged anterior part of the basisphenoid (basipterygoid processes) has grown backward still further and, together with the quadrate and pterygoid, has enclosed the anterior part of the eustachian system, converting the sub-basisphenoid recess into the *Me* plus the *Mea*. The median ridge on the lower surface of the basisphenoid of *Pelagosaurus* is probably derived from the mid-line fusion of the basipterygoid processes of a *Sphenosuchus*-like form, whereas the transverse ridge corresponds to their posterior edges. The precarotid and postcarotid recesses of *Sphenosuchus* do not occur in *Pelagosaurus*.

The work of Müller (1967) gives further evidence, on the one hand, of the correctness of the homologies established for the principal pneumatic sinuses of *Sphenosuchus* and, on the other, supports the suggestion that the anterior part of the eustachian system has been progressively enclosed during crocodilian history. Müller studied the embryology of the head of *Crocodylus cataphractus*. She regards the adult crocodilian basisphenoid bone as including an anterior element, the presphenoid, itself divided into a dorsal and a ventral portion. During the development of the chondrocranium cartilaginous infrapolar processes originating from the basitrabecular regions grow backwards below the basal plate (cf. also Shiino (1914)). These later ossify to form a dorsoventrally flattened bony plate which encloses the anterior part of the eustachian system (*Mea*) and builds the anterior boundary of the *Me*. These ossified infrapolar processes she terms the 'ventral presphenoid', though this is doubtfully distinguishable from the basisphenoid. In later stages the basicranium grows ventrally so that the *Me* is drawn out to form a canal. Thus the state of affairs seen in the braincase of *Sphenosuchus* can be compared to the earlier stages of the modern crocodilian skull, when the *Me* is a relatively wide aperture, corresponding to the wide open sub-basisphenoid recess of *Sphenosuchus* and confirming the correct identification of the latter. As in the case of the nasopharyngeal duct discussed by Müller, the ontogenetic development of the basicranium in *Crocodylus* parallels the evolutionary history. The anterior portion of the basisphenoid ('ventral presphenoid') grows back in the embryo to enclose the median anterior part of the eustachian system, a process also suggested by the conditions in *Sphenosuchus* (late Triassic or early Jurassic) and *Pelagosaurus* (early Jurassic).

This comparison with fossil forms suggests that the lower part of the 'original' basisphenoid (basisphenoid s.s. of Müller (1967)) is represented in modern crocodiles only by the paired descending tongues on either side of the *Me*, whose fluted posterior surfaces suture against the basioccipital. These correspond in their positions on the basioccipital tubera and their relationships to the *Lee*, to the posterior tongues of the basisphenoid in *Sphenosuchus* and *Pelagosaurus*.

The remainder of the ventral part of the basisphenoid in modern crocodiles, including the thin anterior rim of the *Me* and the thin posterolateral wings which overlap the *Lee*, is derived from the 'ventral presphenoid' of Müller and appears to represent, in a highly compressed state, the basipterygoid processes of *Sphenosuchus* and the corresponding regions of *Pelagosaurus*.

The original division between the basipterygoid processes and the posterior part of the basisphenoid in *Sphenosuchus* seems, in modern crocodiles, to lie at the position of the *Le* grooves transversely and immediately below the *Mea* and *Meall*.

It may be noted that Müller has established that there are no basitemporals in *Crocodylus cataphractus*: the paired elements in crocodiles given this name by Parker (1883) and Shiino (1914) and regarded by them as dermal bones are the ossified infrapolar processes, the 'ventral presphenoid', a cartilage-bone. It would seem to follow from the arguments put forward in the preceding pages that the large, backwardly directed structures in *Sphenosuchus* described by me as basipterygoid processes (Walker (1972) and this paper) are the homologues of the crocodilian 'basitemporals' and thus represent ossified (and pneumatized) infrapolar processes. However, de Beer & Barrington (1934) have stated that the infrapolar processes of crocodiles and birds are different structures from the basitrabecular processes and are not simply basitrabecular processes directed backwards. If so, the infrapolar process cannot give rise to the basipterygoid process. It would therefore seem that only the basipterygoid facet and its base in *Sphenosuchus* represents the basitrabecular process, and that the use of 'basipterygoid process' for the large structure in *Sphenosuchus* is a misnomer. On the other hand, the course of the palatine nerve in relation to the infrapolar process is regarded by de Beer & Barrington as anomalous in the crocodile, yet in *Sphenosuchus* the presumed course of this nerve in relation to the large 'basipterygoid process' seems quite normal, in comparison with the situation in *Sphenodon* (Säve-Söderbergh 1947). This problem lies outside the scope of the present paper, and the term 'basipterygoid process' will continue to be used as before for the large structures in *Sphenosuchus*.

The precarotid (2) and postcarotid recesses (4) of *Sphenosuchus* have no homologues in Recent crocodilian skulls and in fact represent a pneumatization of the floor of the embryonic chondrocranium. It is as if the anterior part of the crocodilian braincase had been 'blown up', increasing the distance between the pituitary fossa and the original floor of the basisphenoid. This floor in the modern crocodilian skull is *above* the transverse sinus already noted.

The rostral recess (1), the cavities in the basipterygoid processes (3), and the precochlear cavities (10) are likewise unrepresented in present-day crocodiles.

Two other cavities leading off the prootic recess, however, have clear equivalents in the modern crocodilian skull. These lie below the prootic flange. The more anterior is anterodorsal to the facial foramen hence, because it seems to lack a name, I have termed it the 'facial antrum' (8). It corresponds to a pocket constantly found in this position in all modern crocodilian skulls which I have examined. It is seen, for example, in *Gavialis gangeticus* (Walker 1972, fig. 1d). The more posterior cavity is larger and lies entirely within the prootic, although it approaches the supraoccipital (or epiotic) closely. This cavity (9) evidently represents, in a less developed form, the mastoid antrum (Hasse 1873: 'antrum mastoideum') of Recent crocodiles. In these forms the *ma* is large and crosses the skull from side to side mainly through the supraoccipital/epiotic. Nevertheless, in species with small supratemporal fossae (*Alligator*, *Caiman*, *Osteolaemus*, at least some species of *Crocodylus*) the entrance is completely ringed by prootic, although the posterior part of the ring is thin and easily broken away when the quadrate is disarticulated. In forms with large supratemporal fossae (e.g. *Gavialis*) the ring of prootic is incomplete posteriorly. In comparison with *Sphenosuchus*, the *ma* in Recent crocodiles has expanded posteriorly and dorsally, so that the prootic buttress has thinned down to a ledge of bone separating the *ma* from the postquadrate foramen. The pneumatic cavity has penetrated through into the supraoccipital/epiotic and joined up with its antimere. The depressed, thickened skull-roof of modern crocodiles allows space for a large cavity, which would scarcely have been possible in the thinner, higher vault of *Sphenosuchus*.

It should be noted that the crocodylomorph mastoid antrum is not the homologue of the avian upper tympanic recess (antrum pneumaticum dorsale) as implied by Whetstone & Martin (1979). The mastoid antrum penetrates the otic capsule itself, probably starting in the prootic if *Sphenosuchus* is any guide, and later in evolution entering the supraoccipital/epiotic, whereas the upper tympanic recess lies *above* the otic capsule, being essentially floored by prootic and roofed by squamosal. The temporal canal of *Sphenosuchus*, in fact, is the homologue of the avian upper tympanic recess. Whetstone (in Whetstone & Whybrow (1983)) regards the temporal canal and mastoid antrum in eusuchians as constituting one sinus, the 'antrum pneumaticum dorsale', a term which should be reserved for birds, and errs in stating that *Sphenosuchus* has only a single pneumatic sinus in this region. I was myself in error, however (Walker 1972) in comparing the 'postquadrate canal' (postquadrate foramen of this paper) of *Sphenosuchus* to the avian posterior tympanic recess (antrum pneumaticum caudale), whereas in fact the postquadrate foramen enters the temporal canal.

There is no representative of the postfenestral depression (12) (incipient homologue of the bird posterior tympanic recess) of *Sphenosuchus* in Recent crocodiles. The cavity in the dried skull behind the fenestra ovalis and below the mastoid antrum is the medial side of the recessus scalae tympani, lying beneath the secondary tympanic membrane. It does not, in any case, encroach on to the prootic. In *Sphenosuchus* the postfenestral depression lies *above* the sharp ridge (crista interfenestralis) to which the secondary tympanic membrane was attached.

The temporal canal (11) and postquadrate foramen of *Sphenosuchus* have clear homologues in the crocodilian skull (see §8). These cavities, especially the temporal canal, are large in *Sphenosuchus* and are believed to have been pneumatic. According to van Beneden (1882), however, the temporal canal is not pneumatized in living crocodiles and thus there is, strictly speaking, no homologue of the avian upper tympanic recess (as a pneumatic space) in living forms. In Recent crocodiles the postquadrate foramen and anterior part of the temporal canal have become the route by which the temporo-orbital artery and vein pass from the cranio-quadrate passage to the supratemporal fossa (Rathke 1866; Hochstetter 1906). There is little doubt that the stapedial or temporo-orbital artery took the same route in *Sphenosuchus*, but there is no reason to think that a major vein accompanied it (see §5*d*).

The pit in the posterior surface of the quadrate (13) of *Sphenosuchus* appears to be comparable to the foramen in modern crocodiles (except *Gavialis*) which passes through the quadrate from side-to-side, directly in front of the otic incisure and beneath the tympanic membrane. It has the same spatial relationship to the line of attachment of the tympanum as in crocodiles, except that the tympanum was much larger in *Sphenosuchus* and occupied most of the quadrate height (figures 13*d* and 15*f*), so that the 'otic incisure' in this case corresponds to practically the entire posterior concavity of the bone. Hecht & Tarsitano (1983) figure five widely distributed foramina in the dorsal surface of the quadrate of *Protosuchus*. It seems fruitless to attempt to equate any one of these with the pit of *Sphenosuchus*; more probably the whole group broadly corresponds to this pit.

Continuing with the air spaces which are linked to the tympanic cavity, there can be little doubt that the cavity in the medial side of the articular (14) of *Sphenosuchus* compares directly with that typically found in living forms. However, the canal leading to it (siphonium) was not enclosed in the quadrate as it is in present-day forms. In *Sphenosuchus* the foramen aërum in the articular is a larger aperture than the inconspicuous hole of Recent crocodiles. There appears to be no representative in any extant form (or in any bird) of the foramen in *Sphenosuchus* leading forwards out of this cavity.

Modern crocodiles lack an antorbital fenestra or fossa (15) and a channel in the upper surface of the maxilla–jugal (16). These features will be considered later (see p. 85). They also lack a cavity in the ectopterygoid (17). In certain theropod dinosaurs, e.g. *Deinonychus* (Ostrom 1969), *Saurornitholestes* (Sues 1978) and tyrannosaurs (Russell 1970), a deep pocket of unknown function on the lower surface of the ectopterygoid has been described. The ectopterygoid of these forms differs greatly from that of *Sphenosuchus*, however, and the pocket is said to face 'medially and slightly forward', or 'ventrally', whereas the cavity enters anteroventrally in the case of *Sphenosuchus* and is more anteriorly placed on the bone. Thus it seems unlikely that there is any homology between the two cases. The cavity in *Sphenosuchus* does not seem to be suitably orientated for a part of the origin of the pterygoideus musculature and is more likely to have been pneumatic. The same considerations apply in the case of the cavity entering the pterygoid (18) which runs backwards into the bone. In living crocodiles the pterygoid may be pneumatized, but it gains its air from the narial passage. These cavities will be considered further below (p. 85).

In modern crocodiles there is a number of air-filled diverticula entering the bones which surround the naso-pharyngeal tube (Wegner 1958). None of these, in fact, seems to occur in *Sphenosuchus* which has only a short secondary palate. However, the large chamber in the anterior part of the palate (19) may possibly have been pneumatic, because it has a large medial aperture communicating with the narial passage. The cavity appears to be homologous with a much smaller one in some Recent crocodilian skulls which opens downwards at the lateral side of the palate by a foramen between premaxilla and maxilla, and medially to the naso-pharyngeal duct by a small foramen between the same bones. This cavity does not seem to be pneumatic in any living form and the medial foramen is for a nerve, according to Wegner (1958). The palatal entrance in crocodiles seems to be simply a larger member of the usual series of vascular foramina which occurs medially to the alveoli, and is matched in *Osteolaemus* by a large foramen in the same series behind the fifth maxillary tooth. The possible significance of the anterior palatal cavity in *Sphenosuchus* will be given further consideration in §5*d*(i).

To conclude this section, the following items on the above list of cavities in the *Sphenosuchus* skull are considered to have pneumatized equivalents in the modern crocodilian skull: numbers 5, 6, 7, 8, 9, 13 and 14.

(ii) *Comparison with birds*

There is a large literature dealing with the pneumatization of the bird skull, which it is beyond the scope of this paper to review. In spite of this, a more modern comprehensive description of the main cavities than those by Stresemann (1927–34) and Marinelli (1936) seems to be lacking. The three principal cavities (anterior, posterior and superior tympanic recesses) were first clearly named and described by Pycraft (1902), building on the work of Parker (1869) and Suschkin (1899). These cavities are also known as the 'antrum pneumaticum rostrale', 'caudale' and 'dorsale', respectively (Baumel *et al.* 1979).

Comparison of the pneumatic cavities in the skull of *Sphenosuchus* with those found in modern bird skulls is made difficult by the fact that many adult bird skulls are so highly pneumatized that it is possible to find a cavity or connection in almost any desired position if one looks hard enough. However, the three recesses cited above are the most constant in occurrence, being found in nearly all bird groups, and are present from an early stage, beginning in a simplified form as diverticula from the tympanic cavity and acquiring their complexity and interconnections later on. Determination of the basic character of these cavities in terms of which bones surround them is made difficult by the obliteration of most sutures in the adult skull, but is critical to any discussion of homologies. I have not attempted to study the formation of the pneumatic cavities in the bird skull in a systematic manner, but have assembled a number of juvenile skulls in the course of a study of the composition of the avian otic capsule, part of which has been published (Walker 1985). These juvenile skulls have been used in the comparison which follows.

It is particularly difficult to obtain such specimens at the right stage to display the definitive suture pattern in the braincase before it is obliterated by fusion. In earlier stages too much cartilage intervenes, and one needs a close succession of growth-stages over the short critical period (when the skull is about half adult size) to determine all details. Those specimens the young of which are the easiest to obtain (fowl, duck) are not necessarily the most primitive while, in those groups usually regarded as primitive, juveniles tend to be difficult to acquire. Coverage of groups therefore tends to be patchy and no significance should be attached to omission of particular groups. It should be added that the term 'juvenile' is used here in a general, rather than in the strict ornithological, sense.

The anterior tympanic recess (ATR) lies above and partly lateral to the bony tube which usually encloses the internal carotid (or cerebral carotid) artery, and reaches back as far as the facial foramen and anterior wall of the cochlear recess. Its medial wall is formed by the basisphenoid and prootic, its lateral wall by the 'alaparasphenoid' (Jollie 1957) or 'tympanaler Flügel' (Erdmann 1940). The latter varies in posterior and ventral extent. The paired recesses are confluent in front within the basisphenoid complex, extending into the rostrum and usually surrounding the carotid tubes as they converge and join to pass up into the pituitary cup. The tubes, however, may lie directly against the anterior surface of the basisphenoid, as in *Fulmarus glacialis*.

The ATR proper communicates broadly between the carotid tubes with a trabeculate air space lying below the basisphenoid and above the basitemporals (a term introduced by Parker (1861)) (= 'basi-parasphenoids' of Jollie (1957)) and extending back into the basioccipital. Whether this ventral space should be regarded as part of the ATR is uncertain.

There is an obvious resemblance between the anterior pneumatic spaces in the skull of *Sphenosuchus* and those of birds. The ATR is represented in *Sphenosuchus* by the rostral recess (1), the pre- and postcarotid recesses (2 and 4), and the prootic recess (7). The relationships of the postcarotid and prootic recesses to the palatine nerve and internal carotid artery were evidently as in birds. The palatine nerve ran down the prootic to join the internal carotid artery near the prootic–basisphenoid suture, which slants downwards and backwards. Like the bird, but unlike the crocodile, the palatine nerve appears to have accompanied the artery for a short distance at the base of the postcarotid recess, before diverging from it. In the crocodile, the nerve crosses the internal carotid canal nearly at right angles.

The rostral recess in *Sphenosuchus* was at least partly divided by a horizontal septum, such as occurs in some birds, e.g. *Fulmarus*, *Gavia* and *Larus*. The cartilaginous interorbital septum ended posteriorly in contact with the air space above this septum, conditions in *Sphenosuchus* being identical to those in young birds with well-pneumatized skulls. The carotid pillar with the internal carotids converging and running up its sides, and the pituitary cup, both surrounded by air spaces (figures 21 and 23), closely resemble the situation in birds. The anterior base of the carotid pillar in *Sphenosuchus* has a central mid-line swelling between paired depressions. In birds there is often a prominent bony trabecula or group of trabeculae supporting the pituitary cup in the mid-line, between the converging carotid tubes, seeming like a hyper-development of the situation in *Sphenosuchus*. In birds also the abducens nerves frequently run in bony tubes at the top of the ATR behind the pituitary cup. In *Sphenosuchus* similar tube-like ridges arch across the roof of the postcarotid recess, carrying the VIth nerves.

The two precochlear cavities (10) of *Sphenosuchus* recall the penetration of pneumatization in this region in young bird skulls, until the bony cochlear recess is largely supported by trabeculae alone in the adult skull. In some birds, gulls providing a good example, there is a tendency for a strong pillar or group of trabeculae to persist halfway down the anterior wall of the cochlear recess, dividing the pneumatization into two regions.

In birds the lateral wall of the ATR is largely made up by the alaparasphenoid, which in ontogeny grows backwards from the basisphenoid along the side of the prootic, below the trigeminal foramen. In *Sphenosuchus* the lateral wall of the homologue of the ATR is largely formed by the pterygoid and the quadrate. However, the overhanging prootic–basisphenoid flange makes a partial lateral wall, and there seems to have been a small expansion of this flange on the basisphenoid which may perhaps be regarded as an incipient alaparasphenoid.

Theoretically, the pattern of connections between the ATR and its ventral extension in birds can be derived from that seen in *Sphenosuchus* by imagining that the channels for the internal carotid arteries in the latter, which lie at the base of the postcarotid recess (figures 28 and 49), have been spread apart, so that this recess and the sub-basisphenoid recess have become confluent between them. In birds the basicranium has become flattened and the carotids converge at a wider angle than they do in *Sphenosuchus*. At the same time it must be postulated that the large basipterygoid processes of a *Sphenosuchus*-like form have extended back still further (as it seems that they have done in crocodilian evolution), joined, and become greatly flattened, overlapping on to the basioccipital and forming the basitemporals. The pneumatic cavities within the basipterygoid processes (3) would have become merged within the general trabeculate space below the basisphenoid. The walls of these processes in *Sphenosuchus* are already pierced by several pneumatic foramina. On this view, the sub-basisphenoid recess of *Sphenosuchus* would be the partial homologue of the ventral extension of the ATR of birds.

The basioccipital recesses (5) of *Sphenosuchus* may be the homologue of the pneumatic space extending back into the basioccipital of birds, but the fact that pneumatization seems to affect this bone at a relatively late stage in development tends to throw doubt on this assumption.

The facial (8) and mastoid (9) antra have no clear-cut homologues in the bird skull, but in many birds there is a group of air cells in the comparable position, above the facial foramen and in front of the prootic articulation for the quadrate. These cavities also tend to link up with the upper tympanic recess (STR) beneath the anterior entrance to the latter. In some cases, e.g. *Fulmarus glacialis*, it is as if the original floor to this entrance has disappeared, so that a passage (probably that called the 'suprahyomandibular tunnel' by Saiff (1974)) leads directly from ATR to STR. How such a connection could arise is shown by the proximity of the mastoid antrum of *Sphenosuchus* to the floor of the anterior temporal foramen (figure 21*c*).

However, the derivation of the ATR and its associated cavities from a pattern similar to that of *Sphenosuchus* would depend upon a view of homologies which is not widely accepted, because the basitemporals and alaparasphenoids of the bird skull are commonly regarded as being dermal bones and not outgrowths of the basisphenoid. Jollie (1957) has said that 'the ossifications in the basis cranii present one of the most difficult problems of the bird skull', and describes the chicken basisphenoid complex as arising from nine centres, seven of which are of dermal origin, the actual paired basisphenoid ossifications being quite small. Kesteven, on the other hand, (1942), considered the entire complex to be of basisphenoid origin, the elements considered dermal by other authors being derived from the inner layer of the perichondrium by a process he termed 'extraperichondrial ossification'. They would thus appear to be membrane bones in the sense of Patterson (1977). Kesteven's views have not found general acceptance, however. Some support for the phylogenetic derivation of the bird basitemporals from the basisphenoid comes from the situation in crocodiles. Very similar flattened elements in this group were also termed basitemporals by Parker (1883) and were long regarded as dermal bones, until Müller (1967) showed that they are the ossified infrapolar processes and are thus outgrowths from the basisphenoid. The avian embryo also possesses infrapolar processes (Sonies 1907) which are very similar to those of crocodiles, so that it does not seem impossible that the bird basitemporals have ultimately been derived from these structures. The complexity of the process of ossification of the bird 'basisphenoid' may perhaps be viewed as a 'solution' to the problem of creating a bony framework around a complicated and enlarging series of air spaces, which has led to a proliferation of centres of ossification.

In *Sphenosuchus* there is little doubt that the palatine nerve and artery curved medially round the posterior supporting 'strut' of the basipterygoid process, whereas on the bird comparison the expected position for these structures would have been for them to have passed down behind the basipterygoid facet. De Beer (1926) pointed out that the palatine nerve in the bird runs lateral to the infrapolar process, whereas it passes medial to it in the crocodile. De Beer & Barrington (1934) explain the difference by assuming that, in the crocodile, the palatine nerve has slipped medially over the free end of the infrapolar process. *Sphenosuchus*, therefore, would have been crocodilian in this character.

The superior or upper tympanic recess (STR) lies mainly above or dorsolateral to the otic capsule; it is essentially floored by prootic and roofed by squamosal. It may extend medially so that the epiotic enters the floor and the parietal forms part of the roof. The paired recesses are frequently in communication via the parietal or supraoccipital or both. The STR lies above, or lateral to, the stapedial artery.

The temporal canal (11) of *Sphenosuchus* is directly comparable to the bird STR. Its floor is composed largely of prootic, with the opisthotic entering only at the rear, and the squamosal forms the greater part of the roof. The epiotic enters the medial wall. Its large size compared with that of modern crocodilians suggests that it was pneumatized.

In *Sphenosuchus* the temporal canal has two relatively large entrances, one anterior to the quadrate head (the anterior temporal foramen), the other (the postquadrate foramen) posterior to it. The first of these corresponds to the anterior entrance to the STR in birds ('foramen pneumaticum dorsale') and, as in birds, is situated entirely between squamosal and prootic, adjacent to the articular area for the quadrate head. In birds this entrance may be (*a*) large and usually at least partly pneumatic (e.g. many procellariiforms and pelecaniforms), in which case a posterior entrance is usually lacking, or (*b*) reduced to a vascular channel (e.g. many galliforms, anseriforms, *Ardea*, *Falco*, *Strix*, *Columba*, Alcidae, many passerines).

The postquadrate foramen in *Sphenosuchus* corresponds to the avian posterior entrance, as seen most clearly in the juvenile fowl and duck. It lies mainly between the squamosal and prootic, but in the bird what is probably ossification of the metotic cartilage (Stresemann 1927–34) comes close to it at the posterior end, so that behind it the squamosal rests on both prootic and metotic. In *Sphenosuchus* the appearance is similar, but it is more primitive in that the paroccipital process was almost certainly made up of opisthotic, and it is doubtful whether the squamosal actually contacted the prootic at the rear end of the postquadrate foramen in the undistorted skull. However, the squamosal has undoubtedly moved forwards as a whole in the bird skull so that it is not difficult to see how such a contact could have been established. It seems also that, in the bird, the opisthotic contribution to the paroccipital process has been reduced (Jollie 1957), with the increase in importance of the metotic cartilage, which ossifies as part of the adult exoccipital (Stresemann 1927–34).

Modern birds tend to fall into two groups, one in which there is a well-developed anterior entrance to the STR (i.e. in front of the quadrate socket or sockets) but no posterior entrance (i.e. behind the quadrate socket or sockets), and the other in which the posterior entrance is well developed but the anterior entrance is reduced to a vascular channel for the ramus occipitalis of the stapedial artery. In *Sphenosuchus* both entrances are large.

In birds the squamosal and prootic articular areas for the quadrate are frequently separate, and the anterior and posterior entrances are often confluent in the dried skull. These two conditions do not necessarily occur together. Both are presumably derived states within birds. Both could readily be obtained from that in *Sphenosuchus*, because the temporal canal is very close to the quadrate head, and it only requires a separation into two articular areas to give the essentials of the bird condition (figure 48). However, it must be allowed that there is an important difference, in that in birds the prootic articular area lies posteromedially to that on the squamosal, whereas in *Sphenosuchus* it is anteromedial. Theoretically, one disposition might have been derived from the other by improvements in the kinetic mechanism. If one assumes that in the primitive state the quadrate swung purely in a parasagittal plane, a change to the typical avian condition, in which the quadrate swings in an anteromedial–posterolateral plane, combined with forward migration of the squamosal, could conceivably have led to a reorientation of the positions of the articular facets on the skull.

It may be noted in passing that, if one attempts to seek homologies between the parts of the upper end of the quadrate in *Sphenosuchus* and birds, the above gives a much simpler and more plausible comparison than the one previously put forward by me (Walker 1974). I no longer consider that the anterodorsal process of the *Sphenosuchus* quadrate is the homologue of the bird squamosal head. There are several reasons for this, which it would be inappropriate to explain at this point, but the most important is that such a comparison poses difficult problems with regard to the location of the pneumatic cavities and entrances adjacent to the top of the quadrate. It is much simpler and more in

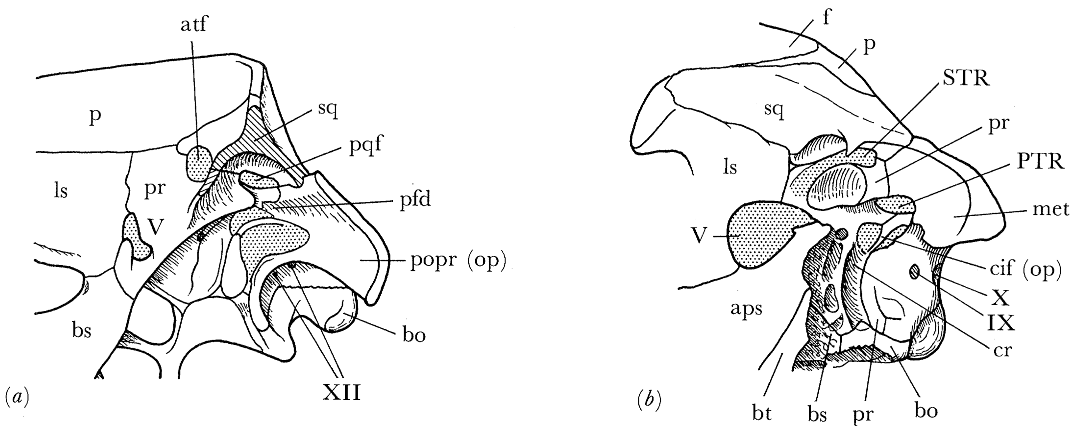


Figure 48. Articulations for the head of the quadrate and adjacent structures in (*a*) *Sphenosuchus*, magn. × 1; (*b*) mallard, *Anas platyrhynchos*, magn. × 2.8. Fenestra ovalis and fenestra pseudorotunda are stippled. The cochlear recess has been opened up in the mallard.

accordance with other morphological features to suppose that a continuous prootic-squamosal quadrate articular surface of *Sphenosuchus*-type has divided into two separate areas in many birds. Another point to be borne in mind is the probability that the anterodorsal process of the *Sphenosuchus* quadrate has arisen by the dorsal migration of a rounded anterolateral process of a type similar to that seen halfway up the quadrate in the thecodontian *Stagonolepis* (Walker 1961). Quadrate/quadratojugal/squamosal relations at and above the anterolateral process in *Stagonolepis* bear a detailed similarity to those at the anterodorsal process in *Sphenosuchus*, save that in the latter the descending process of the squamosal has disappeared and the anterodorsal process is much closer to the quadrate head. (This is not to suggest a direct derivation of one from the other, although stagonolepidids and sphenosuchids may be sister-groups). If this is a valid comparison, then it follows that the crocodylomorph anterodorsal process is not part of the original head of the quadrate, and thus cannot be the equivalent of the bird squamosal head. On the other hand, the latter has every appearance of being the homologue of the normal reptilian quadrate head, while the bird prootic contact of the quadrate, like that of the crocodylomorph, appears to be a derived feature.

The posterior tympanic recess (PTR) is a cavity in the paroccipital process, leading back from the region of the fenestra ovalis and fenestra pseudorotunda. It lies ventrolateral to the external semicircular canal and its entrance is medial to, or below, the stapedial artery and hyomandibular nerve. Its lateral wall is formed by the 'occipital wing' or ossified metotic cartilage; the medial wall is a depression in the otic capsule. In juvenile birds the prootic–opisthotic suture runs up and back from the upper margin of the fenestra ovalis across the medial wall, more or less bisecting it (Walker 1985, figs 2 and 3). The entrance to this recess (foramen pneumaticum caudale) was erroneously labelled 'pqc' in an earlier figure (Walker 1972, fig. 1c). It is emphasized that the prootic forms a substantial part of the upper and medial border of this entrance, and of the recess itself, in the bird. It is doubtful whether a true PTR is present in theropod dinosaurs.

In *Sphenosuchus* a slight but definite concavity behind the fenestra ovalis is considered to represent an incipient PTR. This concavity, or postfenestral depression (12) (figure 20), crosses the prootic–opisthotic suture as the latter runs up and back from the fenestra ovalis. The position of the groove for the hyomandibular branch of the facial nerve in *Sphenosuchus* indicates that this nerve, and the stapedial artery, ran round at some distance lateral to this concavity. In *Dibothrosuchus*, a close relative of *Sphenosuchus* (Wu 1986), there is a much more definite pneumatic sinus in the same position.

As already noted, there is no representative of the PTR in the modern crocodilian skull. The cavity labelled 'ventral sinus' by Whetstone & Martin (1979, fig. 3) is a true PTR in *Hesperornis*, but in their unnamed 'crocodylid' it is too low down to be such, and this cavity is in fact a pneumatization of the subcapsular portion of the exoccipital, being an extension from the rhomboidal sinus.

In birds there is commonly a connection or connections between the STR and the PTR within and behind the curve of the external semicircular canal. This connection misled me (Walker 1972, fig. 1) into comparing the postquadrate foramen (or canal, as it was then called) of *Sphenosuchus* with the entrance to the bird PTR, whereas the postquadrate foramen actually enters the homologue of the avian STR.

In birds there generally seems to be no equivalent of the pit in the posterior surface of the quadrate of *Sphenosuchus* (13). A pneumatic pore in about this position does occur, however, in some birds, e.g. *Struthio*, *Ardea*, and the gulls, where it is somewhat more medially placed. Because the tympanum is, on the whole, more medially placed in birds than it was in *Sphenosuchus*, and in each case the pit is just medial to the tympanum, the pit in these birds may, with some doubt, be regarded as homologous.

The cavity in the medial side of the articular (14) is obviously the homologue of the cavity in this position in the bird articular. The morphology of the articular in *Sphenosuchus* as a whole is, in fact, strikingly bird-like, in the form of the short, hoof-like retroarticular process and the occurrence of a prominent internal ascending process (figure 34). This type of structure is present in many birds, e.g. Laridae and Procellariiformes, to name but two groups. The foramen aërum in *Sphenosuchus* is also large, and the siphonium did not pass through the quadrate. However, I have not been able to discover in any bird a homologue for the foramen leading forwards out of the cavity in the articular. This foramen (figure 34) is too large to have transmitted only the chorda tympani nerve, and it probably supplied an air sac running along the lower jaw such as has been described by Bignon (1889) in the case of some birds, where, however, it is supplied from the orbital (subocular) air sac, or the cervico-cephalic sac.

The function of the antorbital fenestra and its surroundings fossa in archosaurs has been the subject of much debate (reviewed by Ewer (1965) and Osmolska (1985)), although without definite conclusion. Because a homologous opening is present in many bird skulls, where it is frequently the site of a pneumatic sac, a pneumatic explanation of its function in some archosaurs is at least a possibility, although this may not have been its initial function. Such a sac, or an orbital air sac, might also have sent diverticula in *Sphenosuchus* into the dorsal channel in the maxilla-jugal (16), the cavity entering the ectopterygoid (17), and that entering the pterygoid (18). In birds pneumatic diverticula from the orbital sac or the cervico-cephalic sac frequently ramify among the jaw muscles and lie against the bones of the skull in a variety of positions (Bignon 1889). The high degree of pneumatization of the braincase in *Sphenosuchus* suggests the possibility that analogous or homologous sacs may have been present in this animal. However, none of the three cavities mentioned above seems to have an avian homologue, because the maxilla–jugal channel is lacking in birds, the ectopterygoid has been lost, and the pneumatic pore in the pterygoid is usually near the rear end of the bone, which is also of very different shape from that of *Sphenosuchus*.

In the crocodile the bony median and lateral eustachian canals are prolonged ventrally as membranous tubes which join to emerge at a common opening immediately behind the choanae (Owen 1850; Colbert 1946). In birds, on the other hand, there is no comparable median eustachian foramen and the lateral or true eustachian tubes run forwards from the middle ear along the sides of the basitemporal plate to a common anterior opening in the roof of the pharynx. The joining together of the lateral eustachian tubes in the mid-line is a striking point of agreement between birds and crocodiles.

It is not as straightforward as in the case of the crocodilian comparison to list those pneumatic cavities in *Sphenosuchus* which have homologues in the bird skull. However, it may be said that these comprise numbers 1, 2, 4, 7–12 and 14 of the list on p. 75, omitting doubtful examples. It is possible that other cavities (3, 5 and 6) could be regarded as merged in a trabeculate air space within the basicranium of birds, depending upon one's view of bone homologies.

(*d*) *Vessels of the head*

It may be stated at the outset that the vascular system of the crocodilian head has been much modified from the primitive pattern (Hochstetter 1906). *Sphenosuchus*, being partly advanced morphologically along the route towards the modern crocodilian skull, might be expected to have developed some of these vascular modifications to a limited degree. The following section attempts to assess to what extent such changes had occurred.

(i) *Arteries*

The *internal carotid artery* in crocodiles and birds describes a similar sinuous course along the side of the braincase, ascending in a curve in the region behind the cochlear recess, reaching its highest point just outside the lagenar region of the cochlea, descending forwards at the side of the basisphenoid and then curving up again to enter the pituitary fossa. There is good evidence that it pursued a similar course in *Sphenosuchus*. It is convenient to begin with the anterior end, since this is least equivocal. There can be no doubt that the internal carotid entered the pituitary fossa by running up the side of the carotid pillar. The next posterior 'fix' for its position is the 'shoulder' at the lower end of the basisphenoid plate (figures 22 and 23). This shallow notch is considered to indicate the position of the internal carotid, and it is reasonably certain that, in between, the arteries curved down into the paired channels at the posterior base of the postcarotid recess. Appearances on the right side certainly suggest this, the left being more distorted.

More posteriorly, the small accessory flange and groove on the exoccipital (figures 22 and 24) is believed to indicate the position of the stapedial artery, where this curved backwards just above its origin from the internal carotid. The strong ridge of the exoccipital on which this flange is based is believed to indicate a certain development of a subcapsular process ossification in *Sphenosuchus*, like that of living crocodiles but not so extensive. It is convenient to term this strong exoccipital ridge in crocodylomorphs the *subcapsular buttress*. The situation in living forms is complicated by the fact that the initial part of the stapedial (or temporo-orbital) artery has been very largely replaced by a secondary vessel passing forwards through the cranio-quadrate passage. However, the original vessel still persists as a slender artery (Hochstetter 1906) which departs from the internal carotid just behind the point where the latter passes close to the lower end of the cochlear recess. This artery climbs up the thin lateral wall of the recessus scalae tympani, immediately behind its free anterior edge (i.e. the anterior edge of the pneumatized subcapsular buttress), to join the secondary stapedial artery at the anterior end of the cranio-quadrate passage.

The small accessory flange in *Sphenosuchus* is considered to represent the much more extensive anterior edge of the exoccipital (subcapsular buttress) in living crocodiles, which lies within the tympanic cavity. There is an even closer resemblance in the case of birds, where there is usually a lateral flange of bone directly

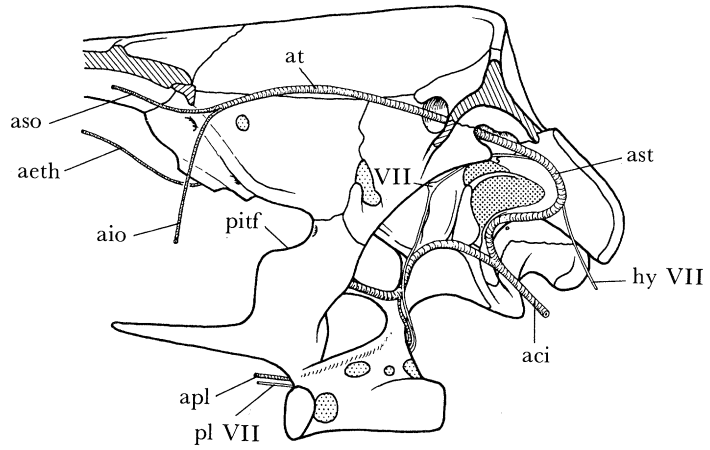


Figure 49. *Sphenosuchus acutus* Htn. Braincase with main arteries and branches of the facial nerve restored, magn. × 1.

above the origin of the stapedial (or external ophthalmic) artery. The latter is given off in the bird at the same position as in the crocodile, after which it curves round the back of the tympanic cavity. In the fulmar, *Fulmarus glacialis*, the bony scaffolding which encloses these arteries to a greater or lesser extent in the otic region of most birds is reduced to a small lateral flange, grooved for the stapedial artery. This is very like that of *Sphenosuchus*, but it is more laterally placed, because it arises from the metotic buttress, representative of the embryonic metotic cartilage which ossifies as part of the adult exoccipital. The avian metotic cartilage is very similar to the subcapsular process of crocodiles, and the two may be homologous; it encloses the IXth and Xth nerves, as does the subcapsular buttress in the crocodile.

These comparisons are considered to establish that the position of branching of the internal carotid artery in *Sphenosuchus* was closely similar to that of living birds and crocodiles. From this point to the 'shoulder' of the basisphenoid plate the artery would have curved in a gentle upward arch, passing first close to the cleft between pro- and opisthotic at the base of the cochlear recess, and then close to the lower edge of the prootic. The constraints mentioned above leave little room for doubt concerning the course of the internal carotid artery.

The *stapedial artery* in *Sphenosuchus* would have passed laterally to the IXth and Xth nerves, as it does in crocodiles and birds. It may have described a tighter curve round the tympanic cavity than as shown in the restoration (figure 49). The glossopharyngeal nerve foramen in birds usually lies directly medial to the origin of the stapedial artery, so that it is a little more anteroventral than seems to have been the case in *Sphenosuchus*. However, this does not apply to all birds; in *Alca* and *Uria*, for example, IX runs somewhat more posteriorly across the floor of the recessus scalae tympani. Because of the wide open cranio-quadrate passage in *Sphenosuchus*, there is no reason to think that any by-passing of the initial portion of the stapedial artery had commenced.

As already stated, the anterior temporal foramen, temporal canal and postquadrate foramen of *Sphenosuchus* have clear homologues in the modern crocodilian skull, although they are relatively smaller in living forms and there are certain differences. Because of this resemblance, and the different build of this region in thecodontians, there can be little doubt that the stapedial artery in *Sphenosuchus* followed a similar course to that of the crocodile (Rathke 1866; Hochstetter 1906) which, after the junction described above, passes through the postquadrate foramen, runs forwards in the temporal canal, emerges at the anterior temporal foramen, and then crosses the supratemporal fossa. This part of its course in the crocodile is unusual in that the artery appears to pass forwards *above* part of the quadrate head, whereas in other reptiles and in birds it normally passes forwards *below* that structure. However, the artery actually passes over the prootic contact of the quadrate, medial to the original, i.e. squamosal, head. In the modern crocodile the squamosal head is only that portion of the proximal end which hooks back above the otic incisure, a small proportion of the apparent 'head'. This prootic contact in the modern crocodile is on the same level as the true head or original squamosal contact, but in the more primitive *Sphenosuchus* the prootic contact is at a lower level and is much smaller than the original squamosal head which is clearly recognizable as such (figure 16). Nevertheless, the position of the stapedial artery in the modern crocodile requires an explanation, but this must be deferred until later (see §5*d*(iv)).

In the Recent crocodile, the proximal part of the *mandibular artery* has disappeared even in the embryo, and neither Hochstetter (1906) nor Shindo (1914) was able to find any trace of it. The distal part of the artery is supplied from the A. maxillaris interna. Thus in the crocodile the stapedial artery passes directly into the temporal artery, in the nomenclature of O'Donoghue (1920). Because the origin of the mandibular artery in reptiles is usually in the region where, in the crocodile, the stapedial (or temporo-orbital) artery passes through the postquadrate foramen and temporal canal, it seems likely that the disappearance of the root of the mandibular branch is connected with the enclosure of this artery by the forward movement of the quadrate head. Hence it is assumed that the proximal part of the mandibular artery had already been lost, at least in the adult, in *Sphenosuchus*; it would presumably have been present in the embryo.

In reptiles the stapedial (or temporal) artery usually divides at the upper posterior corner of the orbit into *supraorbital* and *infraorbital* branches, and there is no reason to think that *Sphenosuchus* was unusual in this respect, because it is a relatively primitive form.

The normal *palatine artery* of reptiles has been lost in the crocodile (Shindo 1914), presumably because of fusion of quadrate and pterygoid to the braincase. As such fusion had not taken place in *Sphenosuchus* it is assumed that a normal palatine artery accompanying the palatine branch of the facial nerve was given off from the internal carotid at the base of the postcarotid recess. The groove curving round the back of the basipterygoid process may indicate the artery rather than the nerve, in fact.

As discussed in §5*a*, there may also have been a *sphenomaxillary artery* in *Sphenosuchus* running along the groove below the upper margin of the basipterygoid process and passing over the facet. In birds this artery frequently leaves the internal carotid by a separate bony tube a short distance after the carotid has turned upwards towards the pituitary fossa, whereas the palatine artery is given off at the lowest point of the S-bend.

The small foramen running upwards and forwards through the left laterosphenoid 'bridge' (figure 27*e*) is believed to have been for one of the paired *ethmoidal arteries*. In reptiles this name, correctly applied, refers to a small artery which arises from the ventral side of the brain as a branch from the anterior ramus of the intracranial internal carotid and eventually enters the nasal cavity (Rathke 1857; Dendy 1909; Albrecht 1967), although it may disappear in the adult. In the crocodile the ethmoidal artery is peculiar (Hochstetter 1906) in that, in the adult, it arises from a dorsal branch of the intracranial internal carotid and runs forwards at first dorsally, but then dives down between the olfactory tracts to the ventral side. In the embryo, however, the ethmoidal artery has a ventral as well as a dorsal origin. Thus the crocodile skull shows no foramen through the laterosphenoid for the ethmoidal artery. However, there is a foramen for this artery just above the optic nerve foramen in the bird skull, although it is sometimes mistakenly identified as for the internal ophthalmic artery (e.g. Gadow 1891). The paired ethmoidal arteries in the bird pass through or notch the laterosphenoids on either side of the interorbital septum (Wingstrand 1951; Baumel 1975*a*) in very much the same position as the small foramen in *Sphenosuchus*. This foramen is unlikely to be for an 'ophthalmic' artery (*sensu* Hochstetter (1906) and Romer (1956)), as the latter leaves the braincase along with the optic nerve.

It is unlikely, in fact, that *Sphenosuchus* had an 'ophthalmic' artery in the above sense, since this is found in adult *Sphenodon*, lizards and snakes. Instead, an 'orbital' artery (*sensu* Hochstetter (1906) and Romer (1956)) would more likely have been present. This artery is found only in the embryos of *Sphenodon* (Säve-Söderbergh 1947) and lizards (Hochstetter 1906), but survives into the adult in crocodiles, turtles and birds, where it is usually (and confusingly) termed the 'ophthalmic' or 'internal ophthalmic' artery by embryologists (e.g. Bellairs & Kamal 1981). It has a more posterior origin and is the first branch to be given off from the internal carotid after the intercarotid anastomosis in the pituitary fossa; in *Sphenosuchus* it would have emerged below nerve III, on the crocodilian analogy. The small size of the ethmoidal foramen in *Sphenosuchus* may suggest that regression of the blood supply from the ventral side of the brain was already taking place.

Reference has been made (p. 48 and figure 30*c*) to converging grooves on the upper surface of the basisphenoid plate, which probably represent branches of the *basilar artery*. It is interesting that these tend to form chevrons, as is usually the case in the branches of the basilar artery in birds (e.g. Baumel, 1975*a*, figs 67–69) and are not directed away at right angles, as in crocodiles (Hochstetter 1906, taf. 5, fig. 34).

The groove which runs along the medial side of the maxilla, above the secondary palate (figure 4*d*,*f*) appears to have carried some structure or structures to the large chamber in the anterior part of the palate, because it terminates just behind the broad notch by which this chamber communicates with the nasal cavity. Presumably these structures were an artery and vein which may have supplied a poison gland lodged within the chamber, as the tips of the enlarged anterior dentary teeth must have entered these cavities when the jaws closed. It is unlikely that the cavities had anything to do with Jacobson's organ, as they are too far in front of the choanae and too far removed from the vomers for this to be probable. In lizards in which this organ is well developed, the palatal entrance is the anterior part of the choana, separated from the remainder by an expansion of the vomer.

(ii) *Veins*

The fine grooves on the undersurfaces of the frontals in front of the depressions which mark the position of the olfactory bulbs probably indicate the former presence of veins. Hochstetter (1906) figures in *Crocodylus niloticus* a pair of veins curving over the olfactory bulbs, from which are given off a number of parallel veins running forwards.

The upper foramen in front of the laterosphenoid buttress (figure 6*e*), above that identified as for the trochlear nerve, is in a similar position to a foramen found in several dinosaur skulls. Janensch (1936*a*) considered this to be the equivalent of the fenestra epioptica of living reptiles and suggested that the anterior cerebral vein passed through it in the embryo, as it does in the embryos of living forms. This may have been the case in *Sphenosuchus*.

The trigeminal foramen in *Sphenosuchus* is constricted in the middle; the lower portion is believed to have transmitted the trigeminal nerve itself. The Gasserian ganglion probably occupied the outer part of this portion (Fischer 1852; Hopson 1979), while the middle cerebral vein probably exited through the upper portion. The evidence for this is as follows: (*a*) the middle cerebral vein leaves the cranial cavity above the trigeminal nerve foramen in *Sphenodon* (O'Donoghue 1920; Säve-Söderbergh 1947) and passes down behind the nerve to join the lateral head vein; (*b*) the braincase of *Euparkeria*, a primitive early Triassic archosaur, is closely similar to that of *Sphenodon* (Cruickshank 1971, and personal observations); (*c*) In the iguanid lizard *Ctenosaura*, a pointed supratrigeminal process from the prootic 'divides the trigeminal notch into a dorsal part for the middle cerebral vein and a ventral part for the trigeminal nerve' (Oelrich 1956, p. 16). This is like the situation in *Sphenosuchus*, in which a bulge of the prootic at the posterior side tends to divide the trigeminal foramen into two parts. In *Ctenosaura* the supratrigeminal process is joined by a ligament to a cartilaginous process from the pila antotica. The crocodilian laterosphenoid is, of course, an ossification in the pila antotica, so that a similar cartilaginous process or ligament may have spanned the trigeminal foramen in *Sphenosuchus*; (*d*) in the thecodontian *Stagonolepis* a horizontal bar made up of prootic and laterosphenoid divides the trigeminal foramen into two parts (Walker 1972, fig. 1a). Previously (Walker 1961) the upper foramen was tentatively identified as for V_2 and V_3, the lower as for V_1, but because of the situation in *Ctenosaura*, it seems more likely that the upper foramen was for the middle cerebral vein and that the trigeminal nerve was confined to the lower foramen; (*e*) in the earlier embryos of living crocodiles a middle cerebral vein is present, but it has disappeared by a late embryonic stage (Hochstetter 1906). However, this loss is connected with the disappearance in late stages of the lateral head vein, into which the middle cerebral vein normally opens, and this in turn is no doubt due to the fusion of quadrate and pterygoid to the braincase, blocking the route of the lateral head vein. There is no reason to think that the lateral head vein had been lost in *Sphenosuchus*, however, in which these bones are still free; (*f*) some birds have a vein which leaves the skull through the foramen for V_2 and V_3, or from the upper portion of this foramen which becomes cut off at maturity from the lower part by a bony bar. Such a vein is described by Neugebauer (1845, p. 557) in *Meleagris gallopavo*, and Pycraft (1899*a*, *b*) in the Procellariidae, Gaviiformes and Sphenisciformes. Pycraft calls this vein the 'vena cephalica posterior'. It may be the homologue of the reptilian middle cerebral vein, for although van Gelderen (1924–25; 1933) states that the avian primary 'stem-vein' (mainly a lateral head vein) is replaced in ontogeny by a secondary 'stem-vein', there is some doubt as to whether this is true of all bird groups, and in any case the vessel exiting above nerves V_2 and V_3 may still be a primary vein, as van Gelderen (1924–25) investigated only *Gallus*, *Anas* and *Vanellus*.

As noted on p. 74 the transverse sinus is probably indicated in *Sphenosuchus* by a broad shallow depression curving down the interior of the prootic to the trigeminal foramen (figure 46*a*). In *Sphenodon* (Dendy 1909) this sinus discharges from the cranial cavity by means of the middle cerebral vein.

In the descriptive section (p. 18) it was noted that a small foramen enters the medial wall of the temporal canal between parietal and epiotic. Another small foramen enters on the occiput between the same bones. This latter foramen is also present in some dinosaurs, e.g. *Allosaurus* (Madsen 1976, fig. 13) and *Tyrannosaurus* (Osborn 1912, fig. 4), and probably in *Euparkeria* (Cruickshank 1971, fig. 1, labelled as part of post-temporal fenestra). These two canals in *Sphenosuchus* probably join internally and emerge on the inner cranial wall, also between parietal and epiotic (figure 30*a*). The groove running forwards internally from this latter foramen seems to enter the depression taken to indicate the transverse venous sinus (p. 4). There is a resemblance here to *Sphenodon* (O'Donoghue 1920), in which the vena capitis dorsalis passes through the post-temporal fenestra and enters the skull by a small foramen in a comparable position to that in the temporal canal of *Sphenosuchus*. It then enters the transverse sinus. Bruner (1907) describes a similar course for the vena capitis dorsalis in *Lacerta agilis*. The foramen by which it enters can be seen in lizard skulls between parietal, prootic and supraoccipital. Bruner states that the dorsal head vein joins the 'middle cerebral vein' (i.e. the transverse sinus) within the cranium. From these comparisons it is concluded that the foramen in the medial wall of the temporal canal of *Sphenosuchus* transmitted the *vena capitis dorsalis*, which drained the occipital region via the post-temporal fenestra.

Corroboratory evidence from present-day crocodiles is difficult to obtain. Romer (1956) says that the post-temporal fenestrae are 'traversed by blood vessels' but does not give details. Hochstetter (1906) did not describe any vessels entering the post-temporal fenestra, although van Beneden (1882, p. 527) mentions a vein coming into it from the occiput and joining the temporo-orbital vein within the temporal canal. Examination of crocodilian skulls reveals a foramen passing forwards between 'supraoccipital' (probably epiotic) and parietal, at the anterior end of the floor of the temporal canal. This foramen runs in along the contact between 'supraoccipital' and parietal and emerges internally at the junction of these bones with the prootic and laterosphenoid (in *Osteolaemus*). It thus appears to correspond to the foramen in the medial wall of the temporal canal in *Sphenosuchus*, and its inner opening seems to correspond to the projection on the endocranial cast of *Caiman* labelled 'vc' by Hopson (1979 fig. 1: 'branch of longitudinal sinus'). In *Caiman* (Hopson 1979, fig. 2C) this represents a vein which enters the 'recessus lateralis' of Hochstetter (1906). The latter appears to be the homologue of the transverse sinus of Dendy (1909), because it runs down from the longitudinal venous sinus to just above the trigeminal foramen, and overlies the junction of the optic lobe with the cerebellum. Hochstetter denied that the 'recessus lateralis' of the crocodile is a transverse sinus; however, both he and Shiino (1914) use the term 'transverse sinus' in the mammalian sense, for a more posterior vessel which discharges through the vagus foramen. There is little doubt that the 'recessus lateralis' is a transverse sinus in the sense of Dendy (1909), who in fact (p. 423) states that the crocodile has a transverse sinus. It thus seems probable that the vena capitis dorsalis is recognizable in the crocodile, although it was not described by Hochstetter

(1906). Whether there is a more medial tributary vein from the occiput, as appears to have been the case in *Sphenosuchus*, is practically impossible to decide from an examination of skulls alone.

It seems probable also that the foramen between epiotic and parietal on the occiput in *Sphenosuchus*, adjacent to the supraoccipital, is the homologue of the foramen for the external occipital vein of birds, commonly occurring just lateral or dorsolateral to the foramen magnum. In juvenile birds the epiotics, which are relatively larger than in *Sphenosuchus*, are attached only at their bases to the supraoccipital, and the veins run dorsally into the intervening slits which extend up to the parietals (e.g. Pycraft 1898, pl. LXI, fig. 4). There is, in fact, a close resemblance between the inverted shield-shaped supraoccipital of *Sphenosuchus*, with its attached epiotics and its vein-foramina, to the arrangement and proportions of these bones in many birds, before obliteration of sutures takes place. The veins (or sinuses) in birds arch forwards on the inner walls of the cranium, running in grooves or tunnels just above the anterior vertical semicircular canals (which form prominent ridges), curving down anteriorly on the prootics and often running into the upper ends of the foramina for nerves V_2 and V_3. In the higher part of its course the vein (or sinus) lies along the suture between parietal above and epiotic and prootic below. The intracranial part of the vessel is termed the petrosal sinus, divided into rostral and caudal portions (Kaku 1959; Baumel 1975*a*). The caudal petrosal sinus appears to correspond broadly to the concealed portion of the vein from the foramen on the occiput of *Sphenosuchus*, the rostral petrosal sinus to the exposed intracranial portion. The rostral petrosal sinus would also appear to correspond to the intracranial vena cerebralis media or transverse sinus of reptiles. However, there seems to be no foramen medially in the upper tympanic recess of birds corresponding to that for the vena capitis dorsalis of reptiles.

There is nothing other than very slight hints in the interior of adult skulls of modern crocodiles of the reniform cavity posterodorsal to the otic pyramid of *Sphenosuchus*, from which a groove runs down into the upper end of the metotic foramen (figures 28*b* and 30*a*, *b*, *d*). A juvenile skull of *Caiman* sp. in my possession shows two separate depressions with small foramina in them on the epiotic and opisthotic, respectively, which might correspond to the upper and lower ends of the cavity in *Sphenosuchus*, but there is no gutter into the metotic foramen. This gutter was originally wider in the undistorted fossil skull. There appears to be nothing in the literature relative to this point. It seems unlikely that the cavity housed a gland or a ganglion, and a vascular function, presumably venous, seems the most probable explanation for it. In reptiles the posterior cerebral vein discharges via the metotic foramen or the foramen magnum, or both exits may be used (Romer 1956). In living crocodiles (Hochstetter 1906; van Gelderen 1924–25) the posterior cerebral vein runs out through the metotic fissure in earlier embryonic stages to join the lateral head vein, but in later stages it is replaced by the occipital vein passing through the foramen magnum. Again, this change would seem to be connected with the loss of the lateral head vein in ontogeny in the crocodile, as the primitive adult reptilian condition (compared with that of lower vertebrates) is for the posterior cerebral vein to exit through the metotic foramen, as in *Sphenodon* (O'Donoghue 1920). There thus seems no reason why it should not have done so in the adult *Sphenosuchus*. Dendy (1909, p. 413) states that the posterior cerebral vein in *Sphenodon* 'adheres closely to the inner surface of the cranial wall... lying just behind the projection of the auditory capsule'. He figures (pl. 31, figs 1 and 3) an expansion of the vein posterodorsal to the auditory capsule; his text figure 7 shows the vein entering the posterodorsal end of the metotic foramen. The reniform cavity in *Sphenosuchus* would thus seem to have housed a venous sinus on the posterior cerebral vein, and the vein itself probably discharged through the upper end of the metotic foramen via the gutter.

As previously remarked (p. 48) the small recess just behind the upper end of the metotic foramen in *Sphenosuchus* is considered to have housed a diverticulum of the longitudinal venous sinus, such as occurs in modern crocodiles (Hopson 1979, p. 51, and figs 1, 2: 'vcp').

Because there seems to be good evidence for a persistent middle cerebral vein in *Sphenosuchus*, and somewhat less certain evidence for a posterior cerebral vein passing through the metotic foramen, there is no pressing reason to suppose that the lateral head vein was greatly reduced, particularly as the quadrate and pterygoid were free from the side wall of the braincase and the quadrate was not greatly inclined. There is ample room between the quadrate wing of the pterygoid and the basisphenoid for the lateral head vein to have passed backwards from the orbit. The space above the stapes close to the fenestra ovalis appears in a lateral view to be somewhat restricted for the passage of a vein; however, the posterior end of the flange on the prootic projects laterally as well as posteriorly and there is more room here than might at first be thought. The lateral head vein probably passed back lateral to the 'anterior strut' of the basipterygoid process, and then curved dorsally, keeping close to the free edge of the prootic-basisphenoid flange (cf. *Varanus*: Säve-Söderbergh 1947). The middle cerebral vein probably passed downwards and backwards to join it behind the posterodorsal extremity of the quadrate wing of the pterygoid, where there seems to have been a gap between this bone and the quadrate. After passing over the stapes in company with the hyomandibular branch of the facial nerve and the lateral cranial sympathetic trunk it would have curved downwards and been joined by the posterior cerebral vein coming from the rear end of the metotic foramen.

In the crocodile the temporo-orbital vein accompanies the temporo-orbital (stapedial) artery and plays a large part in the drainage of blood from the orbit. With the V. maxillaris interna it replaces the lateral head vein (Hochstetter 1906). However, there is no reason to think that these changes had progressed very far in *Sphenosuchus*, so that it is unlikely that any important vein accompanied the stapedial artery through the temporal canal in this form.

(iii) *Impressions and foramina in upper part of orbit*

It was suggested (Walker 1972) that *Sphenosuchus* had salt-excreting (nasal) glands on the skull-roof in a similar position to those of many living sea-birds, but smaller. The reasons for this inference were (*a*) the shallow, paired depressions separated by a median ridge, on the upper surfaces of the frontals; (*b*) the presence of four or five marginal notches and foramina piercing the orbital rim on each side of the depressions (figure 6); (*c*) the 'ill-defined fan-shaped impression' referred to on p. 17 which converges downwards to a foramen entering the crista cranii in the upper wall of the orbit; (*d*) the arching canal leading through the bone from this foramen, which emerges as a group of foramina in the dorsolateral angle of the channel for the olfactory tract, just behind the impressions of the olfactory bulbs; (*e*) the prominent foramen between frontal and prefrontal in the anterodorsal corner of the orbit, which was assumed to have transmitted the duct of the gland, together with other vessels.

Collectively, these features resemble the structures seen above and within the upper part of the orbit in many sea-birds. The depressions for the salt-glands are usually bordered by notches or foramina in the frontals through which pass veins and arteries supplying the glands. In many bird skulls a series of grooves is seen converging downwards from these foramina or notches to another more medial foramen or notch in the upper part of the orbit. From this a groove arches over inwards below the cranial roof, behind the depressions which house the olfactory bulbs. The posterior part of the gland is supplied with blood from the supraorbital artery, a branch of the external ophthalmic (stapedial) artery, the anterior part from the ethmoidal artery, with which the supraorbital artery anastomoses (Marples 1932; Fänge *et al.* 1958; Baumel 1975*a*; Midtgard 1984). The supraorbital vein drains the posterior part of the gland and anastomoses with the ethmoidal vein from the nose which drains the anterior part, forming the ophthalmic vein. From near the junction a vein passes inwards to join with the intracranial olfactory venous sinus which surrounds the olfactory bulbs (Neugebauer 1845; Marples 1932; Kaku 1959; Baumel 1975*a*). This latter vein evidently follows the groove mentioned above which curves over below the skull roof, and is probably the 'V. facialis interna' of Kaku (1959, figures 9 and 10), although he does not describe this.

There is little sign in modern crocodilian skulls of the pattern of grooves and foramina seen in the upper part of the orbit of *Sphenosuchus*. There may occasionally be marginal notches on the frontals as in *Crocodylus acutus* and *Gavialis*, but I have been unable to find anything corresponding to the impressions in the upper part of the orbit, the foramen in the crista cranii, or the canal curving medially through the frontal from the latter. Hochstetter (1906) figures a plexus of veins dorsally between the olfactory bulbs at the beginning of the longitudinal sinus in *C. niloticus*, from which veins pass laterally over the anterior ends of the bulbs and curve round to make connection with the orbital veins. There seems to be a general resemblance here to the canal passing through the crista cranii of *Sphenosuchus*, but the correspondence in detail is not close, and there is no sign in crocodilian skulls of this cross connection. The venous arrangement in the corresponding regions of *Sphenodon* (O'Donoghue 1920) and lizards (Bruner 1907) seems, as far as one can gather from the descriptions, less similar still.

Altogether, the venous pattern in the upper part of the orbit of *Sphenosuchus* seems to have been quite similar to that seen in birds, more so than in crocodiles, except that the vein arching over laterally from the olfactory venous sinus to the foramen in the upper part of the orbit passed through the crista cranii of the frontal (which is very much thicker in *Sphenosuchus*) instead of running below the bone itself as it does in birds.

However, examination of a skull of *Struthio* in my possession shows one or two notches in the posterior part of the frontal edge, a faint pattern of grooves leading down to a notch in the edge of the crista cranii, and a groove running medially from this, as in other birds, yet the nasal gland is located at the anterior dorsal corner of the orbit, with its upper surface in the large elliptical foramen in the plane of the frontal surface (Technau, 1936). There are no depressions for the nasal glands on the posterior part of the skull roof. Pycraft (1900) figures six or seven marginal foramina in *Dromaius*; according to Technau (1936, p. 612) the gland is lacking in the 'Casuarii'. Evidently, therefore, the occurrence of a particular pattern of marginal notches or foramina, grooves, etc. in a bird skull or in the *Sphenosuchus* skull is not proof that a nasal gland was directly associated with this pattern.

Conversely, absence of depressions on the skull roof is not proof of the absence of extensive nasal glands, because there may be large glands above the orbits, but no or only very slight impressions on the skull roof (Anseriformes). The gland may extend laterally beyond the edge of the frontal in the upper orbital membrane, and marginal notches or foramina may be absent (Marples 1932, and personal observations).

The question of what vessels or other structures passed through, and in what positions, from the upper part of the orbit into the nasal cavity is also difficult to resolve in *Sphenosuchus*, since apart from the olfactory tracts and bulbs, there would have been at least one ramus of the ophthalmic nerve, probably a medial and a lateral ethmoidal (or nasal) artery, and an ethmoidal (or nasal) vein. Neither these structures nor their precise course in relation to the skull have been properly described in crocodiles. Detailed published information of this kind on other living diapsid reptiles is also meagre.

Among close relatives of *Sphenosuchus*, paired depressions occur on the frontals of *Hesperosuchus* (Colbert 1952), and apparently in *Dibothrosuchus* (Wu 1986), but not in *Terrestrisuchus* (Crush 1984) nor, apparently in *Pseudhesperosuchus* (Bonaparte 1971). The situation in *Saltoposuchus* (von Huene 1921) is unknown. The frontals of *Hesperosuchus* lack the marginal notches and other grooves seen in *Sphenosuchus*.

From the above considerations, it seems that the presence or otherwise of nasal glands on the skull roof of *Sphenosuchus* and its allies must remain an open question. The apparently bird-like vascular pattern in the upper part of the orbit may have been a general one in early archosaurs and the evidence of its presence in *Sphenosuchus* is perhaps partly due to the unusual depth of the crista cranii frontalis in this skull. The most that can be said at present seems to be that this pattern was already established in the late Triassic or early Jurassic so that when in birds the nasal glands eventually extended back on to the skull roof, the adjacent vascular supply required little modification.

(iv) *The stapedial artery and its enclosure*

The course of the stapedial or temporo-orbital artery in modern crocodiles has already been described (pp. 85–86). At the time that the hypothesis of a particularly close relationship between crocodiles and birds was first put forward (Walker 1972), it was realized that the different position of the artery in the two groups (in crocodiles above the prootic contact of the quadrate head, in birds below this contact) posed a problem, but it was believed that, in this part of its course, the crocodilian stapedial artery is a bypass or replacement vessel. This was partly because of its unusual position, and partly because the temporo-orbital vein which accompanies it is known to be a replacement. It was thought likely that the former course of the stapedial artery in the crocodile is shown to a large extent by that of the lateral cranial sympathetic trunk, which normally accompanies the stapedial artery in reptiles and also in birds. In the modern crocodile this nerve (Fischer 1852; Killian 1890; Bellairs & Shute 1953) is unusually large. It commences from the superior cervical ganglion and enters a foramen (the 'foramen vasorum' of Hasse (1873)) lying dorsolaterally within the external 'vagus' foramen. From here it passes steeply upwards and forwards, emerging towards the upper or lateral end of the recessus scalae tympani and then arching high over the top of the mastoid antrum, keeping close to the edge of the prootic buttress, before dropping down to pass between prootic and quadrate to the trigeminal ganglion. Its more anterior course does not concern the present discussion. The large size and dorsal position of the mastoid antrum in modern crocodiles has no doubt considerably distorted the original path of the nerve, which in *Sphenosuchus* would have followed a similar, but less extreme, sinuous course. It is to be noted that the entrance to the mastoid antrum lies between the lateral cranial sympathetic trunk (above) and the hyomandibular nerve (below). In the crocodile the subcapsular buttress has enclosed the sympathetic nerve, which was not the case in *Sphenosuchus*. In the crocodile the nerve passes to the trigeminal foramen below the broad area on the quadrate which sutures to the prootic and laterosphenoid, and it is thus below the prootic contact of the quadrate. Hence, if this nerve indicates the former position of the stapedial artery, the latter would also have passed below the prootic contact, in the primitive position.

However, there is little indication in the work of Hochstetter (1906) on the development of the cranial vessels in crocodiles that the main part of the stapedial artery is replaced, although he was not able to describe the earliest stages of its development. In contrast, the complex series of changes in the later stages, giving rise to the formation of the artery through the cranio-quadrate passage which to a large extent replaces the initial portion of the stapedial, was documented in detail by him. In one of the few other studies dealing with the development of the cranial arteries in reptiles Hafferl (1921*a*), in work on the gecko *Platydactylus annularis*, showed that the supraorbital artery in this form appears as a main branch of the stapedial by Stage V, but by Stage VI it has almost entirely disappeared except for a terminal portion now supplied from the A. ophthalmica. It seems probable, therefore, that replacement of the main portion of the stapedial artery in the crocodile would have been detected by Hochstetter, if it occurs.

Romer (1956, p. 42) states that the stapedial artery 'has three main branches which are, in considerable degree, associated with the three main rami of the trigeminal nerve'. Lower down the same page he continues: 'For example, in some reptiles the vessels join the nerve rami at a point close to that at which the rami diverge'. This state of affairs is shown in his created a lateral or upper wall to the newly formed *Sphenodon*, but the diagram is quite different from the actual arrangement of the arteries in that form (O'Donoghue 1920). Despite an extensive search of the literature, I have not been able to find an instance in which the arteries, in the adult reptile, adopt the pattern shown in Romer's diagram (although I have paid little attention to snakes) and the usual reptilian arrangement seems to be similar to that which Romer himself briefly described in *Sphenodon* (1956, p. 42), and which he seems to regard as unusual. This pattern is that, after giving off the mandibular artery well behind the trigeminal foramen, the stapedial (now the temporal in O'Donoghue's terminology) climbs steeply just in front of the quadrate head, crosses the supratemporal fossa (or the equivalent region) fairly high up or superficially to a point just behind the upper posterior corner of the orbit and then divides into the supraorbital and infraorbital arteries. The infraorbital artery then descends steeply behind the orbit and often joins the maxillary branch of the trigeminal nerve. In this pattern the supraorbital and infraorbital arteries join the ophthalmic and maxillary branches of the trigeminal nerve respectively well in front of the point of divergence of the main nerve rami, and the mandibular artery is given off well behind this point. This arrangement is often found in turtles and is probably primitive for the group, although the stapedial artery may be much reduced (Shindo 1914; Albrecht 1967, 1976). It is also found in *Sphenodon* (O'Donoghue 1920), and lizards (Corti 1847; Rathke 1857; Shindo 1914; Bhatia 1929; Oelrich 1956). In turtles the stapedial artery is enclosed in a canal between prootic and quadrate, but its position in relation to the opisthotic is basically the same as in the other groups. In the crocodile the artery crosses the supratemporal fossa superficially, dividing and re-joining, and then branches more or less in the usual manner behind the orbit (Rathke 1866; Hochstetter

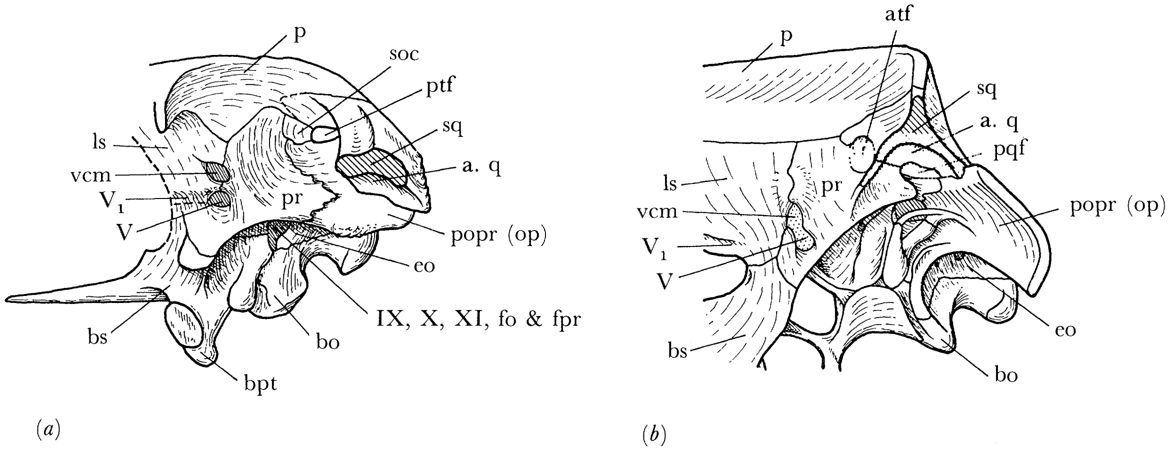


Figure 50. Left lateral views of the braincases of (*a*) *Stagonolepis*, magn. ×0.55; and (*b*) Sphenosuchus, magn. ×1. In (*a*) the otic opening has been reduced in size by compression of the paroccipital process.

1906). As already noted, the proximal part of the mandibular artery has been lost. It is thus not the high position of the crocodilian stapedial artery which is unusual, but its passage above the prootic contact of the quadrate.

If it be assumed that the disposition of the stapedial artery in thecodontians was similar to that in modern reptiles, i.e. that it climbed steeply immediately in front of the quadrate head, then its enclosure in a canal and its course above the prootic contact of the quadrate in crocodiles is not too difficult to understand, and appears to follow from the forward movement of the quadrate head which has taken place in crocodylomorphs (Walker 1972). It is instructive in this connection to compare *Sphenosuchus* with the late Triassic thecodontian *Stagonolepis* (Walker 1961) (figure 50). It is convenient to use this form because I have two skulls in Newcastle, one in which the bone is preserved, the other in the form of flexible casts made from natural moulds. In the latter skull the squamosal had become detached *post mortem* and its cast can be fitted on to the braincase and variously manipulated to help make intelligible the enclosure of the crocodilian stapedial artery.

In *Stagonolepis* the stapedial artery was probably given off behind the ridge of exoccipital which forms the posterior boundary of the combined otic–metotic opening. There is a slight notch where the prootic/opisthotic suture runs round the crista prootica, and this probably indicates the upward passage of the artery on to the side of the braincase. Since the supratemporal fossa in *Stagonolepis* faces largely laterally the artery probably did not rise up as far within the fossa, before turning forwards, as it usually does in modern reptiles, but this point is not significant to the present discussion. The position of origin of the mandibular artery is uncertain, but was presumably in the region opposite the posterior tongue of prootic on the anterior face of the paroccipital process. On the *Sphenodon* analogy, it would have passed forwards more or less horizontally to near the trigeminal foramen, and then turned downwards and outwards over the quadrate–pterygoid lamina.

Compared to a form like *Stagonolepis*, the quadrate head in *Sphenosuchus* has moved forwards and inwards along the paroccital process so that it no longer meets the opisthotic, as it does to a certain extent in at least some thecodontians (Price 1946; Walker 1961; Chatterjee 1978), but has gained instead a small contact with the prootic (Walker 1972) (figures 16 and 18). The main socket for the quadrate below the squamosal has moved inwards and forwards, and the bone itself has expanded forwards to allow for this. An overhang has thus been created behind and at the side of the quadrate head, and this extends forwards along the top of the infratemporal fenestra. In each skull the posterior tongue of squamosal runs about halfway down the anterior surface of the paroccipital process. It is not clear that streptostyly was necessarily involved in this transition, although the quadrate head in *Sphenosuchus* has the appearance of having been streptostylic. During this change the stapedial artery presumably sank into a notch which formed at the prootic/opisthotic suture, allowing the quadrate head to move past it. This notch was spanned by the squamosal which, meeting the prootic anterior to the notch, created a lateral or upper wall to the newly formed postquadrate foramen. (The modern crocodilian condition, in which the quadrate head enters this wall, is a derived state.) The forward expansion of the squamosal and its contact with the prootic converted the post-temporal fenestra from being essentially a window in the rear wall of the temporal fossa to a tunnel leading forwards, out of which the stapedial artery emerges at the rear of the supratemporal fenestra. As the result of a change such as this the stapedial artery in *Sphenosuchus* is thought to have passed above and medial to the prootic contact of the quadrate.

The strong ridge of prootic in *Sphenosuchus* which forms most of the lower border of the postquadrate foramen is probably comparable to the posterior tongue of prootic in *Stagonolepis* which lies on the anterior surface of the paroccipital process. There is a considerable difference between the two skulls in that the prootic/opisthotic suture which runs up to the supraoccipital in *Stagonolepis* is on the side wall of the braincase, whereas in *Sphenosuchus* the corresponding region is on the nearly horizontal floor of the temporal canal.

It seems likely that the forward and inward movement of the quadrate head has been responsible for the elimination of the original proximal part of the mandibular artery in crocodiles, as already pointed out (p. 86). However, short-circuiting of what was becoming a tortuous course for the blood supply to the lower jaw may also have been a factor.

As well as the quadrate head moving past the stapedial artery in crocodilian phylogeny, it is possible that the artery actually gains its position above the prootic contact in early ontogeny in the living animal. The pattern of branching of the artery in Romer's diagram (1956, fig. 27), in which the three main divisions are given off close to the origin of, and accompany, the three main branches of the trigeminal nerve, may be one which tends to occur early in the embryos of all living reptiles, and the typical adult pattern, in which the stapedial (or temporal) artery rises up to a dorsal position well behind the trigeminal origin, may be one which is attained during ontogeny. The pattern of the diagram is also one which tends to predominate in fishes, although it is not always fully developed (Allis 1897, 1923; O'Donoghue & Abbott 1928; Millot *et al.* 1978), and corresponds to that of the diagram of a primitive tetrapod by Goodrich ((1930, fig. 449); the true supraorbital artery is unlabelled in this figure; the vessel labelled '*ao*, supraorbital' is the orbital, *sensu* Hochstetter (1906)). This pattern therefore appears to be an archaic one in vertebrates, which tends to recur in tetrapod embryos, including Man (Padget 1948).

The quadrate cartilage in the embryo is not closely linked to the chondrocranium, so that it is possible that, in the crocodile, the dorsally migrating stapedial artery could 'slip upwards' through the gap to gain a position above the future prootic contact. The evidence that dorsal migration of the artery takes place in living reptiles is not very great, owing to the fact that very few developmental studies of the cranial arteries have been made. A comparison between the figures of Wyeth (1924) of embryos of *Sphenodon* with the adult arrangement as shown by O'Donoghue (1920) shows that dorsal migration must take place in that form. In the embryo of the gecko *Platydactylus annularis* (Hafferl 1921*a*), the stapedial artery at Stage V branches close to the trigeminal ganglion into supraorbital and mandibular branches which accompany V_1 and V_3, respectively. Unfortunately, the supraorbital artery soon regresses and the infraorbital artery is anomalous, but in the adult of the related *Hemidactylus flaviviridis* (Bhatia & Dayal 1933) the temporal and supraorbital arteries are in the usual high position. However, whether the stapedial artery in the crocodile does actually move up between the quadrate cartilage and the chondrocranium during development must await confirmation from further embryological studies.

Goodrich (1930, footnote on p. 411) points out that 'the articulation of the otic process appears to shift along the crista parotica or lateral edge of the capsule. In Selachii it meets it anteriorly at the postorbital process, and in Reptilia posteriorly where the crista forms a paroccipital process'. This raises the interesting possibility that the position of the quadrate articulation in crocodylomorphs may be the result of neoteny, i.e. a failure of the articulation to move backwards in ontogeny, rather than a forward movement in phylogeny. Such a suggestion rests on the assumption that the quadrate cartilage in reptilian embryos normally migrates backwards in relation to the chondrocranium during ontogeny. The development of the relevant region of the chondrocranium of crocodiles has still not been studied, and a preliminary survey of the literature on the embryology of other reptiles suggests that it would be very difficult to determine whether such a change actually occurs.

In birds the pattern of branching of the stapedial (external ophthalmic) artery corresponds closely to that of Romer's diagram. The stapedial artery branches close to the maxillo-mandibular foramen of the trigeminal, and its supraorbital, infraorbital and mandibular branches are, to a large extent, closely associated with the three main rami of the trigeminal nerve (Assenmacher 1953; Lucas 1970; Kilgore *et al.* 1976; Bubień-Waluszewska 1981; Midtgard 1984). This pattern is almost certainly neotenic. The basic pattern of branching of the stapedial artery in birds, unlike that in reptiles, changes very little during development (Twining 1906; Hughes 1934; Midtgard 1984), at least in the fowl and herring gull; in the lapwing the supraorbital branch becomes modified (Hafferl 1921*b*). The adult arrangement is essentially that of the embryo 'writ large'. It is thus possible that birds passed through a stage in early evolution in which the stapedial artery passed above the prootic contact of the quadrate, but have reverted to a state in which the artery is secondarily below this contact, because the artery has ceased to migrate dorsally in ontogeny. If this is the case, the problem of the different position of the artery in birds and crocodiles has been resolved, and the'proquadrate condition' in the two groups (Walker 1977) is restored as a primary synapomorphy, together with the associated suite of auditory improvements.

It follows from the above that birds would have acquired a prootic cantact of the quadrate head by the late Triassic (because early crocodiles had such a contact). *Archaeopteryx* would thus be anomalous, if the interpretation presented by me (Walker 1985) is correct.

(*e*) *The Ear*

The ear of *Sphenosuchus* provides evidence of good general hearing ability. Its construction throughout, with an external auditory meatus, a large middle ear space with extensive diverticula, an elongated cochlear recess, and a large, laterally placed perilymphatic sac, resembles the ears of birds and crocodiles, both of which have good auditory faculties (Baird, 1970; Wever 1978; Kühne & Lewis 1985; Smith 1985). The tympanic membrane was evidently large. The forward and inward position of the quadrate head and the consequent overhang of the squamosal posteriorly and at the side allowed the tympanum to be sunk below the skull-roof in a protected position and guarded from the main effects of the depressor mandibulae muscle (Walker 1972; Carroll 1977). The removal of the tympanic membrane from the head surface into a stable framework allows it to be larger and more delicate than if it remained on the surface, with a consequent improvement in sensitivity and an extension of the high-frequency response (Henson 1974). A large middle ear cavity reduces the damping of the tympanic membrane by giving a large volume of air for it to push against. As a result, the frequency sensitivity is extended to lower ranges (Webster 1966). In birds 'the more spacious middle ear cavities and those with the most extensive communication with air spaces, are found in birds with good or excellent hearing abilities, such as birds of prey and owls' (Kühne & Lewis 1985).

(i) *External ear*

The overhang of the postorbital and squamosal at the top of the infratemporal fenestra and along the sides of the quadratojugal and quadrate indicates a modest development of an external auditory meatus. The rugose projection from the lateral edge of the squamosal may indicate the existence of a rudimentary superior ear-flap (Shute & Bellairs 1955). The normal crocodilian groove along which this flap is attached is absent in *Sphenosuchus*, but in Recent crocodile skulls there may be an extra rugosity or small extra flange in the same approximate position (about half-way along the postorbital-squamosal bar), e.g. *Alligator*, *Gavialis* and *Crocodylus acutus*. Gow & Kitching (1988) have regarded the presence of a squamosal groove as a criterion for an aquatic mode of life in crocodylomorphs, but it is possible that the ear-flap may have evolved initially in relation to a different function, for example in order to protect the tympanum from windborne detritus.

It is unlikely that an inferior ear-flap was present, as the postorbital–jugal bar is not inset. The pit in the postorbital at the upper posterior corner of the orbit is not likely to have served for the attachment of the ypsilon (Shute & Bellairs 1955) because the alignment of the rugosities associated with it is inconsistent with the expected direction taken by such a structure. In addition, modern crocodile skulls usually show no sign of its attachment on the postorbital.

(ii) *Middle ear*

The line of attachment of the tympanum is clearly seen on the left quadrate and less so on the right (figures 13*d* and 15*f*). Evidently the drum was relatively large, taking up most of the height of the quadrate. Its posterior limit was presumably at the posterior contact of the squamosal with the paroccipital process. The stapes is not preserved.

The middle ear was an extensive cavity with many diverticula entering adjoining bones and the lower jaw. These cavities have been dealt with already and require no further comment.

In modern crocodiles and birds the crista interfenestralis is usually a slender bar as it is in *Sphenosuchus*. Although thin, this bar has an appreciable width mediolaterally, and in these living forms the annular ligament of the footplate of the stapes is often attached towards the medial edge of the bar whereas the secondary tympanic membrane covering the fenestra pseudorotunda is often attached to its lateral edge. The secondary tympanic membrane is thus 'set up' in relation to the stapedial footplate. Conditions in *Sphenosuchus* were presumably similar. The anterior boundary of the annular ligament would have been the strong rear edge of prootic which runs up above the cochlear prominence, but the upper and posterior boundaries are only faintly indicated (figures 23 and 24). The entrance to the vestibule was more deeply set down anteriorly than posteriorly with respect to the footplate, as is also the case in crocodiles. On the other hand, the fenestra ovalis in *Sphenosuchus* was not bordered by a recessed rim, as it is (particularly at the anterior end) in the crocodilian skull, and in this respect it resembles more the usual situation in birds.

In *Sphenosuchus* the secondary tympanic membrane (figure 51 *a*) would have been attached along the crista interfenestralis, down the posterior edge of the expansion of the opisthotic which helps to form the cochlear prominence, and would then have run close to the outer margin of the subcapsular buttress. Its posterior corner would have followed a curved line which is faintly visible running round from the subcapsular buttress to the rear end of the crista interfenestralis (figures 23 and 24). The area enclosed by these boundaries is the fenestra pseudorotunda, below which lies the recessus scalae tympani.

Fenestra ovalis and fenestra pseudorotunda together form an approximately triangular area with the fenestra pseudorotunda taking up the greater moiety. A moderate development of the subcapsular buttress has extended the recessus scalae tympani laterally, so that the secondary tympanic membrane was in the same plane as, or at a large obtuse angle to, the fenestra ovalis (apart from the step-effect at the crista). In the modern crocodile the subcapsular buttress has extended more dorsally than in *Sphenosuchus*, so that the secondary tympanic membrane is at right angles to the fenestra ovalis (Wever 1978, fig. 24-17). The recessus is more constricted laterally in the crocodile than in *Sphenosuchus*, and it seems that its greater dorsal extension compensates for this: Shiino (1914) states that as the subcapsular process extends dorsally in the growth of the embryo, the secondary tympanic membrane shortens. Thus the relative size of the perilymphatic sac may not have increased very much in the modern crocodile. Many birds, particularly those in the orders generally regarded as primitive, have a very similar configuration of fenestra ovalis and fenestra pseudorotunda to that of *Sphenosuchus*, that is forming a triangular area with the footplate of the stapes and the secondary tympanic membrane essentially in the same plane, or set at a large obtuse angle. These include representatives of the Sphenisciformes, Gaviiformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Charadriiformes and Strigiformes, to name but those in which the secondary tympanic membrane has been observed in place.

In some other groups of birds the secondary tympanic membrane is set approximately at right

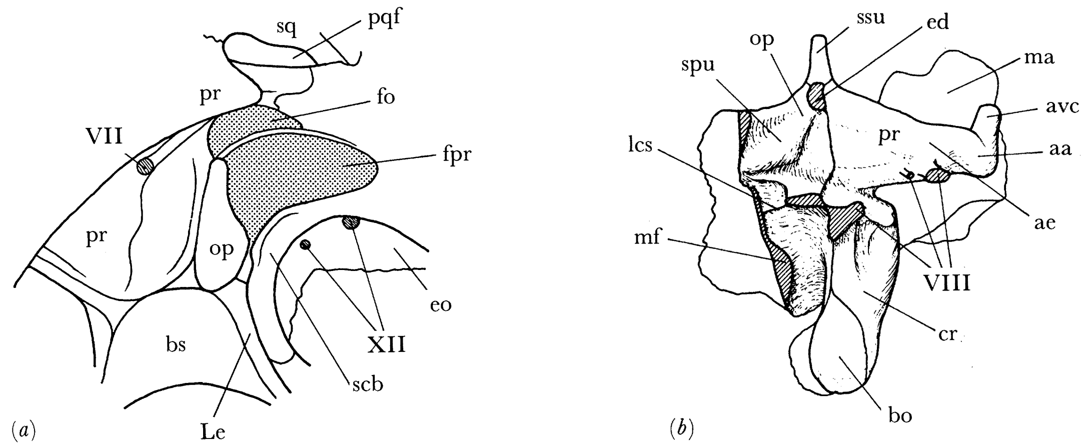


Figure 51. *Sphenosuchus acutus* Htn. (*a*) Diagram of the left otic region, magn. ×2; (*b*) cast of the left cochlear recess and vestibule, medial and somewhat anterior view, magn. ×3. The loop-closure suture has been opened up a little by distortion behind the posterior auditory foramen.

angles to the fenestra ovalis, e.g. members of the Rheiformes, Anseriformes, Galliformes, Gruiformes, Columbiformes and Passeriformes. There seems to be no hard-and-fast distinction between these two conditions, however, and the second is presumably a more derived state, perhaps connected with a greater development of the metotic cartilage, combined with bony 'scaffolding' around the otic opening, mainly from the tube for the stapedial artery.

(iii) *Inner ear* (*figures 21–24, 28, 29, 51–53, 59 and 60*)

The discussion of the otic capsule which follows below is mainly based on a comparison with the inner ears of living crocodiles and birds. This is possible because of the excellence of the preservation of this region in the specimen of *Sphenosuchus*. A detailed comparison with the otic capsules of the various fossil archosaurs described in the literature will not be attempted at this stage. It is assumed that soft-part anatomical structures in the inner ear of *Sphenosuchus* were similar to those of living crocodiles and birds, which agree with each other very closely in most respects (Baird 1974*a*, *b*). Thus the cochlear duct would have been elongated. Although strictly speaking not part of the otic capsule, one cannot at the same time avoid consideration of the recessus scalae tympani and its floor which is formed by the subcapsular buttress. The perilymphatic duct in *Sphenosuchus* would have passed out of the capsule through the foramen perilymphaticum and expanded within the recessus to form a large perilymphatic sac. Laterally the sac would have joined with the mucous membrane of the tympanic cavity to form the secondary tympanic membrane. The sac would also have sent an extension medially through the lower part of the metotic foramen to contact the cranial meninges. De Beer makes the curious statement (1937, p. 263) that, in the crocodile 'the ductus perilymphaticus does not pass through the foramen perilymphaticum'; that this is an error is shown by the work of Retzius (1884), de Burlet (1934, fig. 1156), and Baird (1960).

The construction of the otic capsule has been investigated in representatives of the following groups of birds: Ratites (*Struthio*, *Dromaius*, *Casuarius*, *Rhea*), Sphenisciformes, Procellariiformes, Anseriformes, Galliformes, Charadriiformes. By this is meant that the suture-pattern has been determined just before the fusion and disappearance of the sutures.

The otic capsule of *Sphenosuchus* closely resembles that of a modern crocodile. Externally, prootic and opisthotic form a cochlear prominence in crocodiles, housing the tubular lower part of the elongated cochlear recess. The external edges of prootic and opisthotic meet along a straight or slightly sinuous line, the opisthotic contribution to the junction being usually the thicker, as it is in *Sphenosuchus*. The opisthotic is thickened and produced backwards in a lobe at its lower end in *Sphenosuchus* in a manner typical of crocodiles. Prootic and opisthotic also curve apart in crocodilian fashion at the lower end of the recess, leaving a space at the side of the lagenar region which would have been closed off in life by cartilage. The pattern of sutures is very similar to that of modern forms, but there are significant differences which will be pointed out.

Most of the above features are also found in the otic capsule of birds, which in some respects shows a greater resemblance to that of *Sphenosuchus* than does that of crocodiles, but in this case also there are differences. The cochlear prominence of birds is usually more marked in pulli; in the adult the basitemporal or the bony tube for the internal carotid artery, or both, may conceal it, as in the spongy basitemporals of *Gallus*. Also, the metotic ossification (part of the 'exoccipital') which plays the same rôle in relation to the otic capsule as does the subcapsular buttress in the crocodile, forms a strong buttress below the paroccipital process; this merges with the lower end of the cochlear prominence and tends to obscure it. The lobed area of the opisthotic occurs in the pulli of some birds (e.g. *Daption*, *Eudyptes*, *Pygoscelis*, *Larus* (Walker 1985, figs 2 and 3)), but does not extend down to the lower end of the cochlear recess, since the metotic commonly intrudes into this region. Also in pulli the lateral wall of the cochlear recess closes in development from the top downwards, so that an unossified, cartilage-filled cleft persists for a time at the lower end between prootic and opisthotic + metotic or, in later stages, between prootic and

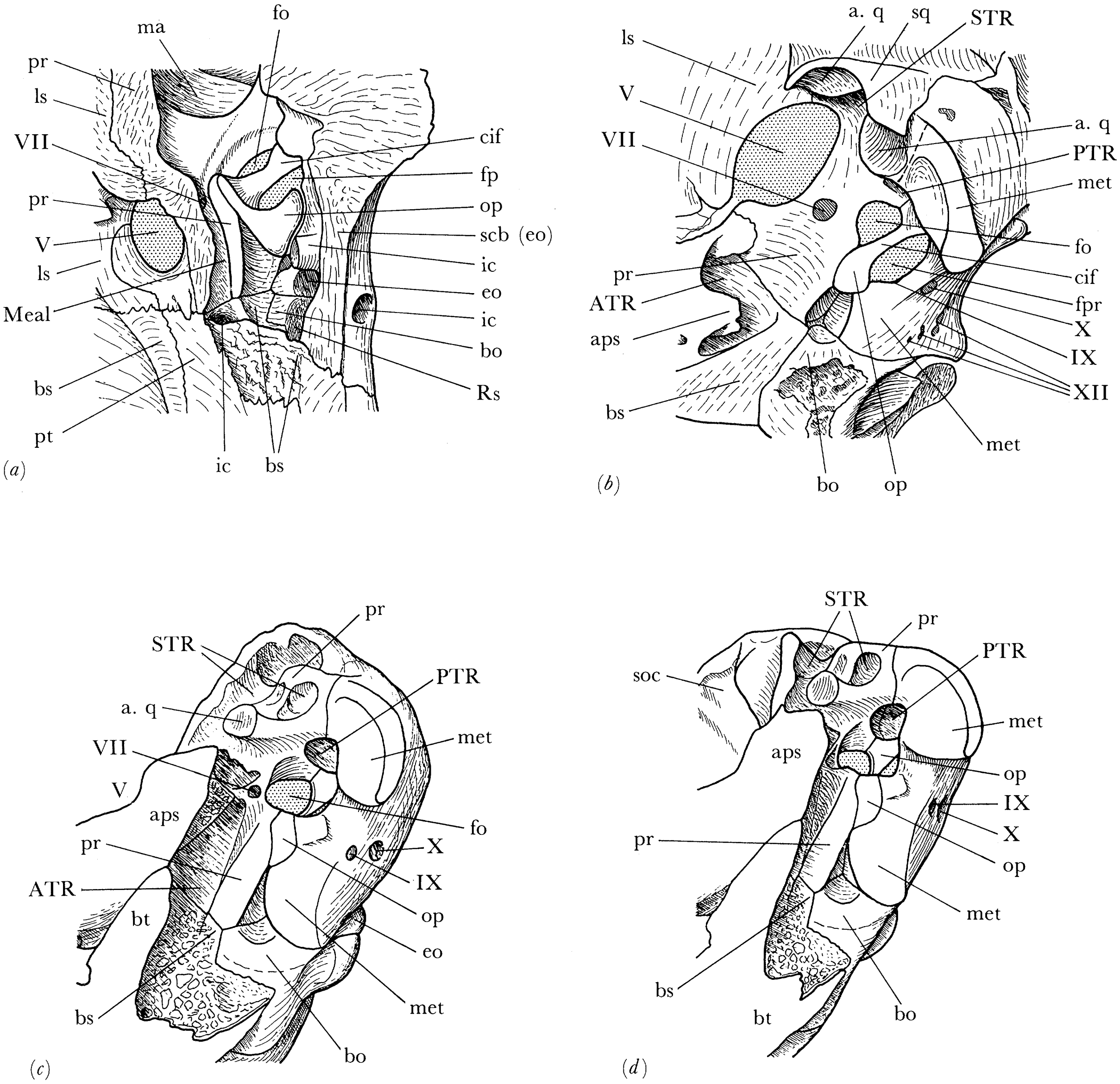


Figure 52. Otic capsules. (*a*) *Osteolaemus*, adult. Foramen perilymphaticum stippled. (*b*) *Daption*, juv., fenestra pseudorotunda stippled. Occipital condyle missing. (*c*), (*d*), *Gallus*. juv. Squamosal removed and basitemporal partly dissected away. (*a*)–(*c*): left lateral views; (*d*): anterolateral view. (*a*): Magn. ×2.5; (*b*)–(*d*): magn. ×4.8.

metotic. (An exception to this is the situation in *Anas* and *Somateria* in which the tubular part of the cochlear recess is largely made up of prootic and the metotic does not enter it.)

The superior sinus of the utriculus and the anterior vertical semicircular canal are expressed as ridges on the interior of the *Sphenosuchus* braincase (figure 28*b*), enclosing a depression for the floccular (auricular) recess (p. 48). This resembles the conditions in birds, but in a less marked form, rather than in crocodiles; in the latter these features are not detectable on the interior of the cranium.

In certain other respects the general build of the capsule in *Sphenosuchus* is more avian than crocodilian. Thus the marked geniculation of the cochlear recess of the crocodile is lacking. As a result of this geniculation, the tubular lower portion of the recess is vertical in the crocodile, the entrance to the vestibule is set back relative to it, and so as a consequence is the foramen for the endolymphatic duct within the vestibule, and the sinus superior of the utriculus. In *Sphenosuchus*, on the other hand, the cochlear recess runs down and slightly forwards from the vestibular entrance in a gentle continuous curve, also curving a little medially. The endolymphatic duct foramen and sinus superior utriculi in *Sphenosuchus* are in line with the long axis of the cochlear recess. The capsule is tilted back at about 13° to the vertical in *Sphenosuchus*, using as reference a line running through the superior sinus of the utriculus and the cochlear recess, and taking the straight posterior part of the basioccipital/exoccipital suture to be horizontal (in figure 51*b* the capsule is viewed from a slightly anterior angle; figure 22*a* shows a true lateral view). The vestibule also seems to have been smaller compared with the cochlear recess in *Sphenosuchus* (allowing for the compression of the left side) than in modern crocodiles. In all these features *Sphenosuchus* shows a closer approach to the conditions in birds than those in crocodiles.

The upper end of the cochlear prominence projects strongly laterally in modern crocodiles, which is not the case in *Sphenosuchus* or in birds. This appears to be a consequence of the different orientation of the fenestra ovalis in the crocodile, which generally faces more dorsolaterally than in *Sphenosuchus*, presumably because of the smaller and more dorsally placed tympanum.

In *Sphenosuchus* the opisthotic forms a complete loop round the foramen perilymphaticum (figure 24), the perilymphatic loop (Walker 1985), meeting itself at the loop-closure suture. This is situated, as in crocodiles, towards the posterior end of the opisthotic ledge (as viewed laterally). In the juvenile birds that I have investigated this complete loop of opisthotic is found only in the Galliformes (*Gallus*, *Perdix*, *Phasianus*). In other groups the 'exoccipital' (probably in this region the ossified metotic cartilage) intervenes, meeting prootic at the lower end of the ledge and breaking the continuity. The ledge in most bird groups is thus not an 'opisthotic ledge' but an 'opisthotic–metotic ledge', and the equivalent of the loop-closure suture is set towards the anterior or ventral end of the ledge.

Turning to the cochlear recess itself, in *Sphenosuchus* the basioccipital forms a large part of the lagenar region at the base of the recess, and **V**'s upwards medially between prootic and opisthotic which meet it at contacts of approximately equal length (figures 22*a*, 23*b* and 24). The exoccipital does not enter the recess. In the crocodile the basioccipital only enters the recess at the posteromedial corner, three quarters of the base being taken up by the basisphenoid. Birds, on the whole, adhere more closely to the *Sphenosuchus* pattern, with the lagenar region lying in the basioccipital and forming an upward **V** medially, but 'exoccipital' (probably ossified metotic cartilage) intervenes to a greater or lesser extent in different groups, taking the place of opisthotic at the lower end of the recess (figure 52). (This region is incorrectly labelled 'op' in Walker (1972, fig. 6b).) In the mallard, *Anas platyrhynchos*, and eider, *Somateria mollissima*, however, the prootic makes up most of the tubular part of the recess and the metotic does not enter, except for a short space at the medial border of the foramen perilymphaticum. It is likely that this is also the case in other anseriforms. On the other hand, the basisphenoid proper usually does not take any part in the formation of the recess in birds, although it may come very close to it, and the basitemporal may lap alongside the lagenar region.

The crocodile differs from *Sphenosuchus* in that the 'exoccipital' (probably part of the subcapsular buttress) just enters the lower part of the cochlear recess, intervening between basioccipital and opisthotic in the medial wall (figure 52*a*). It thus presents a certain similarity to the situation in birds. As a result, the lobed portion of the opisthotic is retracted dorsally in crocodiles (less so in the gavial), somewhat as in birds. However, the perilymphatic loop in the crocodile is entirely composed of opisthotic, unlike the situation in most bird groups investigated. The 'exoccipital' meets the prootic below or medial to the opisthotic in crocodiles, again as in birds (figure 53). In *Gavialis* the exoccipital does not quite meet the prootic but the pattern is essentially the same as in other crocodilians. The sharp dorsal arch of the internal carotid artery seems to be responsible for the retraction of the opisthotic in modern crocodiles, so that the arch of this vessel presumably lay a little lower down in *Sphenosuchus*.

This anterior process of the 'exoccipital' which enters the recess medially in the modern crocodile is identifiable in *Sphenosuchus* as the small triangular projection of exoccipital with a flat base which rests on basioccipital (p. 34 and figure 23*b*). It is of very similar form to its counterpart in the crocodile. It lies immediately behind the opisthotic lobe in *Sphenosuchus* but does not enter the cochlear recess. Pneumatization has entered the subcapsular buttress in crocodiles, so that there is a passage leading upwards from the rhomboidal sinus, separating the anterior process of the 'exoccipital' referred to above from the remainder of the buttress.

As regards the semicircular canal system, it seems that the superior sinus of the utriculus or crus commune in *Sphenosuchus* is relatively shorter than in *Alligator* (Retzius 1884), and the anterior and posterior vertical canals continue to rise, after diverging, for a little further than they do in that form. The fine cavities of the canals could only be cleared for a short distance, but a latex cast gives one the impression that the arch of the anterior canal would rise higher than that of the posterior, if followed further, much as in *Alligator*. The anterior canal appears to be orientated more anteroposteriorly and the posterior canal more transversely, than in crocodiles, but it is difficult to be sure of this because of the effects of distortion. In birds the anterior canal is usually orientated close to the parasagittal plane, with the posterior canal at right angles to it. In *Sphenosuchus* the anterior canal is given off partly from the medial side of the posterior canal, rather than from directly in front of it as in the crocodile. This shows some similarity to the situation in birds where, probably because of the large size of the floccular recess, the anterior vertical canal is given off at first backwards and then arches forwards medial to the curve of the posterior canal, that is, its point of origin has been rotated medially and posteriorly. The external canal in *Sphenosuchus*, as far as can be seen, does not present any unusual features.

An outwardly broadening groove on the opisthotic on the floor of the vestibule (figures 22 and 51*b*) is taken to indicate the position of the posterior sinus of the utriculus. A similar but shallower groove is sometimes seen in large Recent crocodilian skulls, e.g. *Crocodylus porosus*.

In *Sphenosuchus* the second or middle of the three foramina for the branches of the acoustic nerve is very small, markedly smaller in diameter than the anterior foramen (figures 22*d* and 51*b*) whereas, although in Recent crocodiles the middle foramen is smaller than the anterior one, the disparity in size is usually not very marked. The macula of the sacculus in the crocodile has a double innervation, one (larger) branch from the anterior acousticus passing to it through the middle foramen, and another (smaller) from the same nerve passing to it through the posterior foramen (Retzius 1884; Glatt 1975). Turtles and lizards also have a double innervation of the saccular macula (Retzius 1884; Baird 1970). The small size of the middle foramen in *Sphenosuchus* suggests a reduction in the importance of the anterior nerve to the macula sacculi, which is of interest because of the fact that birds have only a single innervation of this macula, and also have a very small sacculus compared with that of crocodiles. There is a close correspondence between the three main divisions of the auditory nerve, in terms of the sensory structures supplied by each, in birds and crocodiles. A comparison between the figures of Bubień-Waluszewska (1981, fig. 7.17) and Glatt (1975, fig. 1) shows that the 'caudal vestibular ramus' of the bird (which includes the saccular nerve) corresponds to the posterior part of the 'radix VIII anterior' which passes (along with the cochlear nerve) through the third or posterior foramen in the crocodile, hence it is the anterior nerve to the sacculus which has been lost by the bird, and which is apparently reduced in *Sphenosuchus*. On the crocodilian comparison, the bird has lost a foramen for the anterior nerve to the sacculus, but gained one for the posterior nerve. This is not unlikely, because the nerve to the anterior ampulla has acquired (compared with the crocodile) a separate foramen in birds, and so also has the nerve which supplies the posterior ampulla and the macula neglecta. Birds thus commonly have five foramina for the branches of the auditory nerve (the cochlear nerve making the fifth), as against the crocodilian three. There is no sign of a posterior innervation of the sacculus (apart from the posterior foramen) in *Sphenosuchus*, but neither is there any trace of this nerve on the interior of the capsule in present-day crocodiles.

The nerve which supplied the posterior ampulla and the macula neglecta in *Sphenosuchus* ran back from the posterior acoustic foramen in a groove which crosses the threshold of the vestibule (p. 37 and figures 22*a* and 24*b*). It was thus partly sunk into the bone. A groove for this nerve is not seen in modern crocodilian skulls. In birds, on the other hand, the nerve travels in a canal through the bone, running outwards and backwards from just behind the saccular and cochlear foramina, to the cavity for the posterior ampulla. In some birds, e.g. *Fulmarus glacialis*, the canal is often exposed in the adult as an open groove running along the threshold into the vestibule. The groove is variable in extent and probably tends to close up in old birds. *Sphenosuchus* thus shows an approach to the avian condition in this respect also.

The foramen for the endolymphatic duct in *Sphenosuchus* is in the crocodilian position, but there is no sign of a depression for the endolymphatic sac on the interior of the cranium, such as is sometimes seen in modern crocodilian skulls. One would expect this sac to have lain dorsoposterior to the foramen, on the epiotic adjacent to the opisthotic, close to the reniform cavity. Retzius (1884, pl. X) figures the endolymphatic sac in *Alligator* in this position and states in the legend that its upper end lies over a venous sinus, which affords some support for the suggestion made earlier that the reniform cavity in *Sphenosuchus* housed a venous sinus on the posterior cerebral vein.

The otic capsule of *Sphenosuchus* is of a type from which both that of the crocodile and that of the bird can readily be derived, but in certain features it is more primitive than either. The first of these is in the modest development of the subcapsular buttress, not enclosing IX, X and the internal carotid artery. The metotic cartilage of birds may be the homologue of the subcapsular process of crocodiles, and the two groups may be sister-groups, nevertheless further elaboration of this structure must have occurred independently in each case. Furthermore, it seems likely that a subcapsular process developed, perhaps several times independently, in a number of dinosaur groups (Walker 1985).

The failure of the 'exoccipital' to enter the lower end of the cochlear recess in *Sphenosuchus* is correlated with the modest development of the subcapsular buttress in this form. The fact that the opisthotic extends down to meet the basioccipital is thus likely to be a primitive feature, particularly as this also occurs in *Varanus*. That this is indeed the case is borne out by the following comparison, which adds more detail to the brief exposition of otic capsule changes in archosaurs given previously (Walker 1985).

The crista interfenestralis and its continuation, the thickened posterior wall of the cochlear prominence, of *Sphenosuchus* correspond to the ventral process of the opisthotic in such forms as *Sphenodon*, *Prolacerta*, *Chasmatosaurus* and *Euparkeria* (Cruickshank 1971, 1972; Gow 1975; Evans 1986, and personal observations). In these forms the ventral opisthotic process is a strong pillar, tending to form an anteroposteriorly compressed lamella. It is deep mediolaterally and merges gradually with the paroccipital process at its upper end. The foramen perilymphaticum notches its inner margin in *Sphenodon*, *Prolacerta* and *Euparkeria*, and almost certainly did so also in *Chasmatosaurus*. At its lower end it rests on basioccipital or in a socket shared by basioccipital and basisphenoid. The opisthotic process projects much more strongly laterally than does the exoccipital, which forms the posterior boundary of the metotic foramen. The thickened portion of the opisthotic in *Sphenosuchus* has essentially the same relationships to adjacent bones as in the forms cited. It forms the posterior portion of the lagenar or cochlear region, rests on basioccipital at its foot, probably just touched the basisphenoid lateral to this contact, and is still fairly prominent laterally. The 'clubbed tip' of the ventral ramus of *Prolacerta*, *Euparkeria* and *Mesosuchus* (Evans 1986) presents a certain resemblance to the lobed lower portion of the opisthotic of *Sphenosuchus*. The crista interfenestralis, on the other hand, has thinned down very considerably and retreated medially at its upper end, compared to the upper portion of the opisthotic lamella which lies behind the fenestra ovalis of the more primitive forms.

The foramen perilymphaticum of *Sphenodon* and *Euparkeria* and, by extension, also of *Prolacerta* and *Chasmatosaurus*, faces posteromedially and its inner margin would have been completed in cartilage in the fossil forms. To arrive at the situation seen in *Sphenosuchus*, crocodiles and birds, one must imagine that this foramen has rotated and migrated laterally so that it faces posterolaterally in *Sphenosuchus*, postero-

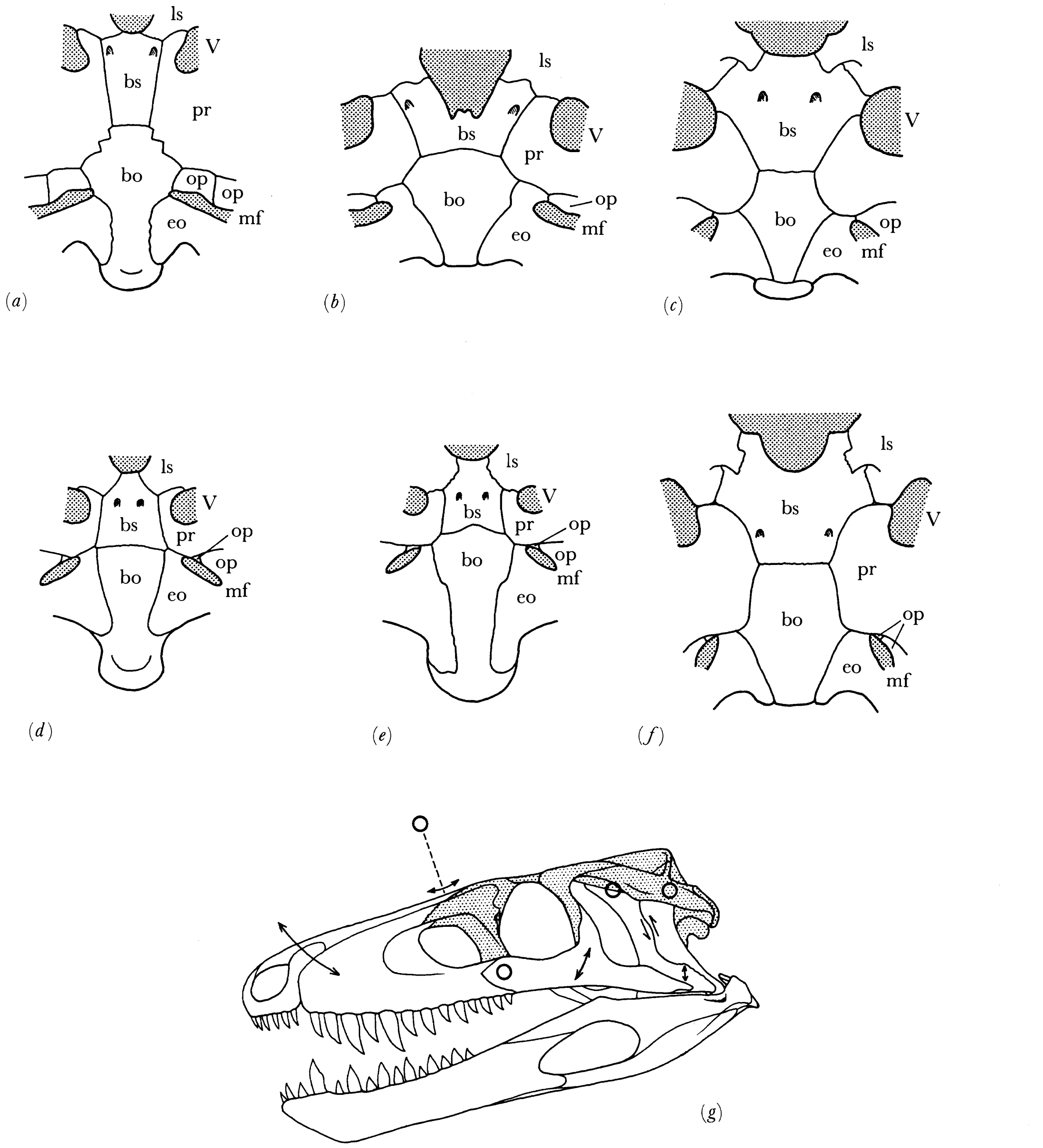


Figure 53. Diagrams of sutures on the braincase floor in crocodylomorphs and birds. (*a*) *Sphenosuchus acutus*, magn. × 1.1; (*b*) *Pygoscelis papua*, juv.; (*c*) *Anas platyrhynchos*, juv., magn. × 2.5; (*d*) *Osteolaemus tetraspis*, magn. × 0.85; *Alligator* and *Caiman* show essentially the same pattern; (*e*) *Crocodylus acutus*, magn. × 0.5; (*f*) Gallus gallus, juv., magn. × 3.5. The alaparasphenoid has been omitted in the case of the birds. (*g*) Diagram of possible kinetic movements in the skull of the juvenile *Sphenosuchus*. Cranial unit stippled. Open circles show the positions of pivots, that of the nasal-frontal slide lying dorsal to the skull.

laterally with a small dorsal component in some cases in crocodiles, and posteroventrally in birds. Basioccipital intervenes at the base of the foramen in *Sphenodon* and probably did so also in *Euparkeria* and *Chasmatosaurus*, so that as well as ossifying in the cartilage forming the inner margin, the opisthotic must also have extended round ventrally to complete the loop around the foramen perilymphaticum. The inner margin or opisthotic ledge (opisthotic + metotic in most birds) thus comes to be visible in a lateral view. In the primitive archosaurs the anterior margin of the metotic foramen is formed externally by the opisthotic lamella. In crocodylomorphs and birds most or all of this margin is formed by the ledge.

The formation of a complete loop of opisthotic is evidently relatively primitive, because it occurs in lizards, *Sphenosuchus* and crocodiles, whereas the situation in most birds, in which metotic intervenes, is fairly clearly more advanced, as it is associated with the formation of the metotic cartilage.

Lateral rotation of the foramen perilymphaticum coupled with development of a subcapsular or metotic buttress and concomitant lateral extension of the recessus scalae tympani probably permits enlargement of the perilymphatic sac. This enlargement and lateral placement, together with increase in the area of the secondary tympanic membrane, may perhaps improve the efficiency of the system as a pressure-release mechanism.

The development of the subcapsular buttress in *Sphenosuchus* has added bone to the lateral edge of the exoccipital behind the metotic foramen. The relative amounts of lateral projection of the opisthotic lamella and the anterior edge of the exoccipital are thus largely reversed in *Sphenosuchus* compared with *Euparkeria*, the strong lateral projection of the opisthotic having yielded primacy to that of the subcapsular buttress. This discrepancy is taken further in birds and crocodiles.

One might expect that the construction of the lower end of the cochlear recess in *Sphenosuchus*, with the basioccipital taking the major share and forming an upward V between prootic and opisthotic, would be primitive compared with that of modern crocodiles. Without more detailed information from more primitive archosaurs this point is difficult to settle. In *Euparkeria* the basioccipital takes up a little more than half of the base of the lagenar recess, lying behind the basisphenoid, compared to the quarter share taken up by the basioccipital in the modern crocodile, which affords some slender support for the above supposition. Although more preparation has been done on the otic capsule of *Stagonolepis* (Walker 1985), which it is hoped to describe at some future date, no information has been forthcoming on this point. The basioccipital is rather elongated in *Sphenosuchus* (figure 53), but the large participation of this bone in the lagenar region is not necessarily correlated with this. In *Pelagosaurus* the braincase is also elongated, but the relationship of the basioccipital to other bones at the base of the cochlear recess is essentially as in living forms.

As suggested earlier (Walker 1972), the geniculation of the cochlear recess in typical crocodiles may be connected with the flattening of the skull which has taken place in these forms, and would thus be a derived character with respect to *Sphenosuchus*. The strong lateral projection of the upper end of the cochlear prominence in modern forms may similarly be correlated with flattening of the skull and amphibious habits. The further elaboration of the subcapsular buttress, enclosing nerves IX and X and the internal carotid artery, and entry of the exoccipital into the base of the cochlear recess, are evidently also derived characters in typical crocodiles.

As derived osteological characters of the avian otic capsule compared with that of *Sphenosuchus*, first of all we see the considerable development of the metotic buttress, enclosing nerves IX and X. The metotic usually enters the lower part of the cochlear recess (not in Anseriformes), and usually also enters the perilymphatic loop (not in Galliformes). The cleft at the side of the lagenar region in *Sphenosuchus* (and crocodiles) may be a primitive feature. In *Sphenodon* the side of the lagenar region remains persistently cartilaginous. The braincase of *Euparkeria* is extremely like that of *Sphenodon*, and Evans (1986) figures a gap between prootic and opisthotic in this region in South African Museum no. 7696. From my examination of this specimen, however, the area which she labels 'prootic' is largely basisphenoid and the facial foramen is incorrectly placed, but the prootic does send down a lamina medial to the basisphenoid in front of the lagenar region, so that the similarity to *Sphenodon* seems to be confirmed (depending on the completeness of the bone edges). Thus the closure of the prootic/opisthotic + metotic suture at the side of the cochlear recess in adult birds may be a derived character.

Other derived features of the bird otic capsule, compared to that of *Sphenosuchus*, are that the semicircular canals are more 'looped' or arcuate; the sinus superior of the utriculus is short; the anterior vertical canal is given off low down, is directed at first backwards and then arches over forwards and outwards; the anterior and posterior vertical canals are more nearly in the parasagittal and transverse planes, respectively; there are five foramina for branches of the auditory nerve instead of three; and the floccular recess is very deep.

6. KINESIS AND STREPTOSTYLY

I have attempted to show (Walker 1972, 1974) that streptostyly and kinesis had operated in the skull of the juvenile *Sphenosuchus*, or in a shortly-preceding ancestral stage. The suturing of the squamosal to the outer side of the anterodorsal process of the quadrate, and of the overlapping quadratojugal to its lower end, shows that the bone was fixed in what is presumably an adult skull. Nevertheless, the smooth, rounded head of the quadrate was located in an ample cartilage-lined socket and has the appearance of having been streptostylic. The possibility that streptostyly and kinesis may have occurred in the juvenile stage before the above-mentioned and other sutural contacts had developed has thus been further investigated, taking into account also certain other features of the skull.

Although it appears possible that, as preserved, the 'pterygoid process' of the quadrate is actually the split-off lower portion of the pterygoid wing, nevertheless there was a certain separation of this wing into 'pterygoid' and 'orbital' processes. The 'pterygoid process' articulated by means of a low convexity at its base with a shallow cup on the pterygoid (figure 14*b*) which was set off from the main body of the quadrate wing of the pterygoid. This resembles the situation in birds and suggests the possibility of kinesis. Also, there seems to have been a rather bird-like arrangement of ligaments at the jaw articulation. A ligament comparable to the lower part of the bird postorbital ligament apparently ran from the rear end of the jugal to the deep pit on the side of the surangular just below the cotylus. Another ligament comparable to the avian internal (or medial) jugomandibular ligament (which actually originates from the quadratojugal) seems to have run from the rear corner of the quadratojugal, in a groove in the surangular (figures 33*b* and 34*b*, *c*), passing around the lateral corner of the quadrate, to insert on the lateral corner of the articular at the notch between this bone and the surangular. A third ligament resembling the occipitomandibular ligament of birds no doubt extended from the lowest part of the paroccipital process to the internal ascending process of the articular. Part of the function of these ligaments, particularly the second mentioned, appears to have been to control and stabilize the quadrate in a rather bird-like fashion during the opening of the jaws.

The contact between jugal and ectopterygoid does not seem to have been very firm and it is postulated that, if the pterygoids were pushed forwards by the quadrates, the wedging action of these bones between the vomers and palatines would have protracted and lifted a 'snout segment' consisting of premaxillae, maxillae, nasals, vomers and palatines (figure 53*g*). It is thought possible that, if some degree of anteroposterior rocking of the quadratojugal in its slot below the squamosal was permitted, protraction of the foot of the quadrate would cause the quadratojugal to slide down its anterior edge, thus depressing the rear end of the jugal. Some wedging action of the quadratojugal, sliding forwards within the jugal, may also have contributed to the depression of the jugal as a whole. The postorbital is firmly fixed to the skull roof, but its contact with the jugal appears to have allowed movement between them. The lower quadrate/quadratojugal contact would then have been a slide, rather than, as previously postulated, a pivot (Walker 1972, 1974). Pivoting between maxilla and jugal, and sliding at the overlap between nasal and frontal, would have been as suggested earlier (Walker 1974).

However, this postulated scheme of kinetic movement comes up against the difficulty that, although the right postorbital and jugal (which are detachable) slide past each other very convincingly in a shallow arc when manipulated, the general disposition of the main contact surface on the jugal was originally sub-vertical and facing forwards (figures 8 and 9) (the ascending process of the jugal has been bent forwards on each side, but not to any great extent). It seems unlikely that a large amount of forward movement of the jugal could have been produced without depressing the posterior end of the bone to an unrealistic extent, but some forward movement seems to have been possible.

It is considered probable, therefore, that the system of movements outlined above operated in the juvenile skull, before certain indented sutures had developed. These movements would have been controlled by a set of stretched ligaments, an important member of which was a ligament (equivalent to the upper part of the bird postorbital ligament) passing from the pit in the postorbital to the rear edge of the ascending process of the jugal. This ligament, together with a recoil-stop at the anterodorsal process of the quadrate, is believed to have played a key rôle in returning the system to the zero position with the minimum expenditure of muscular energy. It is hoped to deal with the working of the kinetic system in more detail in a later paper.

7. MODE OF LIFE

The skull of *Sphenosuchus* has been restored at 192 mm (7.5″) long, while the presacral column length is estimated to have been 473 mm (18.5″). The tail, in comparison with closely related forms (*Pseudhesperosuchus*, Bonaparte 1971; *Pedeticosaurus*, van Hoepen 1915; *Saltoposuchus*, von Huene 1921 and *Terrestrisuchus*, Crush 1984) was probably at least half as long again as the presacral length, i.e. *ca.* 710 mm, giving an estimated total length of 1.4 m (4′ 7″). This suggests an animal about the size of a fox or medium-sized dog.

In the absence of so many parts of the postcranial skeleton (forearm and hand, pelvis, femur) it is not possible to say a great deal about the locomotory habits of *Sphenosuchus*. Comparison with closely related forms, which have slender, elongated limbs, would lead one to expect that *Sphenosuchus* was cursorial, and the evidence from the preserved parts of the postcranial skeleton does not contradict this. The humerus is a strong bone, 89 % of the length of the tibia, both bones being hollow. In those sphenosuchids in which this ratio is known the value is less, namely 75 % in *Pedeticosaurus* (van Hoepen 1915) and 60 % in *Terrestrisuchus* (Crush 1981). *Sphenosuchus* thus seems to have had a relatively longer forelimb than in some of its relatives. The construction of the shoulder girdle is in agreement with this, in that the posterior extension of the coracoid is longer and broader than in other sphenosuchids, indicating that the ventral shoulder musculature was correspondingly well developed. The trochlear groove, although exaggerated by crushing, is deep behind the humerus and suggests a wide arc of extension of the forearm, the elbow mainly functioning as a hinge joint. Features of the shoulder girdle and humerus are unlikely to be related to seizure of prey or manipulation of food because, by comparison with close relatives, the manus was probably of small size and unsuited to grasping. *Sphenosuchus* was the largest of the known primitive crocodylomorphs, most of which are of small size, and this is probably reflected in the stronger coracoid and deltopectoral crest of the humerus. There seems little doubt that *Sphenosuchus* was quadrupedal.

The metatarsals in *Sphenosuchus* are elongated, hollow, and rather slender. Metatarsal I is weak and shorter than the others. Metatarsals II and IV are subequal (57 and 55 mm) and shorter than metatarsal III (63 mm), which is the stoutest. Metatarsal V would doubtless have been reduced also. The tendency here to reduce the metatarsus to the three central digits with the axis of the foot through metatarsal III suggests that the foot was digitigrade, although Parrish (1987) considered that crocodylomorphs, apart from *Hallopus*, were plantigrade. Chatterjee (1985) regarded the poposaurid thecodontian *Postosuchus*, with a crocodilian ankle-joint and a somewhat similar foot to that of *Sphenosuchus*, as digitigrade, although in this case the animal was probably a facultative biped. The metatarsal III: tibia ratio in *Sphenosuchus* is 49 %, whereas in *Pedeticosaurus* (van Hoepen 1915) and *Saltoposuchus* (von Huene 1921) it is 43 %, and in *Terrestrisuchus* (Crush 1981) 37.5 %. This relatively high ratio at least does not discount the possibility of digitigrady in *Sphenosuchus*, although elongation of the metatarsus has to be used with caution because of the secondary elongation which has taken place in modern crocodiles in relation to an aquatic existence (Romer 1956). *Sphenosuchus*, however, shows no sign of aquatic specialization in the known features of its anatomy. The orbits, for example, face laterally and the skull shows no sign of flattening. The secondary palate is too short, and the choanae too far forward, to imply any significant degree of crocodilian specialization in this feature; the backward elongation of the coracoid in crocodylomorphs has been suggested (Walker, 1970) as initially an adaptation for cursoriality, specifically for galloping. Parrish (1987) concluded from a consideration of the palaeoecology that the early members of the group probably occurred in more terrestrial environments than do living crocodilians. Gow & Kitching (1988) also considered that the 'Pedeticosauria' were terrestrial–cursorial.

The skull of *Sphenosuchus* is relatively large and the indications are that the animal was carnivorous. The maxillae are strong bones, armed with powerful compressed, recurved and serrated teeth. The lower jaw has enlarged canines biting into deep cavities in the anterior part of the palate, which may have housed poison glands. The more posterior teeth, however, may have been lanceolate. The supratemporal fossae are large, indicating well-developed jaw muscles. Sense organs appear to have been well developed. The nasal chamber is of large size. The orbits are of moderate size, facing laterally and somewhat forwards. There is good evidence for a keen sense of hearing, with a large tympanum and advanced otic capsule.

The holotype of *Sphenosuchus* is from the highest part of the Elliot Formation, just below the Clarens Formation. The fauna from this horizon in South Africa (Kitching & Raath 1984) includes the early mammals *Erythrotherium* and *Megazostrodon* (Gow 1986), the small cynodonts *Pachygenelus* and *Trithelodon* and the somewhat larger *Tritylodon*, fabrosaurid and heterodontosaurid ornithischians, the prosauropod *Massospondylus*, 'pedeticosaurids' and protosuchians. The early mammals were extremely small and probably nocturnal and so perhaps did not form part of the prey of *Sphenosuchus*. Possible prey species include the small cynodonts at this horizon, other sphenosuchids and protosuchians which were generally smaller than *Sphenosuchus*, and other small reptiles that existed at this time, such as sphenodontids and lizards, but which are not actually recorded at this level. The early ornithischians were generally small, about 1 m in total length, but were probably usually too agile to be caught by sphenosuchids. In addition there were the juveniles of the rather larger herbivorous cynodont *Tritylodon* and the dinosaur *Massospondylus* which attains an adult length of 4 m, on which *Sphenosuchus* might have fed. All in all, the picture of *Sphenosuchus* that emerges is that of an agile, predatory reptile.

8. COMPARISON OF THE *SPHENOSUCHUS* SKULL WITH THE MODERN CROCODILIAN SKULL

In the section that follows, the intention is to consider only those characters of the skull which unite *Sphenosuchus* with present-day crocodiles and distinguish it from thecodontians. It is not a direct attempt to establish a series of synapomorphies for the Crocodylomorpha, although it is expected that most of the features discussed will eventually prove to be such, when more complete material of the lesser-known but apparently allied forms has been collected and studied. A number of these characters have already been listed by Clark (in Benton & Clark 1988, list 1, p. 335).

Because the skull of *Sphenosuchus* is probably the best preserved of the primitive crocodylomorphs (the 'Sphenosuchia') known at present, it is hoped that such a comparison will also be useful in establishing a scale against which to measure evolutionary change in the crocodylomorph skull.

In this section the words 'crocodile' and 'crocodilian' refer only to the skulls of living forms. Most attention has been given to *Crocodylus*, *Osteolaemus* and *Alligator*, with less emphasis upon *Gavialis* because of the distortion introduced by the large size of the supratemporal fossae in that genus. A large (*ca.* 220 mm long) disarticulated skull of *Osteolaemus* has been particularly useful in this study.

Gross differences between the skull of *Sphenosuchus* and those of crocodiles lie in the higher skull of the former, with its laterally facing orbits, the more 'thecodontian' shape of the teeth, the presence of a moderate-sized preorbital fenestra, the deeper occiput, the larger supratemporal fenestrae (except in *Gavialis*), and the more upright quadrate. The jaw shape also differs, that of *Sphenosuchus* lacking the upward curve at the rear end seen in the crocodile.

The prefrontal in *Sphenosuchus*, like that of crocodiles, has a medial or descending process which met the interorbital septum but, unlike the crocodile, this ended some 8 mm above the palate. As restored, these processes are *ca.* 28 mm behind the rear ends of the choanae. The descending processes in crocodiles also meet the palatines and pterygoids at a point which, on the upper surface of the *Sphenosuchus* palate, would appear to correspond to the inward curve of the medial border of the palatine behind the palatine 'fan'. This point is about 20 mm behind the choanae, so that it may be that insufficient allowance was made for the compression of the skull when making the restoration. The expansion of the prefrontal within the orbit is larger than in most crocodiles, although the descending process of the prefrontal of *Alligator* is relatively broad. The posterodorsal process of the prefrontal of *Sphenosuchus* is lacking in modern forms. The only comparable instance of a medial process of the prefrontal in thecodontians known to me is in *Stagonolepis*, where there is a substantial process, flattened in the vertical plane, extending some way below the depression which indicates the position of the olfactory bulb, but not reaching the mid-line.

The medial processes of the prefrontals in *Sphenosuchus* appear to have acted as a transverse brace in a skull with large teeth and a vaulted palate, which is relatively taller than the modern crocodilian skull. The flattening of the typical crocodilian skull apparently brought the descending processes into contact with the upper surface of the palate and converted them into a vertical brace. It is noteworthy that the processes are particularly strong in the alligator which has a very flattened snout. The supposition of a bracing action does not appear to account for the effectiveness of a medially directed process in the early stages of its growth, but it is possible that even a small development of a dermal bone layer overlying the planum antorbitale would have helped in stiffening the skull transversely.

The postfrontal is absent in both *Sphenosuchus* and modern forms. It is usually present in thecodontians, the Proterochampsidae being an exception.

The parietals in *Sphenosuchus* are fused, with no trace of a median suture. In crocodiles both frontals and parietals are fused.

There is a moderate amount of lateral overhang of the squamosal in *Sphenosuchus* compared with the broad overhang of Recent forms. As noted earlier, there is no descending process of the squamosal at the posterior margin of the infratemporal fenestra such as usually runs down the front edge of the quadrate in archosaurian skulls. Crocodiles also lack this process. There is, however, in *Sphenosuchus* a short descending flange from the squamosal which sutures to the outside of the anterodorsal process of the quadrate. This flange also occurs in modern crocodile skulls, similarly suturing to the outside of the anterodorsal process. The interlocking junction between the squamosal and the paroccipital process (p. 19) has all the essentials of the complicated relationships seen in the crocodile, but is not as indented. In the crocodile, however, an upstanding flange from the posterior border of the quadrate (part of the secondary contact of this bone with the skull behind the otic notch) has forced its way between the descending tongue of squamosal which in *Sphenosuchus* runs down the anterior surface of the paroccipital process (figure 15), and the process itself.

In *Sphenosuchus* the quadratojugal extends all the way up the front of the quadrate and meets the squamosal at a long contact in front of the anterodorsal process, forming the entire posterior border of the lateral temporal fenestra. It probably did not contact the postorbital. The quadratojugal is likewise elongated in crocodiles, meeting the squamosal in front of the anterodorsal process in *Alligator*, *Gavialis* and *Tomistoma* (Kälin (1933, fig. 3, incorrectly captioned *Gavialis*)). In other forms, e.g. *Crocodylus*, *Osteolaemus* and *Caiman*, the quadratojugal does not reach the tip of the anterodorsal process and fails to contact the squamosal.

The foramen commonly present in archosaurs between quadrate and quadratojugal is absent in *Sphenosuchus*, as it is in crocodiles. This foramen probably transmitted an artery (Bystrow & Efremov 1940) and its loss is probably due to kinesis.

Details of the suture between quadrate and quadratojugal in *Sphenosuchus* (p. 22) are closely similar to those in crocodiles, the gavial in particular showing clearly the four alternating projections seen in lateral view. The lowest of these is a backward projection of the quadratojugal which, in crocodiles as well as in *Sphenosuchus*, overlaps the quadrate and is sutured to it, very firmly in the crocodile. Above this the edge of the quadrate projects forwards and overlaps the quadratojugal at a bevelled edge in *Sphenosuchus*. There is a similar forward projection with some overlap in the crocodile, and the contact is partly a smooth one also. Then follows a backward curve in each case and the junction is completed by a forward curve along the anterodorsal process. The details of the contact differ as between the crocodile and *Sphenosuchus* in the final two curves, and the socket in the quadratojugal which in *Sphenosuchus* receives the apex of the anterodorsal process is not present in the crocodile. The curved 'pivot' at the lower end of the quadrate is also absent in crocodiles. The essentials of the above contacts are present in other living crocodiles besides *Gavialis*, especially the two lower undulations of the suture, but the resemblance is not so obvious because of the lesser sinuosity of the curves and the failure of the quadratojugal to reach the upper end of the quadrate in some genera.

The quadratojugal probably did not meet the postorbital in *Sphenosuchus* so that this contact, which is found in several Recent crocodilian genera, is probably not a primitive character in Crocodylomorpha but has been brought about by the reduction of the lateral temporal fossa to a triangle due to the obliquity of the quadrate. Hence the contact of quadratojugal with postorbital in the poposaurid thecodontian *Postosuchus* (Chatterjee 1985) is probably (*pace* Benton & Clark 1988) a parallelism. This contact has come about in a different manner in *Postosuchus*, in which the quadrate is not greatly inclined, by the quadratojugal meeting the postorbital lower down, thus cutting off a portion of the lateral temporal fenestra at the top from the main body below. Details of the quadrate/quadratojugal suture in *Postosuchus* are not crocodilian and there is a foramen between quadrate and quadratojugal (Chatterjee 1985, p. 407), lacking in *Sphenosuchus* as noted above. The lateral overhang of the squamosal is also different from the crocodilian type in *Postosuchus*, being the posterior end of a continuous lateral ridge running from the prefrontal across the top of the orbit to the squamosal. The latter bone also has a ventral projection between quadrate and quadratojugal (Chatterjee 1985, fig. 4(b)), constituting a marked difference from the *Sphenosuchus* or crocodilian arrangement. The configuration of the lateral temporal fenestra in *Postosuchus* is therefore considered to be a parallel evolution to the crocodylomorph type.

As noted by Brinkman (1981), the quadratojugal is tall in the Middle Triassic *Gracilisuchus* and extends most of the way up the lower temporal fenestra. However, this bone is slender compared with the broader element present in sphenosuchids, and the arrangement of bones at the upper end of the fenestra differs from that in crocodylomorphs, according to Brinkman's restoration. *Gracilisuchus* also has a quadrate foramen and, according to Romer (1972b), quadrate and quadratojugal diverge dorsally to leave a space below the squamosal. The latter, however, may be the result of compression. There is little doubt that the rather elongated quadratojugal of *Gracilisuchus* is also a parallel evolution.

There is a short secondary palate in *Sphenosuchus* formed by the maxillae. The anterior tips of the vomers probably ran forwards above this in crocodilian fashion, but there was, of course, no development of the 'primitive posterior nares' (Huxley 1877) in this region in *Sphenosuchus*, since the primitive choanae are still fully exposed farther back in the roof of the vault. There is little further to indicate the beginnings of the characteristic crocodilian palate, except that the contacts of the palatines with the maxillae laterally are very low down, and the choanae are elevated in the roof of the mouth, so that the development of shelves from the lateral part of the palatines and a backward extension of the secondary palate on the maxillae would place the primitive choanae in the correct position.

The palatine 'fans' of *Sphenosuchus* have virtually disappeared in the crocodile, so that they are represented by the contacts (on the upper surface of the palate) of the palatines with the vomers and pterygoids. This contact has only a very small amount of overlap on the vomer, but the palatine slopes up medially and the suture is slightly convex medially also, representing relics of the *Sphenosuchus* condition. There is also a median dorsal trough in the crocodile, made up of the vomers and pterygoids, showing a marked resemblance to that of *Sphenosuchus*.

The ascending process of the palatine in the crocodile which, along with the pterygoid, meets the descending process of the prefrontal, probably corresponds to the inward swing of the palatine over the pterygoid behind the 'fan' in *Sphenosuchus*, being an exaggerated version of this contact. It has probably developed in the crocodile in response to the contact of the prefrontal with the upper surface of the palate. The curving ridge on the lateral surface of the palatine which runs up this ascending process in many crocodilian skulls may perhaps correspond to the curving ridge on the upper surface of the *Sphenosuchus* palatine, or it may represent the inner margin of the planum antorbitale.

The ectopterygoid of *Sphenosuchus* is similar to that of the crocodile in general form and in the disposition of its outer contact in an arc running from posterodorsal to anteroventral, but it is a shorter element in *Sphenosuchus*. This articulates only with the jugal and lacks the strong contacts seen in the crocodile, the ectopterygoid of which has an extensive junction with the maxilla and also runs some way up the inside of the postorbital. Also the outer contact in *Sphenosuchus* is divided into two parts, unlike the crocodile. The strong ectopterygoid in the crocodile presumably helps to compensate for the failure of the palatine to act as a brace to the lateral side of the skull.

The pterygoids of *Sphenosuchus* have medial pterygoid flanges. These are larger than those of modern crocodiles (although the flanges are quite large in *Alligator*), but are closely comparable to those of *Pelagosaurus*. The quadrate in the crocodile is strongly inclined forwards and inwards and the rear parts of the pterygoids and the ectopterygoids are pulled strongly downwards with respect to the lateral edge of the skull and the palate. This has produced a strong downwards and forwards tilt to the quadrate–pterygoid arch, compared with the primitive condition in archosaurs. This trend has progressed to some extent in *Sphenosuchus*, but the quadrate is only moderately inclined forwards and inwards. The inclination from the vertical is about 18° in *Sphenosuchus*, measured between a line tangential to the most posterior tip of the head and the rear of the condyles, and a line perpendicular to the generalized lower edge of the skull, as seen in a lateral view. In modern crocodiles this angle, which increases with age, may be as much as 55°. The pterygoids do not descend as far in *Sphenosuchus* as in modern forms but, as restored, it would have been possible to see through the skull above them and below the jugals in a lateral view as in most modern forms, and they would have been clearly visible in occipital view. The quadrate–pterygoid arch in *Sphenosuchus* is moderately inclined.

However, the quadrate and pterygoid are not fused to the braincase in *Sphenosuchus* as they are in living crocodiles, although the quadrate ramus of the pterygoid was in the correct relative position, with its posterodorsal apex lying just lateral to the prootic flange below the trigeminal foramen. In modern crocodiles there is a thin skirt of basisphenoid which projects backwards from beneath the quadrate–pterygoid arch and forms a lateral wall to the lateral eustachian canal. This is represented in *Sphenosuchus* by the ventrolateral wall of the large basipterygoid process which projects backwards in the corresponding position (figure 18) and which may have been in contact with the pterygoid. In *Sphenosuchus* this region was widely separated from the lateral eustachian groove.

Sphenosuchus appears to have had an epipterygoid, a bone not present in the modern crocodilian skull.

The quadrate in *Sphenosuchus* shows the characteristic crocodylomorph condition, which distinguishes it from that of other archosaurians. The quadrate head has moved forwards beneath the squamosal so that there is a long overhang behind it. It no longer contacts the opisthotic (paroccipital process) medially, as it does in at least some thecodontians (as noted earlier), but instead the head has gained a small contact with the prootic; there is also a small forward projection of the pterygoid wing which rests in a groove in the prootic. This type of quadrate contact is unique in reptiles; there is some apparent similarity to turtles in that the quadrate meets the prootic, but in turtles the quadrate is broadly sutured medially to both opisthotic and prootic and has not moved forwards at its head, as it has in crocodiles. Thus the two conditions are fundamentally different.

However, the quadrate in *Sphenosuchus* is very primitive in the small size and posterior position of the prootic contact. In modern forms the quadrate is much more inclined both forwards and medially. As a result, the proximal end has very extensive sutural contacts with the braincase, including a meeting with the laterosphenoid and prootic at an irregularly oval facet which also includes the parietal. This facet corresponds to the low protuberance above the trigeminal foramen in *Sphenosuchus* shared by laterosphenoid and prootic. This protuberance is well separated from the quadrate in *Sphenosuchus*, partly because of the more upright quadrate and partly because of the more elongated prootic in this form.

Sphenosuchus is also more primitive than modern

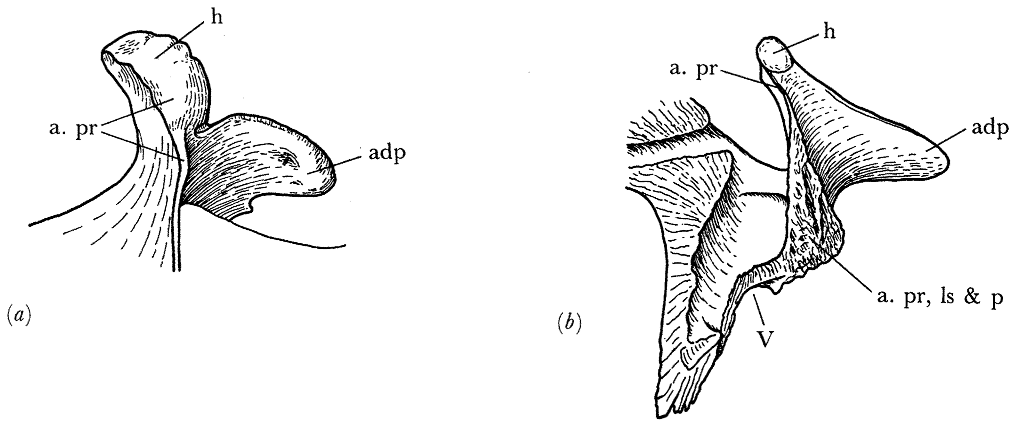


Figure 54. Comparison of proximal ends of left quadrates of (*a*) *Sphenosuchus*, slightly restored, magn. × 1.5; (*b*) Osteolaemus, magn. × 1. Anterodorsomedial views.

forms in that the articulations for the quadrate head on the braincase are situated more laterally, on the outside of the lateral wall of the temporal canal. The articular area is also continuous from squamosal on to prootic. In modern forms the quadrate head has intruded into the temporal canal, slightly separating the primary squamosal socket from the prootic articular area in most cases; the old lateral wall of the temporal canal has, in fact, disappeared in the modern crocodile. The medial wall to the squamosal socket seen in *Sphenosuchus* has gone, and the most posterior section of the prootic contact of the quadrate in the crocodile now lies in the floor of the temporal canal, so that it seems that the lateral edge of the prootic has retreated medially. The quadrate has intruded so far medially and anteriorly in modern forms that it meets the parietal above the prootic in the more anterior section of its medial contact. The anterior temporal foramen is between parietal, squamosal and quadrate with the latter forming the threshold in *Crocodylus* and *Osteolaemus*. The same is true of *Gavialis*, but the foramen is very much drawn out mediolaterally. (In *Alligator* and *Caiman* squamosal and parietal meet above the top of the quadrate, so that the anterior temporal foramen is between parietal and squamosal only.) Prootic begins just within the mouth of the foramen in these forms. In *Sphenosuchus* on the other hand: (*a*) the anterior temporal foramen is entirely between prootic and squamosal, with prootic forming the threshold; (*b*) the squamosal is more deeply inserted into the braincase than in thecodontians or in crocodiles, and extends forwards as a blunt 'V' between prootic and parietal, and (*c*) the prootic is unreduced as in thecodontians. In these last three features conditions in *Sphenosuchus* are more comparable to those in birds than in crocodiles.

In *Sphenosuchus* the squamosal or 'true' head of the quadrate is large and clearly recognizable as the original head (figure 54) in comparison with other archosaurs. The comparison of the various parts of the proximal end is clarified by the observation that the concave area between anterodorsal process and pterygoid wing, which in *Sphenosuchus* faces forwards, has been bent backwards at its upper end in the modern crocodile so that it now faces more or less dorsally. This concavity occupies the rear part of the floor of the supratemporal fossa in crocodiles (but may be partly covered, as in the alligator) and runs back into the mouth of the anterior temporal foramen. It is thus clear that the original head of the quadrate is much reduced in modern forms, as it constitutes only that portion of the proximal end which lies at the posterior end of the concave area, i.e. that portion which hooks back above the otic incisure, and in older animals may form only the posterior extremity of this portion. The upper surface of the head is smooth, covered by a thin coating of cartilage, and fits into a shallow socket beneath the squamosal. This small and inconspicuous socket represents the substantial squamosal socket of *Sphenosuchus*.

The quadrate head in both the crocodile and *Sphenosuchus* comes very close to a peg of the opisthotic which fits into a socket in the squamosal. It does not, however, touch the opisthotic in either case (except possibly in some old individuals in the case of modern forms). In the present-day form a thin ledge of prootic, over which the stapedial artery passes, forms the base of the postquadrate foramen and intervenes on the medial side between quadrate head and opisthotic. This ledge is the attenuated representative of the prootic buttress of *Sphenosuchus* (cf. §5*c*).

The temporal canal is present in the modern crocodilian skull with essentially the same morphological relationships as in *Sphenosuchus*, running from anterior temporal foramen to post-temporal fenestra, with postquadrate foramen entering it behind the quadrate head. The bones surrounding the canal differ somewhat in detail, but the squamosal forms a substantial part of the roof in each case, and the prootic/opisthotic/epiotic relationships are basically the same in its floor.

The above points are adduced to demonstrate that the true head of the quadrate is essentially in the same position in the skull in both *Sphenosuchus* and living crocodiles. It has not moved any further forwards in the modern form than in *Sphenosuchus*, in fact. The long posterior overhang of the squamosal seen in the modern form is basically that of *Sphenosuchus*, except that it has established secondary contacts with the quadrate which are absent in the fossil. The relationship of the

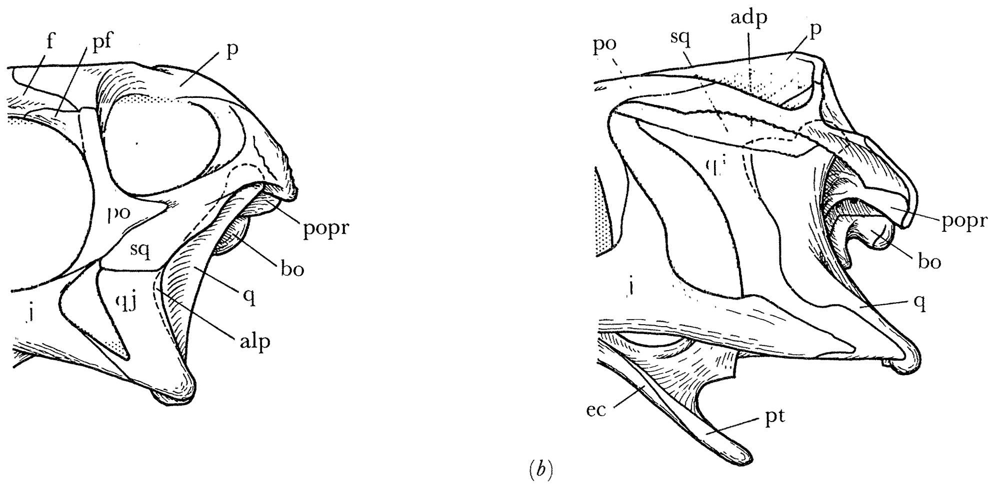


Figure 55. Comparison of quadrates and adjoining bones in (*a*) *Stagonolepis*, magn. × 0.45; *Sphenosuchus*, magn. × 0.7. Profile of quadrate indicated in broken lines. On (*b*) the overhanging part of the squamosal is visualized as having been partly cut away.

outer end of the squamosal to the paroccipital process is closely similar in each case, save that (as noted above) the quadrate has intruded a tongue of bone in living forms.

The great inclination of the quadrate in the modern crocodilian skull has thus largely been brought about, not by a moving forward of the head beyond that seen in *Sphenosuchus*, but by the geniculation of the bone near to its upper end. The quadrate has, so to speak, 'doubled up' on itself, and it is the 'knee-joint' which has moved forwards, not the head, and which has resulted in the telescoping of the upper end of the lateral temporal fenestra and its reduction to a triangle. The braincase, particularly the prootic, has also been shortened; this presumably is the 'verticalization' referred to by Tarsitano (1985). I do not agree with him, however, that the basioccipital has been 'verticalized' in *Sphenosuchus*, since the bone is elongated in this form. The strong geniculation of the modern crocodilian quadrate appears to be due to the restriction of the tympanum to the dorsal end and the deepening of the otic incisure (around which the bone is bent) compared to the generalized condition as seen in *Sphenosuchus* (see §5*c*).

The anterodorsal process in present-day forms has attained the same level as the head proper, mainly apparently because of the reduction of the latter. Owing to the greater inclination of the quadrate, and partly perhaps because of the geniculation of the upper portion of the bone, the apex of the anterodorsal process in modern forms makes a more acute angle than in *Sphenosuchus*. The origin of the anterodorsal process is discussed below.

In view of the differences between the modern crocodile and *Sphenosuchus* with respect to the medial contacts of the quadrate, it is not easy to decide to what the prootic contact of the head in *Sphenosuchus* corresponds in the skull of the present-day form. On a straightforward comparison it would seem to be equivalent to the contact between the medial side of the proximal end and the prootic, which runs anteromedially across the floor of the temporal canal and then disappears beneath the parietal. The initial portion of this prootic contact is usually on the medial side of the head (as defined above) and can be regarded as part of it. It is thus comparable to the prootic contact of the head in *Sphenosuchus*. Its anterior limit in the crocodile is, however, indefinite since it continues to the prootic/laterosphenoid contact area, here regarded as part of the pterygoid wing of the quadrate and not of the head. As observed above, this initial prootic contact in the crocodile is considerably more medial than in *Sphenosuchus*. It is possible also that the small projection at the base of the pterygoid wing in *Sphenosuchus*, which fits into the shallow groove on the prootic, corresponds to the irregular prootic/laterosphenoid contact of the modern form. The achievement of such a contact would have been facilitated by the shortening of the prootic and the geniculation of the proximal end of the quadrate in the modern animal.

'Crest B' of Iordansky (1964) is well represented on the *Sphenosuchus* quadrate and appears to have been quite similar to this crest as developed on the quadrate of *Crocodylus acutus*. Other differences from the crocodilian quadrate lie in the greater development of the pterygoid wing in *Sphenosuchus*, the lack of secondary contacts with the skull behind the otic notch and medially with the subcapsular buttress, and the lack of a perforation for the siphonium. In addition, the quadrate is not pneumatized in the fossil.

Origin of the anterodorsal process

As already noted (p. 84), the anterodorsal process of the quadrate in *Sphenosuchus* shows a marked resemblance in its relationships to adjoining bones to the rounded projection which lies halfway up the lateral edge of the quadrate in the late Triassic thecodontian *Stagonolepis* (Walker 1961) (figure 55). In each case the quadratojugal is broad, with a nearly horizontal contact with the squamosal. The anterolateral projection of the quadrate is at the straight squamosal/quadratojugal contact in *Stagonolepis*; its thickened and rounded anterior edge fits into a groove at the back of the quadratojugal, just below the contact of the latter bone with the squamosal. The rounded edge continues above this for a little way, and then becomes thin. In *Sphenosuchus* likewise the anterodorsal process projects forwards at the straight squamosal/quadratojugal contact. Below the squamosal contact its apex fits into a socket in the rear edge of the quadratojugal. This socket continues upwards and backwards beneath the squamosal.

In *Stagonolepis* the quadrate head is rounded and is separated from the anterolateral projection by a thin edge which fits into a shallow groove below the rear edge of the squamosal. The outer wall of this groove descends a little further than the inner, forming a low posteroventral projection. In *Sphenosuchus* the head of the quadrate is also rounded. The anterodorsal process begins as a thin dorsal edge (figure 12*e*) and then thickens distally. The outer side of its socket below the squamosal descends as a flange which sutures to the outer side of the process, reaching its greatest depth opposite to the thin part of the upper edge.

In *Stagonolepis* the upper edge of the quadratojugal is arched dorsally (Walker 1961, figure 32, plate 10) and the squamosal overlaps its outer surface. In *Sphenosuchus* (figure 7*h*) the upper edge of the quadratojugal is also arched dorsally, but more gently, fitting into a slot below the squamosal. The outer wall of this slot descends farther than the inner wall.

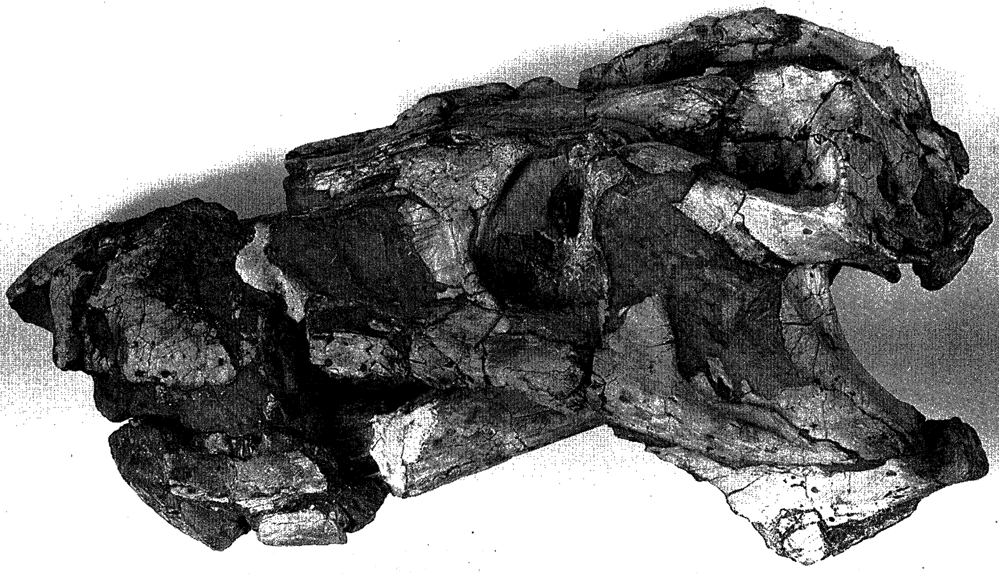
These detailed resemblances strongly suggest that the anterodorsal process of the *Sphenosuchus* quadrate has originated by the dorsal migration of a projection on the lateral edge of the bone similar to that of *Stagonolepis*, taking with it the quadratojugal/squamosal contact. In this way it seems that the quadratojugal extended dorsally until it occupied the entire posterior margin of the lateral temporal fenestra, while the descending process of the squamosal was reduced to vanishing. However, the configuration of the temporal fenestrae in *Stagonolepis*, with the supratemporal opening facing predominantly laterally and the lower opening reduced, is an unlikely one to provide a starting point for this change, and it seems more probable that the ancestral condition for the state of affairs seen in *Sphenosuchus* would have been a skull with a dorsally facing supratemporal fenestra and a laterally facing infratemporal opening, the quadrate being upright or not greatly inclined forwards. The similarity in these bone contacts between *Stagonolepis* and *Sphenosuchus* is further evidence of the close relationship between stagonolepidids and sphenosuchids.

As noted earlier, the crocodylomorph anterodorsal process is unlikely to be the homologue of the avian 'squamosal head' of the quadrate.

Comparing with the modern crocodilian quadrate, it is clear that the anterodorsal process in *Sphenosuchus* has already reached its highest dorsal position in relation to the head of the bone. Subsequent change has resulted in the reduction of the head as already noted, so that process and head are on the same level in living forms. The greater inclination of the quadrate and its tight suturing to adjoining bones no doubt help to brace the jaw articulation and enable the quadrate to resist the forces tending to compress and rotate it. From a mechanical point of view the triangular shape of the lateral temporal fenestra in the crocodile is more stable than the rhomboidal shape seen in *Sphenosuchus*, and the closure of the otic notch adds further strength to the skull.

The braincase in *Sphenosuchus* does not differ greatly in overall proportions from that of a modern crocodile, using as a standard a skull of *Crocodylus acutus* sectioned along the mid-line, but the braincase is greatly shortened ventrally in the modern form, especially in the basisphenoid. The parietal and, especially, the supraoccipital are thicker, and the braincase floor also is thickened or prolonged ventrally in the crocodile (Romer 1956; Tarsitano 1985). The cranial cavity is thus more tubular than in *Sphenosuchus*. The extensive pneumatization of the basisphenoid around the carotid pillar is lacking in living forms. Other differences in the pneumatic cavities have been noted in §5*c*. Differences due to the development of secondary contacts of the quadrate with adjoining bones, and in the passages adjacent to the quadrate head, have been outlined above. The subcapsular buttress (p. 85) is very well developed in present-day forms, blocking up most of the old cranioquadrate passage. This arises from the cartilaginous subcapsular process (Shiino 1914) of the embryo. The development and ossification of the subcapsular process has never been fully studied, so that the processes that lead to the enclosure of the vagus group of nerves and the internal carotid artery are unknown. From previous accounts (Parker 1883; de Beer 1937; Müller 1967; Bellairs & Kamal 1981) and from comparison with the braincases of thecodontians such as *Stagonolepis* (Walker 1961, 1985), it seems probable that the subcapsular process ossifies as the anterolateral and ventral parts of the 'exoccipital'. The division dorsally between the resulting subcapsular buttress and opisthotic is probably at the level of the cranioquadrate passage. The external 'vagus' foramen probably lies between subcapsular buttress and exoccipital s.s., while the internal carotid artery passes through its ventral tongue. In *Sphenosuchus* the buttress was only moderately developed, forming a prominent ridge on the exoccipital but not enclosing the IXth and Xth nerves, the lateral cranial sympathetic trunk or the internal carotid artery. The buttress is pneumatized in modern crocodiles but not in *Sphenosuchus*.

The basioccipital in the crocodile lacks the sheathing of its anterior end by basisphenoid and otic bones which is seen in *Sphenosuchus*, although the descending tongue of the subcapsular buttress is very similar in each case. It is considered that the originally widely separated anterior and posterior ventral portions of the basisphenoid seen in *Sphenosuchus* have been approximated, compressed and fused together in living forms (§5*c*). The basipterygoid facets have disappeared in Recent forms, but their position may be indicated (in *Osteolaemus*) by a pair of descending tongues of bone



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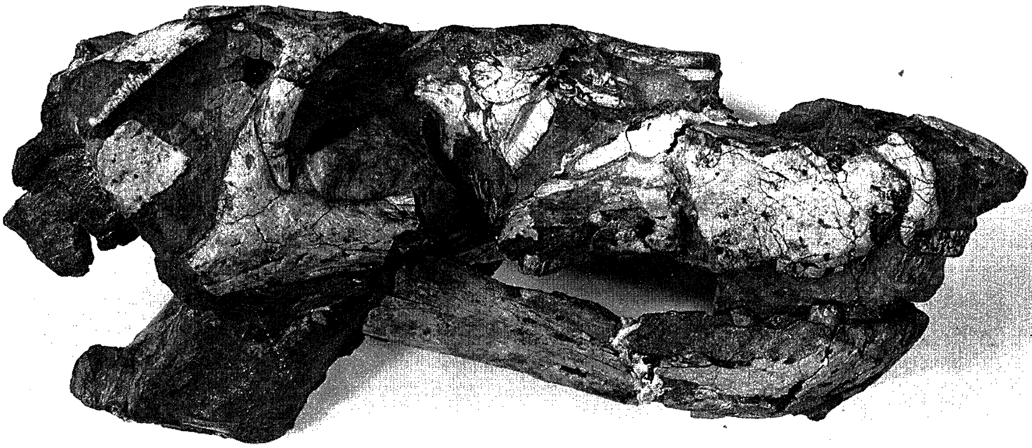

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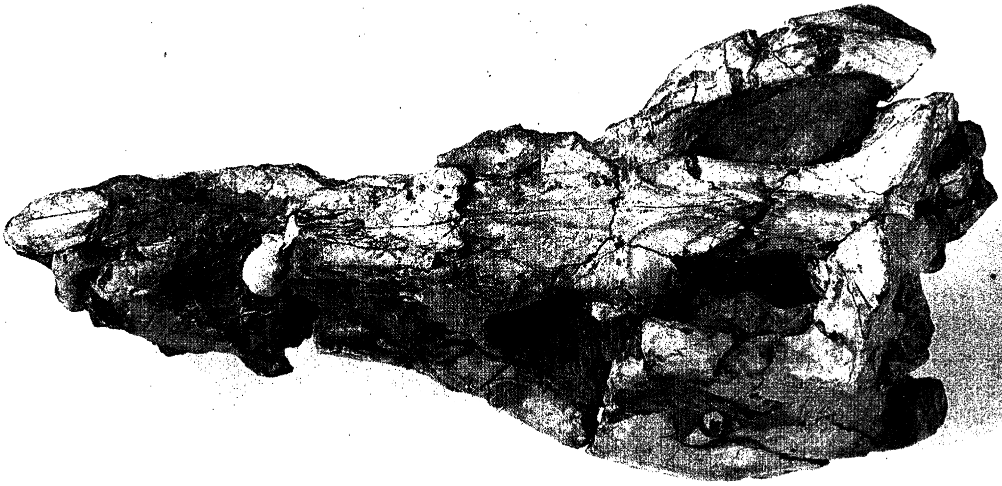

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Figures 56–58. For description see p. 110.

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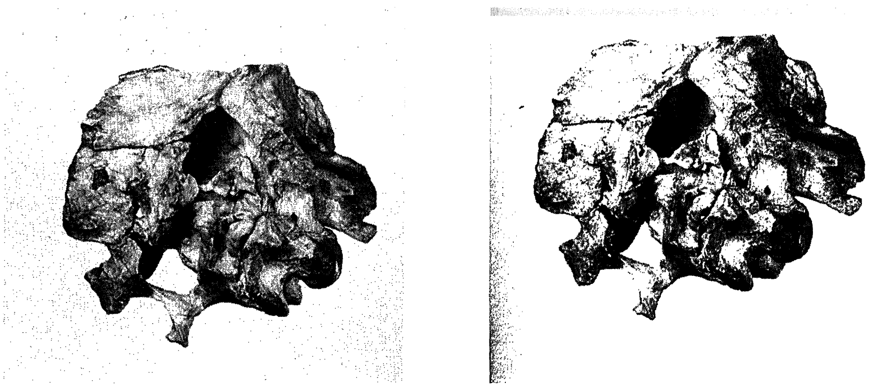

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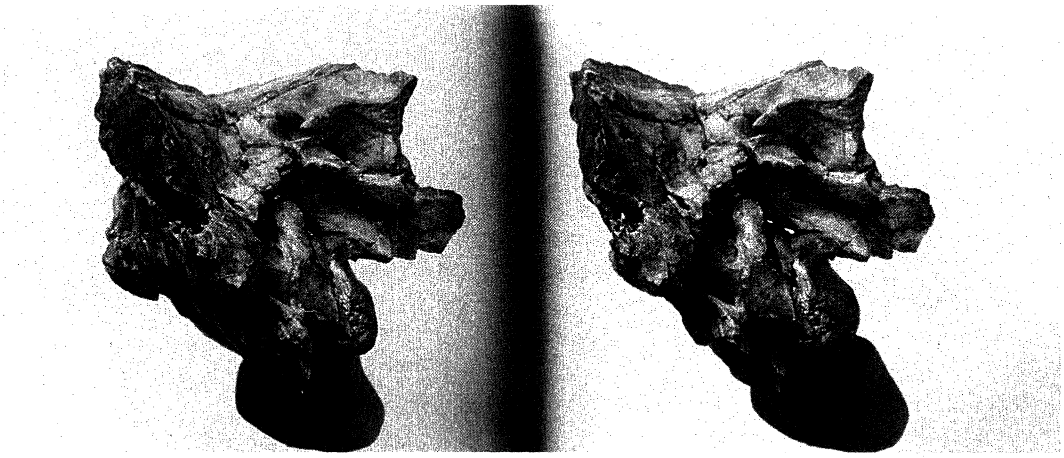

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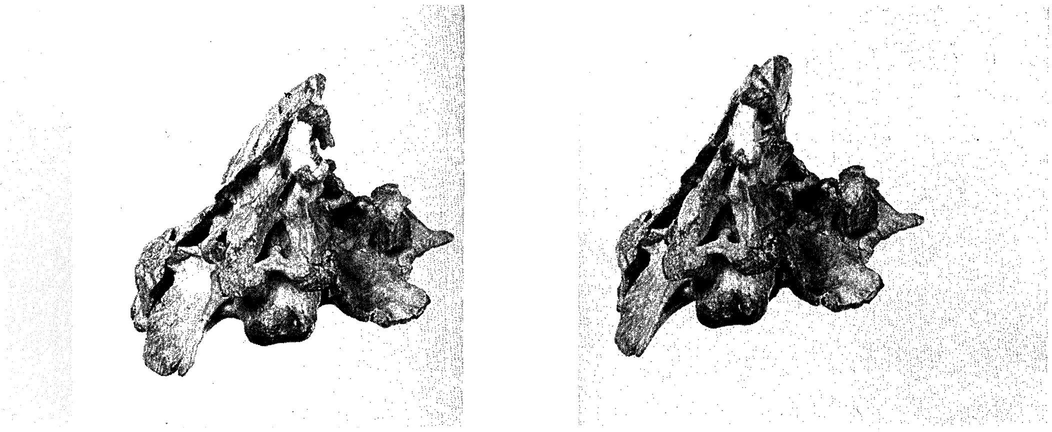

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Figures 59–62. For description see p. 110

situated anteroventrally on the basisphenoid, in front of the anterior rim to the median eustachian opening. The bridge between the laterosphenoid and the rostrum of the basisphenoid usually seen in the crocodilian skull is absent in *Sphenosuchus*.

The otic capsule of the fossil is very similar to that of the living form; resemblances and differences have been dealt with in §5*e*. Sutures between prootic, laterosphenoid and basisphenoid adjacent to the trigeminal foramen conform to the crocodilian pattern in *Sphenosuchus*. The prootic is of normal size in *Sphenosuchus* but considerably reduced in modern forms. The prootic–basisphenoid flange is present also in crocodiles, but partly interrupted by the pterygoid. An important difference is that the exoccipitals do not meet above the foramen magnum in *Sphenosuchus*, whereas this is characteristic of Crocodyliformes (*sensu* Benton & Clark 1988). The supraoccipital shape is reversed in the crocodilian skull, the bone being triangular with apex downwards; in *Sphenosuchus* it is inverted shield-shaped. In *Sphenosuchus* the post-temporal fenestrae are more medially placed than in thecodontians in which these openings are well developed, but not so medially located as in typical crocodiles. The laterosphenoid is elongated in the fossil.

Relationships between dentary, splenial, angular and surangular are closely similar in *Sphenosuchus* to those in crocodiles, with the exception of the coronoid. However, these relationships are also basically crocodilian in several thecodontians including *Stagonolepis* (Walker 1961) and *Ornithosuchus* (Walker 1964) and are evidence only of a primitive archosaurian pattern. The long splint-like coronoid contrasts with the short element of modern forms but is found in Mesozoic marine crocodilians, e.g. *Pelagosaurus* (Eudes-Deslongchamps 1864), *Steneosaurus* and *Metriorhynchus* (Andrews 1913), also in the Middle Triassic thecodontian *Chanaresuchus* (Romer 1971).

The prearticular has been lost in crocodiles, but was of substantial size in *Sphenosuchus*. The angular reaches to the posterior end of the jaw in living forms but not in the fossil. The articular of *Sphenosuchus* differs from the modern type in the shortness and downward inclination of the retroarticular process, the considerably larger size of the foramen aërum, the presence of a foramen leading forwards out of the pneumatic cavity, and the presence of an internal ascending process.

9. THE VALIDITY OF THE CROCODYLOMORPHA AS A TAXONOMIC UNIT

The concept of the Crocodylomorpha as an order of greater scope than the historic order Crocodylia was put forward (Walker 1968, 1970) to accommodate certain forms, then called 'pedeticosaurids', which showed certain crocodilian features but which were difficult at that time to regard as crocodiles in the generally accepted sense of the term.

The diagnosis of the Crocodylomorpha given in 1970 was unsatisfactory in many respects, not least because it omitted certain critical features which only became apparent upon further preparation of the specimen of *Sphenosuchus*. Also, as has been pointed out by other workers, some of the characters listed, such as the crocodilian ankle joint, also occur in thecodontians. Others, such as the quadratojugal, are valid but were incorrectly defined.

The most important character which, it is believed, will prove to distinguish crocodylomorphs from other archosaurs is the nature of the quadrate articulation with the braincase. This has been described in detail for *Sphenosuchus* and it is unnecessary to elaborate on it here. This forward and inward movement of the quadrate head was unsuspected until the braincase had been prepared, so that the order Crocodylomorpha was proposed without the knowledge of this key character. The quadrate as a whole is not greatly inclined in *Sphenosuchus*, so that the change in position of the quadrate head relative to the braincase was not obvious from the exterior. The skulls of sphenosuchids, which on the whole are not well known, tend to be superficially similar to those of thecodontians and unlike those of typical crocodiles in lacking flattening, hence the tendency to deny the relationship. However, this character of the quadrate head is found in typical crocodiles and in no other group of reptiles (the turtle skull is not comparable), and is found also in *Sphenosuchus*. Furthermore, as shown in §8, the true head of the quadrate is in essentially the same position in the modern crocodile as it is in *Sphenosuchus* and has not moved any further forwards in the modern form than it has in the fossil.

The principal advantage of moving the quadrate head forwards would appear to be that of protection for the tympanum beneath the skull roof. Geniculation of the upper part of the bone, which has already

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Figures 56–58. *Sphenosuchus acutus* Htn. The skull as received (magn. × 0.75).

Figure 56. Left side.
Figure 57. Right side; pieces with right quadrate and articular region of right lower jaw omitted.
Figure 58. Upper view.

Figures 59–62. *Sphenosuchus acutus* Htn. Stereopairs of the 'braincase piece' (*ca.* magn. × 0.8).

Figure 59. Right side. The paroccipital process is incomplete.
Figure 60. Left side with 'supraoccipital piece' removed.
Figure 61. Anterolateral view of left side.
Figure 62. Lower view.

occurred in protosuchians (*Orthosuchus*, Nash 1975; *Lesothosuchus*, Whetstone & Whybrow 1983; *Baroqueosuchus*, Busbey & Gow 1984) is an advance on the sphenosuchid condition and would seem to have two main advantages: (*a*) that of tucking the tympanum (which was still large in protosuchians) still further under the skull roof; and (*b*) that of increasing the medial area of contact of the quadrate with the braincase so that it meets the laterosphenoid as well as the prootic. Geniculation appears to be a consequence of flattening.

The nature of the quadrate head articulation in *Hesperosuchus* is unknown, but the braincase is very similar to that of *Sphenosuchus* (personal observations and preparation). In *Pseudhesperosuchus* (Bonaparte 1971) the squamosal has a long posterior overhang which suggests conditions as in *Sphenosuchus*. The same is true of *Terrestrisuchus* (Crush 1984). Crush does not deal with this question, but his reconstructions show the quadrate head placed well forwards along the paroccipital process. Personal examination of the material confirms the closeness of the relationship between *Terrestrisuchus* and *Sphenosuchus*. *Dibothrosuchus* is similar to *Sphenosuchus* in this character (Wu 1986), but is more advanced in that the quadrate is fused to the prootic. The squamosals of *Saltoposuchus* are so similar to those of *Terrestrisuchus* and *Sphenosuchus* that a similar position for the quadrate head can be inferred.

The otic capsule in crocodylomorphs also is advanced over those which are known in thecodontians. These take several forms. There is the type shown by *Euparkeria* (Cruickshank 1971, and personal observations) and *Chasmatosaurus* (Cruickshank 1972; Gow 1975), which is very primitive and basically similar to that of *Sphenodon*, and presumably represents the ancestral archosaurian pattern. The fenestra ovalis is separated from the metotic foramen by a strong pillar of the opisthotic; the metotic foramen is set deeply behind this pillar. The foramen perilymphaticum faces posteromedially and its inner margin is incompletely ossified.

Somewhat different from this is the type displayed by *Erythrosuchus* (von Huene 1911*a*, and personal observations). Fenestra ovalis and metotic foramen are separated by a thin lamella, and are set in a groove. There is no sign of a perilymphatic foramen in B.M.N.H. R 3592 and this must have lain far medially and was probably completed in cartilage. The phytosaurian pattern (von Huene 1911*b*; Case 1928; Camp 1930; Chatterjee 1978; and personal observations) is rather similar to that of *Erythrosuchus*, except that the separating lamella may form an external crest. Camp (1930) describes and figures a slender perilymphatic canal connecting the lagenar region with the metotic foramen. This perforates the opisthotic but appears to be medially placed. The lagena 'was not elongate' (Camp 1930), or was a 'simple sac' (Case 1928).

The braincase has been described by Bonaparte (1975) in the case of *Lagosuchus*. It appears to be somewhat similar to that of *Lewisuchus* (Romer 1972*c*). These forms also seem to be rather similar to *Sphenodon* in the braincase, but the specimens pose difficulties of interpretation.

The braincase of *Postosuchus* (Chatterjee 1985) seems basically similar to the erythrosuchid or phytosaurian type, but Chatterjee states: 'Dorso-laterally, the suture of basioccipital–basisphenoid is excavated into a pair of pockets: the cochlear process for the reception of the elongated lagenae'. This statement is difficult to understand as it seems to refer to an external feature, and requires further substantiation before it can be accepted that the lagena is elongated in *Postosuchus*.

In none of the above forms (with the possible exception of *Postosuchus*) is the lagena elongated; a perilymphatic loop formed by the opisthotic does not appear to be developed; the perilymphatic foramen is medially placed and/or incompletely ossified, and a subcapsular buttress is not present. Only the stagonolepidids among those thecodontians known at present provide an approach to the crocodilian condition. In *Stagonolepis* itself (Walker 1985) the opisthotic loop is present; the crista interfenestralis, however, is a strong bar; the foramen perilymphaticum is fairly large, facing downwards and backwards and only slightly outwards; there is a moderate development of a ridge representing a subcapsular buttress, which projects farther laterally than the crista interfenestralis. The vagus nerve was not enclosed by the buttress; the lagenar region is incompletely preserved but does not appear to have been significantly elongated. Basisphenoid partly conceals prootic in front of the otic opening as in *Euparkeria*. The crista interfenestralis in *Desmatosuchus* (Case 1922) seems to have been rather stronger than in *Stagonolepis*, but the details of the capsule are unknown.

The crocodylomorph otic capsule, as seen in *Sphenosuchus* and typical crocodiles, is characterized by an elongated tubular cochlear (lagenar) recess mainly formed by prootic and opisthotic, which bones have a considerable extension below the fenestra ovalis, and which form an external cochlear prominence. The lagenar region s.s. at the base rests largely (*Sphenosuchus*) or partly (modern crocodiles) in the basioccipital. The crista interfenestralis is a slender bridge and there is a large foramen perilymphaticum enclosed by a loop of opisthotic; this perilymphatic loop lies in a vertical plane. The perilymphatic sac or recessus scalae tympani is large, laterally placed and enclosed posteriorly by a subcapsular buttress forming the posterior border of a fenestra pseudorotunda. The subcapsular buttress is more prominent than the crista interfenestralis. In advanced forms nerves IX–XI and the internal carotid artery are enclosed by the subcapsular buttress.

The otic capsules of *Pseudhesperosuchus* and *Saltoposuchus* are unknown. That of *Dibothrosuchus* has not been described but appears to be closely similar to that of *Sphenosuchus* (Wu 1986, fig. 4A); the nerves of the vagus group are apparently not included within the subcapsular buttress. In *Terrestrisuchus* the capsule is also closely similar to that of *Sphenosuchus* (Crush 1984, and personal observations). Crush's text figure 4D, E shows the subcapsular buttress as continuous with the cochlear recess portion of the opisthotic, which can hardly have been the case. Unfortunately, specimen P.65/67, on which this figure is based, is now missing.

Specimen P.47/22, right side, shows a matrix-filled foramen entering behind the subcapsular buttress, suggesting that the vagus nerve was enclosed in this form. The otic capsule of *Hesperosuchus* is incompletely preserved, but from personal observation and preparation it is evident that, again, the structure was very close to that of *Sphenosuchus*.

Some of these features, such as the subcapsular buttress, are probably found in some dinosaur groups (Walker 1985), and an elongated lagena has been fairly widely reported in dinosaurs, but the precise combination of features which characterize the crocodylomorph type of capsule has not been described in any dinosaur. These features do not necessarily occur in combination, however. In the sauropods, such as *Brachiosaurus* (Janensch 1936*b*) the lagena is elongated, but there is no subcapsular buttress; the foramen perilymphaticum (Janensch's 'fenestra rotunda') faces posteromedially and its inner margin is incompletely ossified. The otic capsule is thus partly advanced and partly primitive. In the ornithopod *Hypsilophodon* (B.M.N.H. R 194) the lagena is somewhat elongated and the vagus nerve was probably diverted back through a subcapsular buttress. However, the perilymphatic loop, if one was present, seems to have been sheet-like and disposed mediolaterally and the foramen perilymphaticum presumably faced downwards and backwards and was probably small. *Zephyrosaurus* (Sues 1980; Walker 1985) appears to have been similar.

The elaboration of the otic capsule displayed by crocodylomorphs is probably connected with the forward and inward movement of the head of the quadrate as part of a general improvement in hearing structures, and denotes a significant advance over the conditions seen in thecodontians, and probably also in dinosaurs.

In 1970 the quadratojugal of *Sphenosuchus* was not fully known and it was thought (Walker 1970) that it was limited to the lower corner of the lateral temporal fenestra. In later preparation the upper half of the right quadratojugal was fortunately discovered lying *in situ* and it was clear that the bone extended all the way up the quadrate to meet the squamosal in crocodilian fashion. In *Pseudhesperosuchus* (Bonaparte 1971) the quadratojugal is similar in shape and extent to that of *Sphenosuchus*, but it appears to have been displaced laterally in the holotype leading to the appearance of a foramen between it and the quadrate. The bone is incompletely known in other sphenosuchids, but appears to have been similar to that of *Sphenosuchus*. In the case of *Terrestrisuchus* it was similarly reconstructed by Crush (1984) who states that its dorsal edge 'buttressed under the squamosal'. In *Pedeticosaurus* the lower parts only of the quadrate and quadratojugal are preserved (van Hoepen (1915), and casts), and their strong inclination has been cited by Bonaparte (1972) as part of his evidence for the supposed protosuchian nature of *Pedeticosaurus*. None of the points cited by Bonaparte are in fact diagnostic, and the lower parts of the quadrate and quadratojugal are quite strongly inclined in *Sphenosuchus* also. Wu (1986) states that the quadratojugal did not meet the squamosal in the case of *Dibothrosuchus*. This, however, is open to question because only the lower part of the bone is preserved, and this situation was thought to obtain in *Sphenosuchus* until the right supratemporal fossa was prepared. A quadratojugal was described for *Saltoposuchus* by von Huene (1921); Crush (1984) regards this as a left quadrate which is unlikely as the left quadrate is unmistakeably present already on the same block. From personal examination I believe the bone to be the rear half of the left parietal.

The dorsal extension of the quadratojugal in crocodylomorphs appears to be correlated with the dorsal migration of an anterolateral process of the quadrate to form an anterodorsal process. An important point, as noted in §8, is that the anterodorsal process has already reached its highest position in *Sphenosuchus* and subsequent change has resulted in reduction of the head of the quadrate so that, in typical crocodiles, process and head are on the same level.

An anterodorsal process similar to that of *Sphenosuchus* occurs on the quadrates of *Saltoposuchus* and *Terrestrisuchus* (personal observations). The quadrate is insufficiently preserved or described in the remaining sphenosuchids for one to be able to state positively that the process is present, but there is no reason to doubt this.

Thus in four key cranial characters *Sphenosuchus*, and with little doubt its allies, have already attained the typical crocodilian condition. These features are: (*a*) the position of the primary head of the quadrate; (*b*) the structure of the otic capsule; (*c*) the nature of the quadratojugal; and (*d*) the formation of an anterodorsal process on the quadrate.

In 1970 little definite evidence for the crocodilian nature of *Hesperosuchus* and *Saltoposuchus* could be adduced, apart from certain resemblances to *Sphenosuchus*, although the crocodilian nature of the coracoid of *Hesperosuchus*, first recognized by Dr K. A. Kermack, was pointed out (Walker 1970, p. 351). I have since had the opportunity of examining the material of *Hesperosuchus* in New York, and subsequently of borrowing and further preparing part of it, by the courtesy of Dr Eugene Gaffney. The left 'premaxilla and maxilla' (Colbert 1952, fig. 5) is, as suggested (Walker 1970), all maxilla. The first tooth, which is almost certainly the first maxillary tooth, is slender, as in *Sphenosuchus*. There is a deep anterior palatal notch, now squeezed nearly shut, and a short secondary palate of similar extent to that of *Sphenosuchus*. The portions of the braincase, particularly the left prootic + opisthotic, also show close resemblance to that of the South African fossil. There are mastoid and facial antra below a flange on the prootic. However, the anterior temporal foramen seems to have been larger and the braincase may have been more highly pneumatized than in *Sphenosuchus*.

The left tibia (Colbert, fig. 28) still had the crocodilian square dorsolateral process of the astragalus fixed to it by matrix when I received it. Removal of this fragment exposed a distal end much more like the tibias of *Sphenosuchus* (fig. 44) and *Saltoposuchus* (von Huene 1921, pl. III, fig. 14) than Colbert's figure would suggest, with a flat, posteroventrally facing distal facet for the dorsolateral process of the astragalus. The medial side of the bone projects distally beyond this facet, as in the other two genera. The curvatures of the distal half of the bone are virtually identical in all three forms.

The 'left manus' (Colbert, figs 24 and 25) is, as has been pointed out by Bonaparte (1971), a foot, part of a right tarsus and metatarsus of crocodilian type. Metatarsal I was evidently a weak bone.

In the same drawer as the unmounted material of *Hesperosuchus* was a right humerus, not mentioned by Colbert, 84 mm long as compared with 94 mm for the figured left humerus (Colbert, fig. 22). This differs considerably from the figured bone and appears to be from an ornithosuchid or a coelurosaur. The left pes figured by Colbert (1952, fig. 31) is considerably larger than the right pes of his fig. 24, and is out of proportion to the distal end of the tibia, as Bonaparte (1971) has noted. These two elements (humerus and pes) suggest that *Hesperosuchus* is to some extent a composite, but with the exception of the large pes there seems no reason to doubt that the figured material belongs to one animal and probably to one individual.

Saltoposuchus is now known to be very close to *Terrestrisuchus* (Crush 1984), indeed Clark (in Benton & Clark 1988) considers them to be at least congeneric and possibly conspecific. I agree with these authors that the two forms are closely related, but am rather doubtful that they are congeneric. Apart from the cranial features already noted, *Terrestrisuchus* has the crocodilian characters of a posteroventrally elongated coracoid (closely similar to the 'problematic bone' of *Hesperosuchus* (Colbert 1952, fig. 26)) and an elongated radiale and ulnare. These characters are also found in *Pseudhesperosuchus* (Bonaparte 1971) and *Dibothrosuchus* (Wu 1986).

Platyognathus (Simmons 1965), on the nature of the coracoid and the presence of ventral armour, is probably a protosuchian.

It is not proposed to review here the distribution within the primitive crocodylomorphs of those characters which are believed to be synapomorphies for the group. Work in progress by Dr James M. Clark, who has had the advantage of examining much of the material at first hand, will deal with character analysis and inter-relationships within the Crocodylomorpha (Clark, 1986). An outline of the results of this work has already been published (Clark, in Benton & Clark (1988)). In many of the early forms the skull and postcranial skeleton, particularly the pelvis, are inadequately known. In the well-preserved skull of *Sphenosuchus* itself, however, the crocodylomorph cranial features are excellently displayed, and it is believed that the apparent absence in other genera of some of them, or apparently anomalous manifestation, is caused by inadequate preservation or preparation, or by distortion. The list of synapomorphies for the Crocodylomorpha which follows is therefore offered as a basis for future discussion.

1. Primary head of quadrate meets prootic (and squamosal) but not opisthotic, creating a temporal canal running from supratemporal fenestra to post-temporal fenestra and communicating by a post-quadrate foramen with the tympanic cavity.
2. Cochlear recess elongated forming cochlear prominence, recess mainly formed by prootic and opisthotic with considerable extent below fenestra ovalis. Lagenar region at least partly in basioccipital. Crista interfenestralis a slender bridge. Foramen perilymphaticum large, surrounded by a loop of opisthotic lying mainly in a vertical plane. Recessus scalae tympani large and laterally placed, bounded behind by a subcapsular buttress, forming posterior margin of a fenestra pseudorotunda. Subcapsular buttress more prominent than crista interfenestralis.
3. Quadratojugal forms entire posterior border of lateral temporal fenestra, extends up quadrate primitively to meet squamosal, primitively does not meet postorbital.
4. Quadrate with anterodorsal process, primitively not meeting postorbital.
5. Prefrontals expanded within orbit, meeting interorbital septum.
6. Postfrontal absent.
7. Squamosal broadly overhangs quadrate laterally and posteriorly.
8. Squamosal lacks descending process in front of quadrate.
9. Squamosal sutured to outside of anterodorsal process of quadrate.
10. Interlocking peg and socket relationship between paroccipital process and squamosal.
11. Foramen between quadrate and quadratojugal absent.
12. Secondary palate formed by maxillae.
13. Medial pterygoid flanges present.
14. Quadrate–pterygoid arch tilted downwards and forwards.
15. Pneumatic cavities present in skull: see numbers 5–9, 13 and 14 of list on p. 75.
16. Coracoid elongated posteroventrally.
17. Clavicles absent.
18. Radiale and ulnare elongated.

Numbers 3, 4 and 8 of the above list are probably correlated characters. Numbers 1, 2 and 7 may also be correlated.

Gauthier (1986) gives a list of synapomorphies which broadly correspond to numbers 1, 3, 6, 8, 12, 16, 17 and 18 of the above list. He also gives:

(*a*) Quadrate and quadratojugal inclined dorsally.
(*b*) Internal jugular vein absent.
(*c*) Post-temporal fenestra very small.
(*d*) Fenestra pseudorotunda present.
(*e*) Entire deltopectoral crest distally placed.

Of the above, (*a*) is difficult to define as a moderate inclination also occurs in some thecodontians; (*b*) is probably incorrect: arguments have been advanced in §5 *d* for the presence of a posterior cerebral (or internal jugular) vein in *Sphenosuchus*; (*c*) does not seem to be valid, as the post-temporal fenestrae are small or absent in stagonolepidids, proterosuchians (Cruickshank 1972) and proterochampsids (see Sill 1967; Romer 1971); (*d*) probably occurs also in some dinosaurs, but otic capsule structure requires more precise definition; (*e*) does not apply to *Sphenosuchus*.

Items 1, 3, 6, 7, 11, 12, 16 and 18 are also given by Clark (list 1, appendix 2, in Benton & Clark (1988)), sometimes in a different form. Clark also gives the following:

(*a*) Post-temporal fenestra small or absent.

(*b*) Prootic does not broadly contact anterior surface of paroccipital process.

(*c*) Pneumatic space in body of basisphenoid.

and as possible:

(*d*) Jugal does not form posterior border of antorbital fenestra.

Of these, (*a*) has been dealt with above; (*b*) is probably acceptable, but (*c*) requires more precise definition because the space in the body of the basisphenoid of *Osteolaemus* is superficially similar to the postcarotid recess of *Sphenosuchus*, but the two are not homologous.

The only character in the above list which is not known for *Sphenosuchus* is number 18, elongated radiale and ulnare. This character occurs in *Pseudhesperosuchus*, *Terrestrisuchus* and *Dibothrosuchus* (and probably in *Pedeticosaurus* (Walker, 1970)); the evidence is lacking for *Hesperosuchus* and *Saltoposuchus*. It is thus highly likely that it occurred in *Sphenosuchus* also.

Characters 1 and 7 of the above list concern the forward and inward movement of the quadrate head, a change in crocodiles which sets them off from all other reptilian groups. Character (or character-complex) 2, the otic capsule, also differentiates crocodiles from other reptiles. These two sets of characters appear to be inter-related and indicate a general improvement in auditory structures in sphenosuchids with the attainment of the essentials of the crocodilian condition. These characters are therefore fundamental to the formation of the crocodilian type of skull, and the fact that they already occur in *Sphenosuchus* clearly allies this form to the Crocodylia in the historic sense rather than to the Thecodontia. In addition, the detailed resemblances pointed out in the preceding section between the skulls of *Sphenosuchus* and modern crocodiles, such as the quadrate/quadratojugal contact and the squamosal/paroccipital contact, and which distinguish the skull of *Sphenosuchus* (as far as is known) from those of thecodontians, speak for a very close affinity.

Thus the initial important shift to the crocodilian condition, particularly in the skull, had already been made by sphenosuchids, and it is considered that phylogenetically this shift is of greater significance than the later changes which led to the 'perfecting' of crocodilian structure seen in the modern representatives, and which seem to have taken place in a more gradual manner. In the Protosuchia, for example, the otic notch was still open behind (Nash 1975; Whetstone & Whybrow 1983; Busbey & Gow 1984) and the secondary palate was still confined to the maxilla as in sphenosuchians, so that these 'typical' crocodilian features had not progressed very far. The otic notch was still not closed behind in some 'mesosuchian' crocodiles and, as is well known, the full development of the secondary palate took until the early Cretaceous to effect. The pattern of crocodilian evolution thus conforms to that familiar from other vertebrate groups, showing an initial major set of morphological changes which establish the basic structure of the group, followed by a more gradual period of refinement and adaptation of these features before the 'typical' condition of the group is attained. The sphenosuchids are therefore grouped here with the protosuchians and more advanced crocodilians in a taxon which so far in this paper has been referred to as the Crocodylomorpha. In a formal hierarchical classification, however, it is perhaps doubtful whether a different name is required, and the group might be more economically known as the order Crocodylia.

Trialestes (Reig 1963; Bonaparte 1982) from the Ischigualasto Formation of Argentina is an apparently anomalous animal, with a crocodilian carpus and a mesotarsal ankle-joint. However, there is some doubt as to the unity of this material and until this is resolved it will be left out of consideration. There is certainly no reason to suppose that the sphenosuchids had a mesotarsal ankle, *pace* Bonaparte (1982), especially because of the clear evidence of *Terrestrisuchus* (Crush 1984). Furthermore, both *Hesperosuchus* and *Saltoposuchus* also have crocodilian ankle joints.

Origin of the Crocodylomorpha

Little can be said on this topic. A primitive form such as *Euparkeria* (Ewer 1965) provides, with the possible exception of the ankle, a generalized ancestor from which the group might have been derived but apart from this rather obvious statement there is little to point to in other thecodontians. Some features of *Chanaresuchus* (Romer 1971) from the Middle Triassic of Argentina are reminiscent of *Sphenosuchus*. The postfrontal has been lost. There are paired oval openings between premaxillae and maxillae in the anterior part of the palate. The jaw symphysis is weak and there is a long, splint-like coronoid. The articular region of the jaw seems rather similar and the ischium (Romer 1972*a*) is somewhat like that of a modern crocodile. However, there is little else in *Chanaresuchus* to suggest a relationship with crocodiles and the backward movement of the external nares which has taken place would seem to rule this out.

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EXPLANATION OF ABBREVIATIONS USED IN FIGURES

Skull and lower jaw

a	angular
aa	anterior ampulla
adp	anterodorsal process of quadrate
ae	external (horizontal) ampulla
alp	anterolateral projection of quadrate
ap	posterior ampulla
aps	alaparasphenoid
ar	articular
atf	anterior temporal foramen
ATR	anterior tympanic recess
aul	auricular (floccular) lobe
aur	auricular (floccular) recess
avc	anterior vertical semicircular canal
a. adp	articular area for anterodorsal process, etc.
bo	basioccipital
bor	basioccipital recesses
bpt	basipterygoid process
bptfac	basipterygoid facet
bs	basisphenoid
bspl	basisphenoid plate
bt	basitemporal
c	coronoid
cav	cavity
ch	choana
cif	crista interfenestralis
cp	carotid pillar
cr	cochlear recess
d	dentary
dia	diastema
dls	diverticulum of longitudinal venous sinus
e	epipterygoid
ec	ectopterygoid
ed	endolymphatic duct
eo	exoccipital
ep	epiotic
eth	foramen for ethmoidal artery
f	frontal
fa	facial antrum
faë	foramen aërum
fo	fenestra ovalis
for	foramen, foramina
fp	foramen perilymphaticum
fpr	fenestra pseudorotunda
gr	groove
h	head (quadrate)
hc	horizontal (external) semicircular canal
hole	hole made in preparation
ibptl	interbasipterygoid lamina
ic	foramen or groove for internal carotid artery
imf	infra-meckelian foramen
imp	impression
j	jugal
l	lachrymal
l.	left
lcs	loop-closure suture
Le	lateral or true eustachian aperture or canal
lig	ligament
lptfl	lateral pterygoid flange
ls	laterosphenoid
m	maxilla
ma	mastoid antrum
Me	median eustachian aperture or canal (foramen intertympanicum)
Mea	anterior branch of median eustachian canal
Meal	lateral division of the above
Mep	posterior branch of median eustachian canal
Mepl	lateral division of the above
met	ossification of the metotic cartilage
mf	metotic foramen
mptfl	medial pterygoid flange
n	nasal
nfl	nasal flange
ob	olfactory bulb
ol	opisthotic ledge
op	opisthotic
‘opq’	‘orbital process’ of quadrate
p	parietal
pbp	parabasal process
pd	perilymphatic duct
pf	postfrontal
pfd	postfenestral depression
pit	pit in surface of bone
pitf	pituitary fossa
pl	palatine
pm	premaxilla
pn	pneumatic cavity
po	postorbital
pocr	postcarotid recess
popr	paroccipital process
‘ppq’	‘pterygoid process’ of quadrate
pqf	postquadrate foramen
pr	prootic
pra	prearticular
prb	prootic buttress
prcr	precarotid recess
prf	prefrontal
pt	pterygoid
ptf	post-temporal fenestra
PTR	posterior tympanic recess
pvc	posterior vertical semicircular canal
q	quadrate
qj	quadratojugal
r.	right
rr	rostral recess
Rs	rhomboidal sinus
sa	surangular
sbr	sub-basisphenoid recess
scb	subcapsular buttress (ossification of subcapsular process)
soc	supraoccipital
sp	splenial
spu	sinus posterior utriculi
sq	squamosal
ssu	sinus superior utriculi
st	groove for stapedial artery

stop	retraction-stop
STR	superior tympanic recess
ts	transverse sinus (vascular)
ty	line of attachment of tympanic membrane
v	vomer
vca?	foramen, probably for anterior cerebral vein
vcd	dorsal head vein
vcm	middle cerebral vein
vcp	posterior cerebral vein
ve	vestibule
vs	venous sinus on posterior cerebral vein

Foramina for cranial nerves in Roman numerals. hy VII, pl VII: hyomandibular and palatine rami of facial nerve, and grooves for same.
chty: foramen and groove for chorda tympani branch of facial nerve.
rap: groove for ramulus ampullae posterioris of nerve VII.
VI: foramen and 'tube' for nerve VI.

Arteries

aci	internal carotid artery
aeth	ethmoidal artery
aio	infraorbital artery
apl	palatine artery
aso	supraorbital artery
ast	stapedial artery
at	temporal artery

Postcranial skeleton

The vertebrae and ribs are numbered consecutively.

abd ribs	abdominal ribs (gastralia)
bt	biceps tubercle
cor	coracoid
hum	humerus
icl	interclavicle
inc	intercentrum
ind fr	indeterminate fragment
l.	left
mt	metatarsal
na	neural arch
ph	phalanx
pro	proatlas
R	rib
r.	right
scap	scapula
tib	tibia

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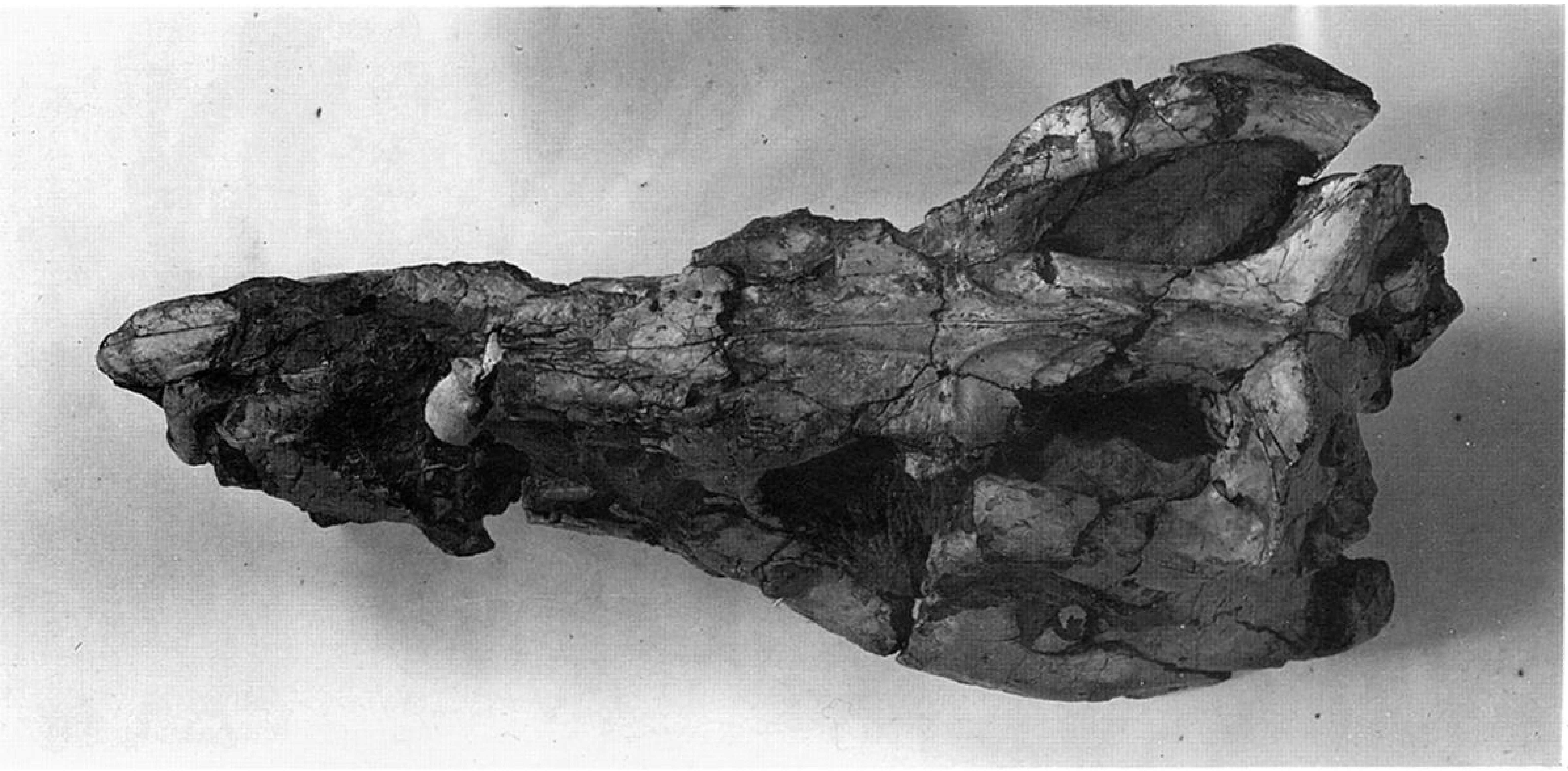

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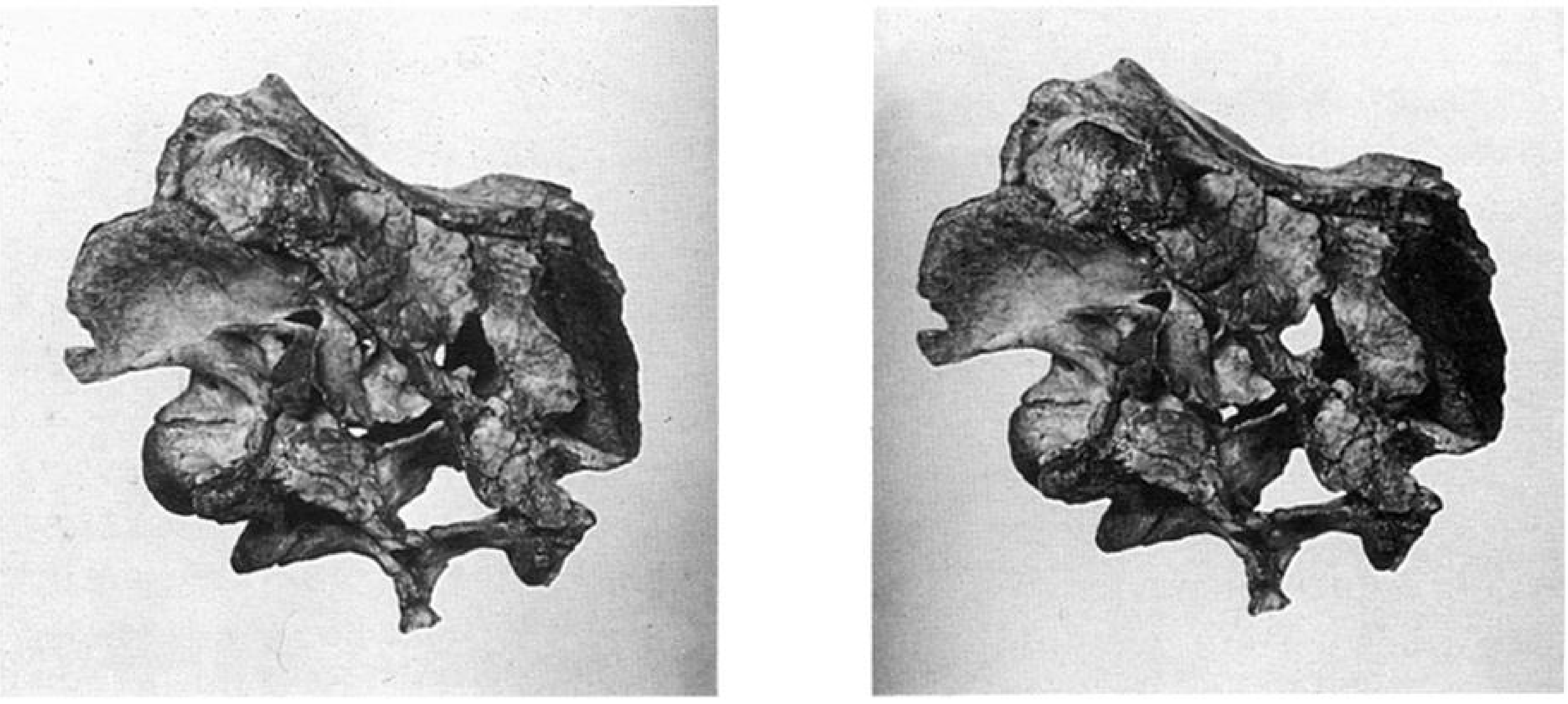
Figures 56–58. For description see p. 110.



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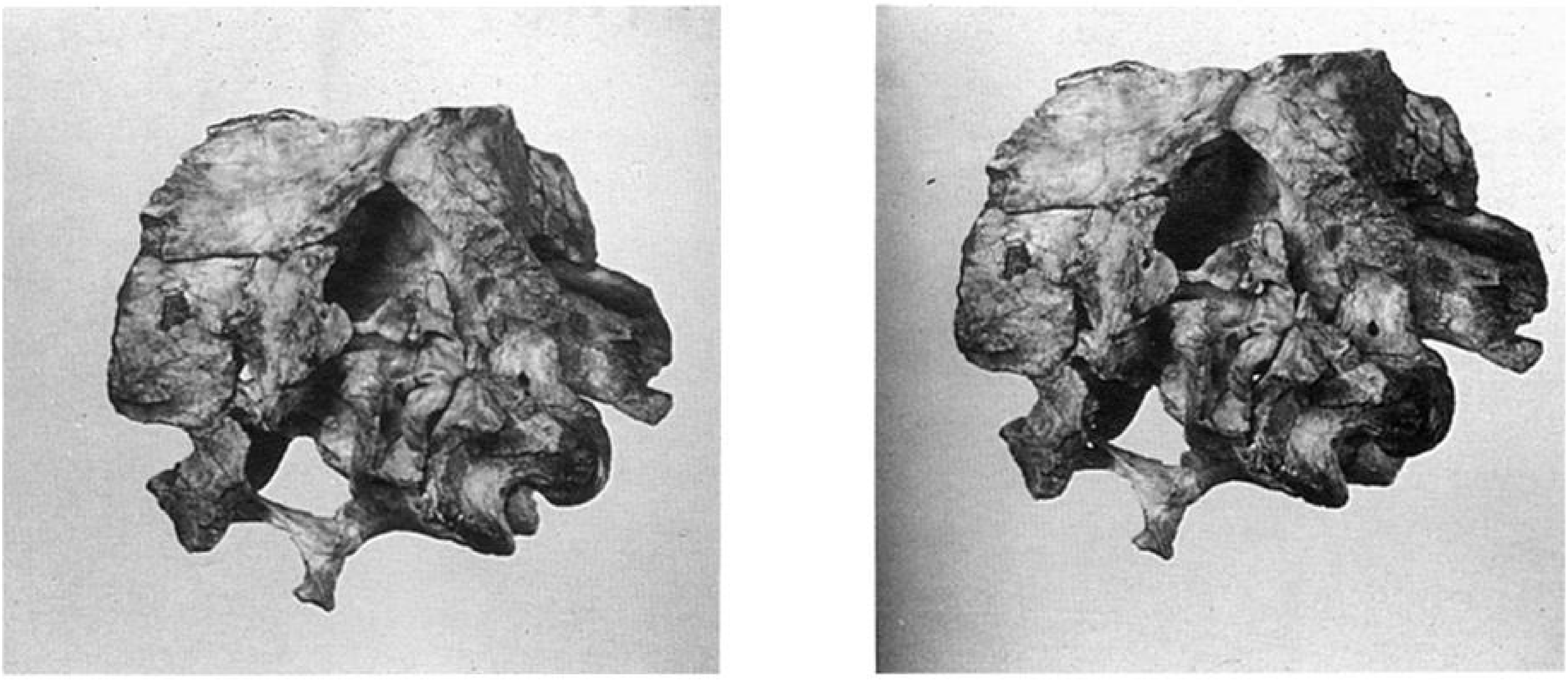

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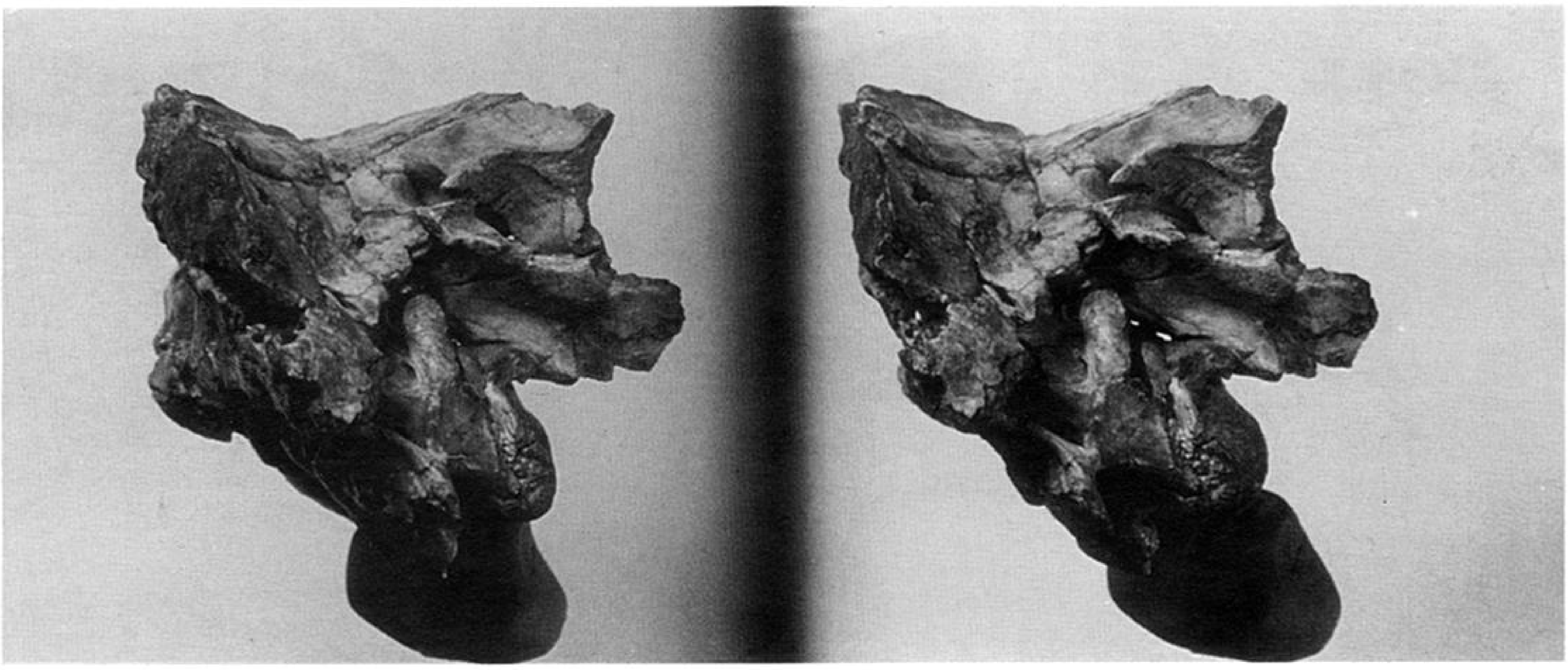

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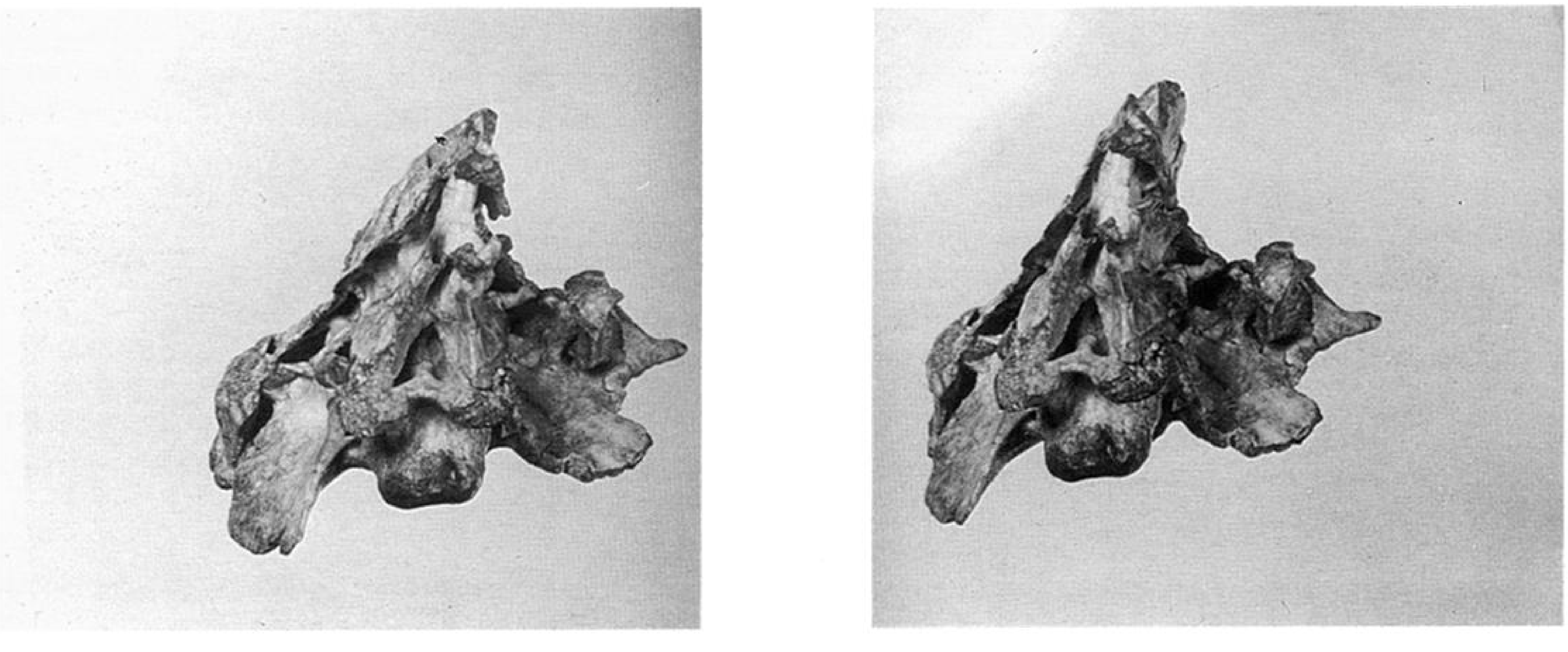

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Figures 59–62. For description see p. 110