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THE OSTEOLOGY AND RELATIONSHIPS OF *CLEVOSAURUS* (REPTILIA: SPHENODONTIDA)

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CONTENTS

The sphenodontid genus *Clevosaurus* from the late Triassic of south west Britain is represented by at least two different species. Exceptionally abundant remains of *Clevosaurus* occur as part of a diverse assemblage of microvertebrates lodged within fissure deposits at localities in Glamorgan and Avon. Although the majority of specimens occur as beautifully preserved disassociated elements, certain associated and articulated remains have been recovered. Contemporaneous vertebrates include other sphenodontians, archosaurs and procolophonids.

C. hudsoni is fully restored as a lizard-like reptile approximately 25 cm long. It was essentially insectivorous, although it may have also been facultatively herbivorous, breaking down food with a well-developed precision shear bite. A smaller species, *C. minor*, is less widespread and its remains are generally not as well preserved. It seems probable that a third species might be distinguished on the basis of dental characteristics, and the occurrence of a fourth species cannot be discounted.

A distinct suite of apomorphic characters separates the Sphenodontida from other lepidosauromorphs and these apomorphies are readily identifiable in *Clevosaurus*. In certain late Triassic sphenodontians the lower temporal arcade was apparently incomplete, but, contrary to Robinson's (*J. geol. Soc. Lond.* **129**, 457 (1973)) description, the lower temporal arcade was unbroken in *Clevosaurus*. However, the articulation between the jugal, squamosal and quadratojugal does not conform to the configuration exhibited by all other sphenodontians in which both temporal arcades are complete. In addition, the possession of a supratemporal in *Clevosaurus* is unique among known sphenodontians. The parietal table in *Clevosaurus* is intermediate between the broad, flat plesiomorphic condition, seen in forms such as *Polysphenodon* and *Homoeosaurus*, and the derived narrow median ridge displayed by *Kallimodon* and *Sphenodon*. Consequently, within the Sphenodontida the position of *Clevosaurus* is unclear; however, on the basis of the prominently flanged additional teeth, some reduction in tooth numbers and at least some partial reduction in the width of the parietal table, it would appear to share certain characteristics with *Sapheosaurus* and *Kallimodon*. *Palaeopleurosaurus*, described by Carroll (1985) as a primitive pleurosaur, may also have affinities with this grouping.

Some of the earliest sphenodontians, such as *Planocephalosaurus* and *Diphydontosaurus*, exhibit fusion of the median skull roofing elements, a short temporal region and retention of a variable degree of pleurodonty in the marginal dentition. Together with *Gephyrosaurus* these genera may constitute a monophyletic assemblage forming the sister group of all other sphenodontians.

1. INTRODUCTION

Sphenodontids are an ancient taxon of reptiles which are superficially very similar to modern lizards. The sole surviving member is *Sphenodon punctatus* which can only be found today inhabiting a few isolated islands off the New Zealand coast. However, recent research has shown that as a group they flourished in the Mesozoic. Two vertebrae from the lower Triassic of Russia, designated to the genus *Scharschengia*, have been attributed to the Sphenodontida (Huene 1940*a*, *b*; Rasmussen & Callison 1981), but the evidence is inconclusive. The documentation of *Polysphenodon* (Jaekel 1911; Huene 1929) from middle Keuper beds near Hanover (Carnian or Norian), *Brachyrhinodon* from the early Norian Lossiemouth Sandstone Formation of northeast Scotland (Huene 1910, 1912; Benton & Walker 1985) and *Elachistosuchus* from the late Keuper of Halberstadt, near Magdeburg (Walker 1966), provide more reliable evidence of early sphenodontid remains. By the late Triassic and Jurassic they were quite widespread, having been located in southwest Britain (fissure deposits in the Blue Anchor and Westbury Formations (Norian and Rhaetian of Fraser Walkden (1983)), Zimbabwe (Forest Sandstone, Norian? (Gow & Raath 1977)), southern Europe (Solnhofen Limestone, Upper Kimmeridgian or Lower Tithonian (Cocude-Michel 1963)), northeast Mexico (La Boca Formation (J. Hopson, personal communication)) and North America (Morrison Formation (Gilmore 1909; Rasmussen & Callison 1981)). Isolated remains are also known from the late Jurassic or early Cretaceous Kirkwood Formation of South Africa (Rich *et al.* 1983) and the Lower Cretaceous Kootenai Formation of southwest Montana (Throckmorton *et al.* 1981) (table 1).

TABLE 1. THE KNOWN RECORDS OF SPHENODONTIDA FROM THE MESOZOIC

	Europe	Americas	Gondwanaland
Lower Cretaceous		*Toxolophosaurus*	unnamed genus (Rich *et al.* 1983)
Upper Jurassic	*Kallimodon*	*Eilenodon*	—
	Homoeosaurus	*Opisthias*	—
Middle Jurassic	—	—	—
Lower Jurassic	*Gephyrosaurus?*	—	—
Upper Triassic	*Clevosaurus*	—	unnamed genus (Gow & Raath 1977)
	Planocephalosaurus	—	
	Brachyrhinodon	—	—
Middle Triassic	*Polysphenodon*	—	—
Lower Triassic	*Scharschengia*	—	—

Perhaps the most prolific sphenodontid fossils are to be found in the fissure deposits of southwest Britain. The genus *Clevosaurus* was first described (but not illustrated) by Swinton (1939) from fragments of jaws, vertebrae, limb and girdle bones discovered by F. G. Hudson in Triassic deposits at Cromhall Quarry (also known as Slickstones Quarry), South Gloucestershire. Robinson *et al.* (1952) reported the discovery of a varied reptilian fauna, from the same locality, which included further remains of *Clevosaurus*. Continued excavation and extensive collecting from the same area revealed associated remains (Robinson 1955) allowing Robinson (1973) to extend the description. However, there are no available details of Robinson's material; no description of the postcranial skeleton has ever been published and neither has there been a detailed account of the cranial osteology.

In 1968 the University of Cambridge acquired more vertebrate-bearing material from the type locality which again included articulated specimens. It is believed that the majority of the Cambridge material originated from Hudson's original deposit, but remains were collected from a spoil heap and no precise sampling details are available. Despite this, the material has yielded much needed information regarding the skeletal morphology of *Clevosaurus*.

More recent research by workers at Aberdeen University has revealed six separate vertebrate-bearing deposits of Triassic age at Cromhall Quarry (Fraser & Walkden 1983). For a description of these fissues see Fraser (1985). Extensive collections were made from all these deposits and a number of different genera, mostly sphenodontids and archosaurs, were identified in the processed material. The most abundant of these is another small sphenodontid, *Planocephalosaurus robinsonae*, which has been described entirely from disassociated remains (Fraser 1982; Fraser & Walkden 1984). The specimens of *Clevosaurus* housed at Aberdeen University originate from five separate fissure fills, and although they too are mostly disassociated, one articulated skull and two lower jaws are to be found among the few articulated remains.

Other localities in the Bristol Channel area have recently been found to contain remains of *Clevosaurus*. These include Tytherington (Whiteside & Robinson 1983) and Pant-y-ffynon Quarries (Crush 1980) (figure 1*a*). Two isolated fragments from Highcroft Quarry are probably also representative of *Clevosaurus* (Fraser 1986*a*, *b*).

Although Swinton (1939) and Robinson (1973) were only able to recognize one species, *Clevosaurus hudsoni*, it has been possible to separate the Aberdeen material into at least two species. *C. hudsoni* occurs exclusive of any other *Clevosaurus* species at one site ('site 1' of Fraser's (1985) nomenclature, see figure 1*b*) and may be occasionally present at two others. More widespread is a smaller species that occurs in four of the six Cromhall fossiliferous fissures, and further species cannot be discounted.

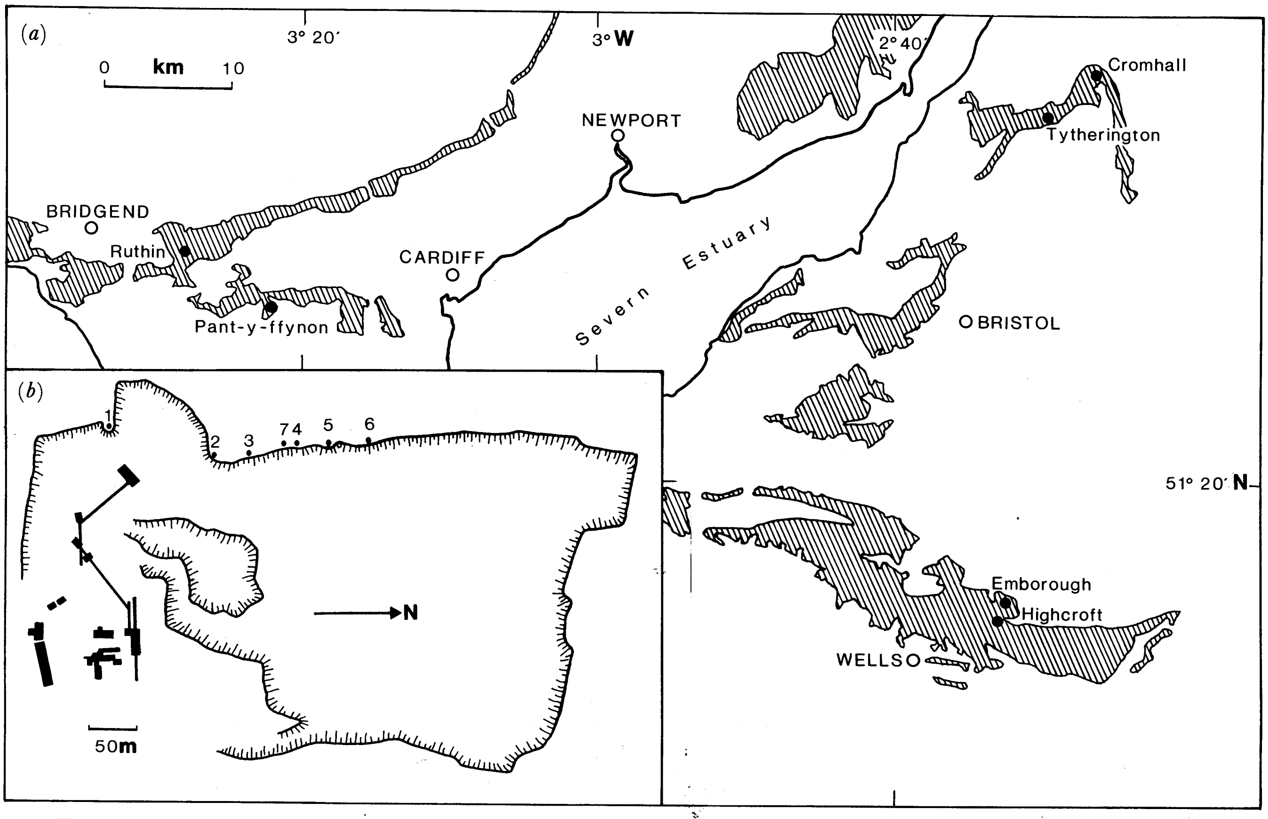


FIGURE 1. (*a*) Localities (solid circles) known to bear *Clevosaurus* in the Bristol Channel area. (*b*) Plan of Cromhall Quarry as in 1984 showing the locations of vertebrate-bearing sediments.

Several *Clevosaurus* jawbones have been recovered from an isolated pocket of one particular feature ('Site 5A', Fraser (1985)). Examination and measurement of the posterior teeth on all the dentary specimens reveals two quite distinct types. The fact that such a distinction can apparently be made at only one of the five sites bearing *Clevosaurus* suggests that it is not indicative of sexual dimorphism or ontogenetic variation.

The correct spelling of the generic name has been the cause of a long-standing dispute. Although first printed as *Clevosaurus* (Swinton 1939), Robinson (1973) believed there was a typographical error in the original manuscript and that *Glevosaurus* [*sic*] was the correct spelling as it originated from the Roman name Glevum which referred to the locality now known as

Gloucester. However, Dr L. B. Halstead (personal communication) suggests that Swinton had actually intended the original spelling, Glevum and Clevum both being acceptable spellings. In any case, under Article 33 of the 1985 *International Code of Zoological Nomenclature*, the name *Clevosaurus* cannot be 'corrected' or emended.

2. MATERIAL

For the general geology of the Cromhall fissure deposits see Fraser & Walkden (1983), Fraser (1985) and Walkden & Fraser (1989). The descriptions of the reptiles are based on material housed in the universities of Cambridge and Aberdeen. All the Cambridge specimens and many of those at Aberdeen were located in a light, buff coloured, bedded limestone. The Aberdeen collections originating from this particular matrix can be precisely located to a single fossiliferous horizon at site one (figure 2, plate 1). It is most probable that the specimens housed in the Cambridge collections were located in the same horizon. This buff-coloured matrix reacts readily with dilute acetic acid and preparation was mostly by acid digestion, although occasional use was also made of a Vibrotool and mounted needles, particularly on the articulated specimens. In addition to *Clevosaurus hudsoni*, the 'site 1' matrix has also revealed remains of the sphenodontid *Diphydontosaurus* (Whiteside 1986), a small thecodont and isolated procolophonid remains.

Other *Clevosaurus* specimens in the Aberdeen collections were derived from acid digestion of bedded crinoidal limestones and marls in fissures 3, 4, 5 and 7 (see figure 1*b* for locations of the fissures) which generally reveal rather fragmentary remains. It is these crinoidal limestones that have yielded the smaller *Clevosaurus* species, and a subsidiary fill at fissure 5 (see Fraser 1985) may contain a third species.

The Cambridge material was prepared by J. Evans and that in Aberdeen by the author. The procedure adopted in reconstructing the disassociated material was essentially the same as that outlined by Fraser (1982) for *Planocephalosaurus*. However, in the present instance the occurrence of articulated specimens has been of immense value in confirming the identification of isolated elements and ascertaining the correct proportions of *C. hudsoni*.

There are over a thousand individual bones of *Clevosaurus* housed in the collections of Cambridge (UMZC) and Aberdeen (AUP) Universities, including a whole range of growth stages. For instance, some complete jaw bones are less than 2 mm in length, and yet teeth and details of articulation facets are all beautifully preserved. Only those specimens referred to in the text are listed below, together with the articulated specimens examined (date of collection in parentheses).

Clevosaurus hudsoni from Cromhall (Slickstones) Quarry

(i) AUP 11088. Left palatine from a juvenile (1980).
(ii) AUP 11143. Left premaxilla (1980).
(iii) AUP 11144. Right maxilla (1980).
(iv) AUP 11146. Left maxilla from a juvenile (1981).
(v) AUP 11152. Right postorbital (1980).
(vi) AUP 11153. Left jugal (1980).
(vii) AUP 11157. Anterior fragment of a left vomer (1980).
(viii) AUP 11158. Left palatine bearing a rudimentary second tooth row (1980).

(ix) AUP 11169. Fragmentary articulated skull exposed in left lateral and dorsal views (1981).

(x) AUP 11171. Cervical vertebra (1981).

(xi) AUP 11172. Dorsal vertebra (1981).

(xii) AUP 11174. Mid-caudal vertebra (1980).

(xiii) AUP 11177. Right scapulocoracoid (1981).

(xiv) AUP 11178. Left ulna (1983).

(xv) AUP 11179. Right humerus (1981).

(xvi) AUP 11180. Right ilium (1981).

(xvii) AUP 11184. Left tibia (1983).

(xviii) AUP 11185. Proximal end of left tibia (1983).

(xix) AUP 11187. Left maxilla (1981).

(xx) AUP 11371. Fragment of a juvenile right dentary (1982).

(xxi) AUP 11372. Fragment of a juvenile right dentary (1982).

(xxii) AUP 11373. Juvenile right dentary (1980).

(xxiii) UMZC T1264. Articulated right nasal and prefrontal, together with an anterior caudal vertebra (1968).

(xxiv) UMZC T1265. Articulated frontals (1968).

(xxv) UMZC T1266. Left squamosal with articulated frontals (1968).

(xxvi) UMZC T1267. Posterior fragment of a right quadrate and quadratojugal (1968).

(xxvii) UMZC T1268. Fragmentary paired vomers (1968).

(xxviii) UMZC T1269. Articulated palate with paired palatines, pterygoids and left and right ectopterygoids (1968).

(xxix) UMZC T1270. Associated fragments of a juvenile skull including paired pterygoids, left palatine, left quadrate and the parabasisphenoid. Also incorporated in the fragmented matrix is a vertebral centrum, a phalanx and an anterior caudal vertebra from a thecodont (1968).

(xxx) UMZC T1271. Articulated skeleton and skull missing the right fore and hind limbs, and the tail posterior to caudal 8. The postcranial skeleton is exposed in ventral view, but with the preserved gastralia obscuring much of the vertebral column. The left manus and pes are in close association with each other. The skull is dorsoventrally compressed and also exposed in dorsal and lateral aspects (1968).

(xxxi) UMZC T1272. Partly preserved articulated skull exposed in ventral view (1968).

(xxxii) UMZC T1273. Left femur with a pathological secondary outgrowth of the proximal head (1968).

(xxxiii) UMZC T1274. Left femur (1968).

(xxxiv) UMZC T1275. Associated right ilium and second sacral vertebra (1968).

(xxxv) UMZC T1276. Left dentary (1968).

(xxxvi) UMZC T1277. A parabasisphenoid (1968).

(xxxvii) UMZC T1279. Left ilium (1968).

(xxxviii) BMNH R5939. Syntypes. Upper jaw portions of right and left mandibles.

(xxxix) BMNH R6100, R9249, R9251, R9252, R9253, R9255–R9258, R9260–R9267. Varied skeletal elements.

Clevosuarus minor from Cromhall Quarry

(xl) AUP 11082. Left palatine missing the anterior vomerine process and with a fragmented maxillary ramus. Paratype (1979).

(xli) AUP 11377. Left maxilla. Holotype (1979).

Clevosaurus sp. from Cromhall Quarry

(xlii) AUP 11191. Right premaxilla (1983).

(xliii) AUP 11374. Left dentary (1984).

Gephyrosaurus sp.

(xliv) UMZC T1278. Fragment of a right maxilla. Collected from Pont Alun Quarry, Glamorgan in 1966 by F. R. Parrington.

3. *Clevosaurus hudsoni*

(*a*) *The skull* (*figure* 3)

The cranial descriptions are based to some extent on the articulated specimens UMZC T1271 (figure 4, plate 2) and AUP 11169, but the numerous, beautifully preserved disassociated elements have provided welcome information, particularly concerning internal structures and details of articulation facets.

The paired premaxillae (figure 5) almost completely surround each anterolateral-facing external naris. A slender internarial process extends dorsally in contact with its counterpart, and wedges between the anterior ends of the nasals. But quite unlike the condition in *Sphenodon* and *Planocephalosaurus*, the posterior border of the naris is also bounded by a dorsal process of the premaxilla (figure 3), from which a forked flange extends backwards underneath the internal surface of the maxilla. The more dorsal process of the two prongs also has a medial facet where it partly overlapped the nasal. Consequently the premaxilla, maxilla and nasal were firmly held together forming a strong brace to the snout. On the internal surface of the premaxilla there is a shallow horizontal groove just below the level of the external naris and this accommodated an anterior process from the vomer. The premaxillary dentition is described in §3*e*.

The maxilla (figure 6) is a robust element that extensively overlapped the premaxilla anteriorly, and dorsally overlapped the nasal and prefrontal anterior to the orbit. Ventral to the orbital margin the maxilla forms a deep vertical wall which tapers posteriorly and bulges laterally where it sheathed the anterior process of the jugal. A variable number, up to about eight, foramina open externally along a line just above the maxillary dentition. The dentition itself is described in §3*e*. In addition to the facets for the premaxilla, nasal and prefrontal, the internal surface of the maxilla displays a prominent facet for the palatine which is pierced by a large infraorbital foramen. Posterior to the palatine facet, and immediately dorsal to the tooth row, the maxilla is produced into a ledge that bears a distinct facet for the ectopterygoid. At this point the ectopterygoid also has a broad lateral contact with the jugal, thereby providing a rigid contact between the palate and the lateral walls of the skull.

The nasal is delicate and not commonly preserved intact, although one specimen (UMZC T1265) (figure 7) is preserved complete and still in association with the prefrontal. Laterally

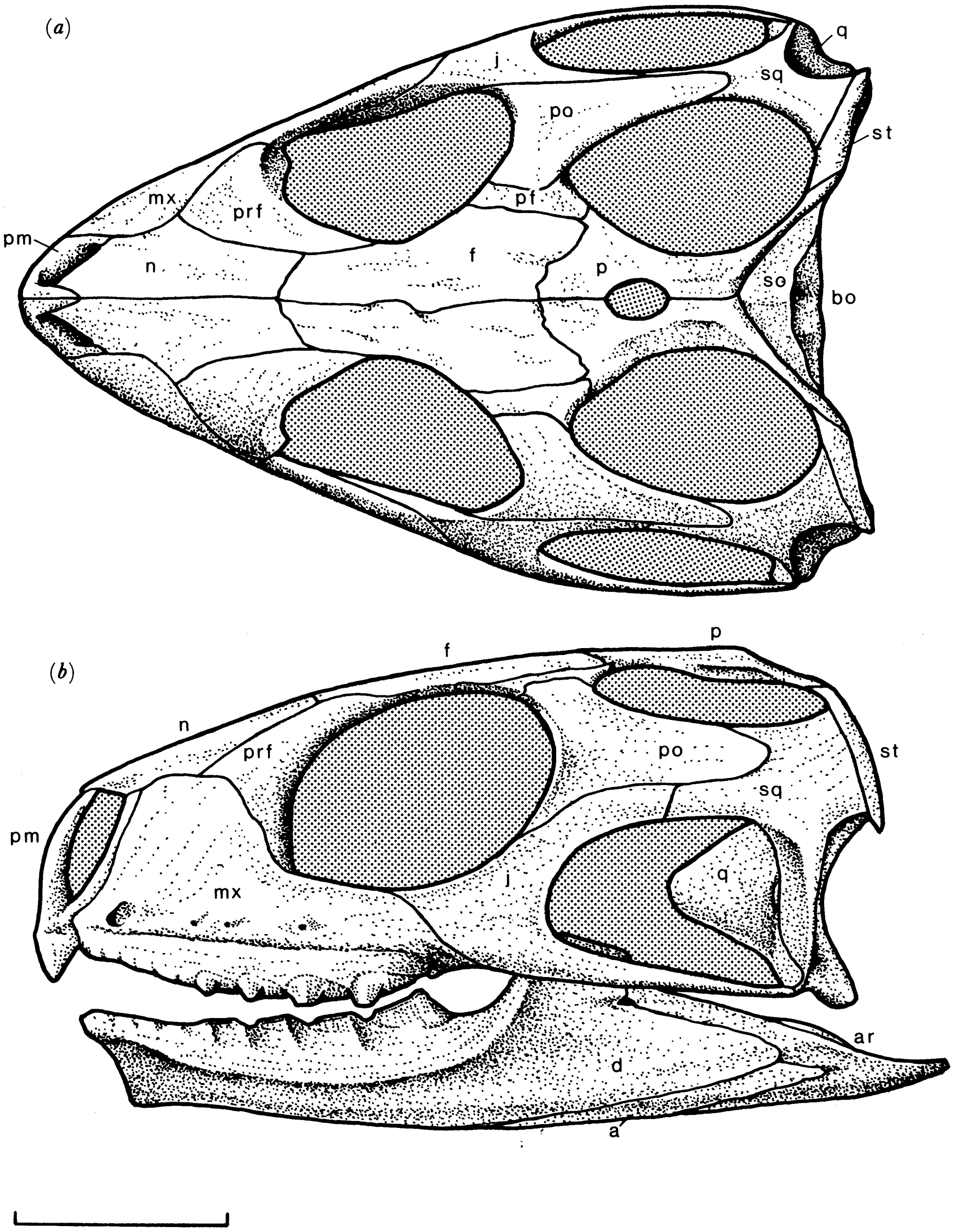
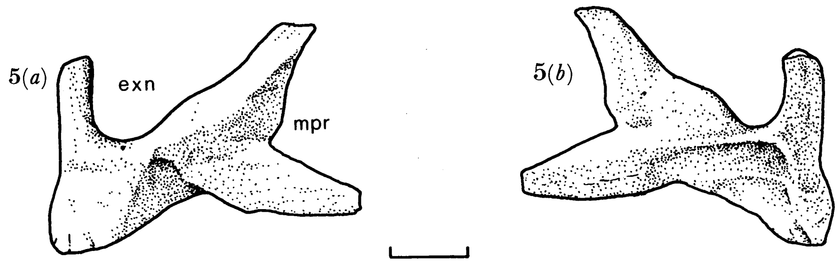
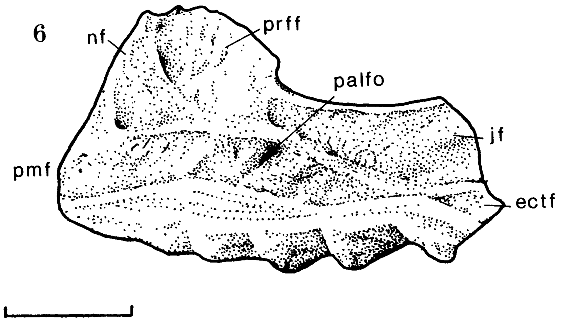


FIGURE 3. *Clevosaurus hudsoni*. Composite restoration of the skull in (*a*) dorsal and (*b*) lateral views. Scale bar 1.0 cm.

the nasal underlay the premaxilla and the maxilla as described above, and posteriorly it overlapped the anterior margin of the frontal. One or two foramina perforate the perfectly smooth external surface adjacent to the maxillary facet. Internally a sharp ridge arises anterior to the articulation with the frontal, curves anterolaterally and terminates at the posterodorsal corner of the external naris. Thus together the ridges of the paired elements delimit a shallow circular depression in the roof of the nasal cavity.

The prefrontal is a large element that marked the anterodorsal edge of the orbit (figure 3). As in *Sphenodon* and *Planocephalosaurus* it had long dorsal contacts with the nasal (figure 7) and





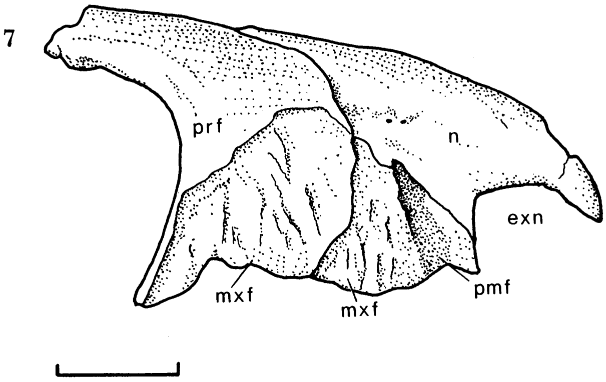


FIGURE 5. *Clevosaurus hudsoni*. Left premaxilla, AUP **11143**, in (*a*) lateral and (*b*) medial views. Scale bar 2.0 mm.

FIGURE 6. *Clevosaurus hudsoni*. Right maxilla, AUP 11144, in medial view. Scale bar 2.0 mm.

FIGURE 7. *Clevosaurus hudsoni*. UMZC T1264, lateral aspect of a right nasal and prefrontal in articulation. Scale bar 4.0 mm.

frontal bones, whereas laterally it was broadly overlapped by the maxilla. A ventral process ran down the anterior edge of the orbit and articulated in a socket on the dorsal surface of the palatine. There was no lachrymal, and the ventral process of the prefrontal was in complete contact with the maxilla so that unlike *Sphenodon* there was no foramen between the two bones (figure 3*a*).

The frontals are flat paired elements that met along the midline in a complex interdigitating articulation (figure 8). Laterally they entered into the supraorbital margin for a short distance and there are shallow grooved articulation facets for the prefrontal and postfrontal. Each element has a well-developed internal strengthening ridge situated parallel and just medial to the dorsal border of the orbit.

The postfrontal is a triradiate bone and was orientated in a horizontal plane. It had an extensive contact along the lateral margin of the frontal and a shorter posterior process overlapped the anterolateral edge of the parietal (figure 3*a*). The laterally directed process formed a tongue in groove articulation with the postorbital, in which the postorbital greatly overlapped the postfrontal on the dorsal surface, but internally there was a more reduced overlap of the postfrontal.

The postorbital (figure 9) is a large triangular bone that formed the posterior margin of the orbit. Ventrally it clasped the front edge of the jugal and posteriorly it strongly overlapped the squamosal to form a fairly broad superior temporal arcade (figure 3) strengthening the lateral walls of the skull. The dorsal process rigidly fixed the position of the postfrontal as described above.

The jugal consists of three slender processes radiating from a central point (figure 10). The anterior process is largely obscured in lateral view by an extensive overlap of the maxilla and on its medial aspect there is a well-pronounced groove against which a broad process of the ectopterygoid abbutted. The dorsal process slopes backwards and is bounded anteriorly and dorsally by the postorbital. Along the dorsal margin of the lower temporal fenestra the jugal met the squamosal and thereby excluded the postorbital from the border of this fenestra. The posterior process of the jugal is long and slender and formed the entire ventral margin of the lower temporal fenestra. Contrary to Robinson's (1973) observations, in at least some instances the jugal would appear to have made a weak contact with the quadratojugal. Frequently the length of the posterior process of the jugal is such that to reconstruct the skull it is necessary that the jugal should have reached and made contact with the quadratojugal. In some specimens there is a small boss on the quadratojugal immediately lateral and dorsal to the jaw articulation which appears to represent the site of the connection between the two bones. The connection may have been partly cartilaginous or even ligamentous rather than strongly sutured. Unlike the condition in *Sphenodon*, or those instances in *Planocephalosaurus* in which the lower temporal arcade is complete, the ventral process of the *C. hudsoni* squamosal does not expand to form a secondary attachment with the jugal. However, in one squamosal specimen (UMZC T1266) the ventral process is produced so that it would have extended around the posterior edge of the quadratojugal and made a weak contact with the extreme tip of the jugal (figure 11).

The squamosal is a large, more or less quadrilateral bone that formed the posterolateral border of the upper temporal arcade. The anterior process bears a broad lateral facet for the reception of the postorbital, whereas the posterior edge is marked by a long shallow depression that received the supratemporal. A ventral process of the squamosal descends along the anterolateral edge of the quadratojugal. This process may have been of variable length, but on occasions it apparently tapers to a narrow point that hooked around the posteroventral margin of the quadratojugal to contact the jugal as described above.

A supratemporal has not been reliably reported previously in any sphenodontid. However, there can be no doubt that one was present in *Clevosaurus* as seen in AUP 11169 (figure 12, plate 3). It is also partly preserved in the crushed specimen UMZC T1271. The bone itself is slender, and bears a slight dorsal convexity. In dorsal aspect it is widest at the point where it overlaps the anterior edge of the posterolateral process of the parietal and superficially separates the squamosal from the parietal. It then continues laterally as a narrow extension over the entire posterior margin of the squamosal.

The parietals are paired elements that formed a narrow, but flat intertemporal roof (figure 3*a*). Each element slopes gently away from the lateral edges of the parietal table and

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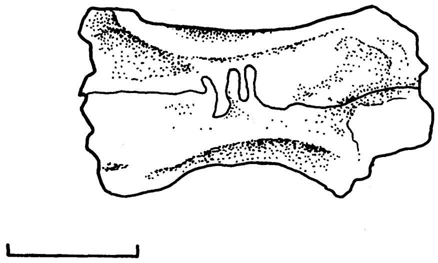

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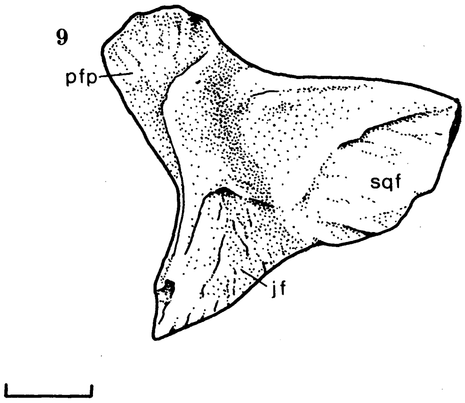
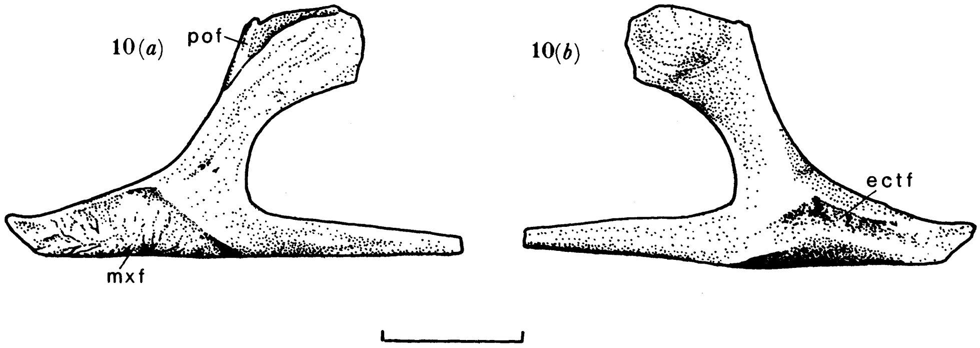


10(*a*)

10(*b*)



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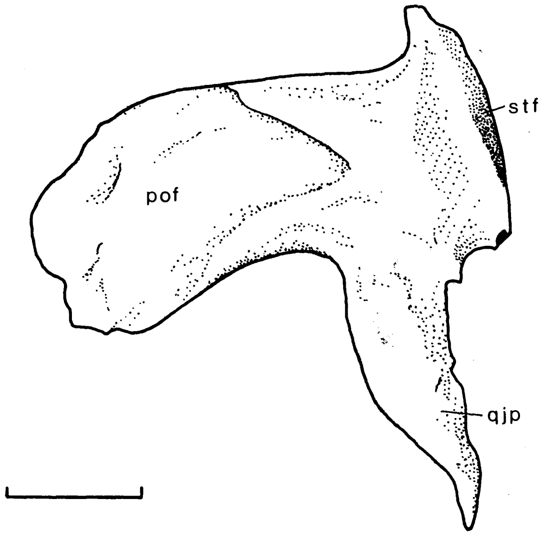


FIGURE 8. *Clevosaurus hudsoni*. UMZC T1265, articulating frontals in cranial view showing the interdigitating articulation. Scale bar 4.0 mm.

FIGURE 9. *Clevosaurus hudsoni*. Right postorbital, AUP 11152, in medial aspect. Scale bar 4.0 mm.

FIGURE 10. *Clevosaurus hudsoni*. Left jugal, AUP 11153, in (*a*) lateral and (*b*) medial views. Scale bar 4.0 mm.

FIGURE 11. *Clevosaurus hudsoni*. Left squamosal, UMZC T1266, in lateral view showing the slender distal process on the quadratojugal ramus that in life is considered to have met the jugal. Scale bar represents 4.0 mm.

forms a medial shelf to the supratemporal fenestra. The bone has separate anterior facets for the frontal and postfrontal and behind these lies the prominent pineal foramen. Behind the pineal foramen the parietal forms a thickened strut, marked ventrally by a longitudinal ridge, which extended posteriorly in contact with its counterpart. Further posteriorly each parietal diverges posterolaterally in a tapering process that met the supratemporal.

The quadrate complex (figure 13) is formed from the quadrate and a very thin quadratojugal normally fused to its lateral surface, except in the region of the quadratojugal foramen which bisects both elements. In a few of the smaller specimens the trace of a suture may still be distinguished immediately above the foramen, and it is frequently particularly prominent on the posterior surface (figure 13*b*).

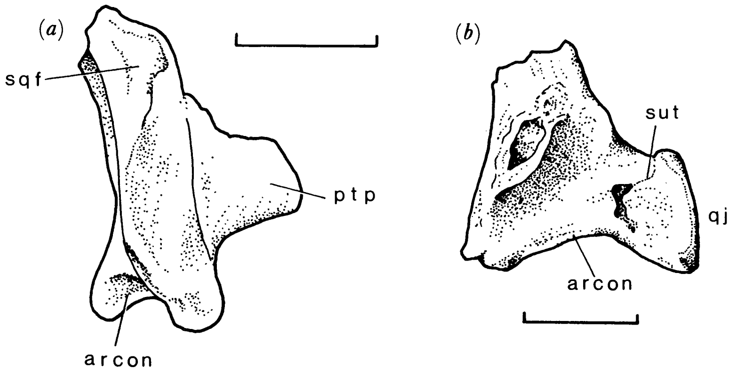


FIGURE 13. (*a*) *Clevosaurus hudsoni*. Fragmentary right quadrate and quadratojugal, UMZC T1267, in lateral view. Scale bar 4.0 mm. (*b*) Juvenile quadrate and quadratojugal, AUP 11376, showing a suture between the two. Scale bar 1.5 mm.

The quadrate condyle is deeply concave from side to side, and slightly convex from front to back. Its anterior–posterior length is short compared with its width. As far as could be ascertained the quadratojugal plays no part in the formation of the condyle. Above the level of the condyle the quadrate forms a narrow pillar running dorsally and aligned transversely. A deep, but thin, quadrate wing passes anteromedially to contact the pterygoid and it is strengthened by a stout horizontal ridge along its ventral edge. The quadratojugal extends posteriorly from the body of the quadrate as a thin lateral flange and bears facets for the jugal and squamosal as previously described. The quadratojugal foramen is relatively larger than that of *Planocephalosaurus*, but smaller than in *Sphenodon*.

(*b*) *The palate* (*figure* 14)

The vomers are thin, fragile elements and consequently poorly represented in the assemblages. No complete isolated specimens are known and they are missing or unexposed in the articulated skulls. The best preserved specimens are AUP 11157 and UMZC T1268. These fragmented vomers are very similar to those of *Sphenodon* and *Planocephalosaurus* and as such can be attributed to *Clevosaurus* with some degree of confidence. The paired elements met in a straight medial contact. Anteriorly there is a slight ventral flexure of each element towards its contact with the premaxilla. Immediately posterior to the premaxillary articulation each vomer is pierced by a foramen which faces anteriorly and would have carried the palatal nerve and blood supply. There are no fragments of the posterior boundary of the vomer preserved, but judging from the orientation of the other palatal bones there was a medial articulation of the vomer with the pterygoid that is typical of sphenodontids. One or two small teeth may occur towards the midline, posterior to the vomerine aperture, or midway along the element; otherwise the vomers are apparently edentulous.

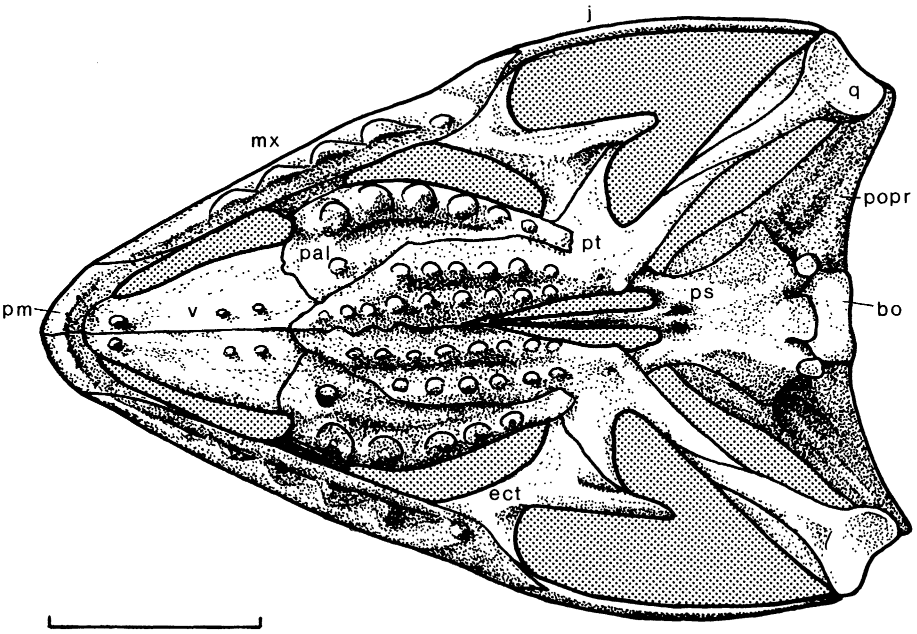


FIGURE 14. *Clevosaurus hudsoni.* Composite restoration of the skull in ventral view. Scale bar 1.0 cm.

The palatine is a large robust bone that medially overlapped the dorsal surface of the pterygoid and it exhibits a slight ventral flexure where it contacted the vomer along the medial boundary of the choanae. The posterior borders of the choanae are bounded completely by the palatines, and in this region an extensive process of each palatine runs anterolaterally to make a strong contact with the maxilla (figure 15, plate 3). This maxillary process is pierced by an infraorbital foramen which carried the maxillary nervous and blood supply. As noted earlier, a facet on the dorsal surface of the palatine, lying adjacent to the maxillary process, received a ventral extension from the prefrontal. A single row of five or six large, obtusely conical teeth occupy the lateralmost margin of each palatine. The largest teeth are positioned anteriorly and they run parallel to the maxillary dentition. These teeth bear lateral wear facets which in all probability were caused by a shearing contact with the lower jaw, although abrasive food material forced through the gap between the palatal and mandibular tooth rows may have been partly responsible. The smaller posterior teeth show less pronounced wear facets and in this region the row diverges slightly away from the maxillary dentition. In mature individuals thickening of the palatal bone extends the lateral tooth row below the general level of the palate. Frequently there is a solitary tooth lying medial to the main tooth row and immediately posterior to the internal naris. However, in one specimen, AUP 11158, three teeth form a rudimentary second palatine tooth row which in the living individual probably aligned with the more lateral of the pterygoid tooth rows.

The pterygoids (figure 16) are large elements that for the purposes of description can be

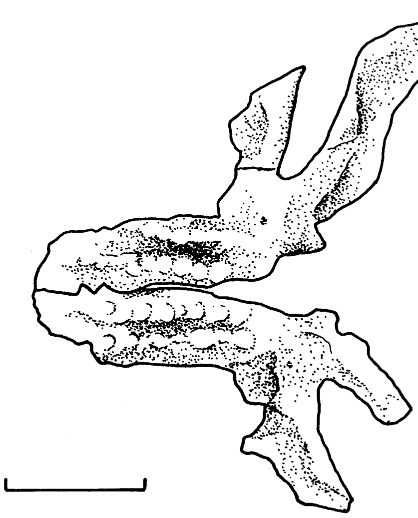


FIGURE 16. *Clevosaurus hudsoni*. Ventral view of paired pterygoids from the partial skull of a juvenile, UMZC T1270. Scale bar 4.0 mm.

divided into three basic regions: an anterior palatal shelf, a transverse process and a posterior quadrate flange. The palatal shelf bears two prominent rows of small teeth (figure 15); the medial row usually bears between nine and twelve teeth and the lateral row approximately six teeth. The two tooth rows are separated by a groove that is particularly evident in mature individuals. Anteriorly the paired pterygoids articulate along the midline by an intricate series of interlocking grooves and flanges, but about halfway along their length they separate to leave a narrow interpterygoid vacuity. The dorsal surface of the palatal shelf is produced as a thin medial septum that is invariably broken along the base, so that its full height is unknown. The facet for the reception of the basipterygoid process is circular, slightly concave, and faces posteriorly. It would appear as though there was some limited movement possible at this articulation. Behind the level of the basipterygoid articulation, the quadrate ramus of the pterygoid forms a thin, high sheet of bone that lay in extensive contact with the pterygoid wing of the quadrate. A recess in the medial surface of the quadrate ramus clearly indicates the position of an epipterygoid just dorsal, and posterior, to the basipterygoid articulation. However, no epipterygoid bones have been positively recognized within the assemblages. The broad transverse flanges of the pterygoid bear pronounced anteroventrally directed triangular facets that broadly overlapped the ectopterygoid.

The ectoptergoid is a large robust bone that had a broad lateral contact with the jugal and the maxilla. This lateral process runs forwards alongside the medial margin of the maxilla until it reaches the posterior extremity of a similar process from the palatine. The suborbital (or palatine) fenestrae are therefore completely enclosed by the ectopterygoids and the palatines (figure 15). The suborbital fenestra is relatively much wider than in *Sphenodon* and approaches the condition in *Planocephalosaurus*, a feature correlated with the divergence of the palatine tooth row away from the maxillary dentition. From the maxillary contact the ectopterygoid runs posteromedially as a rod-like strut where it again contacts the palatine. Behind this secondary palatine articulation the ectopterygoid overlaps the anteroventral face of the lateral pterygoid flange, and extends ventrally and posteriorly into a tapering process that served to align the lower jaws with the upper dentition.

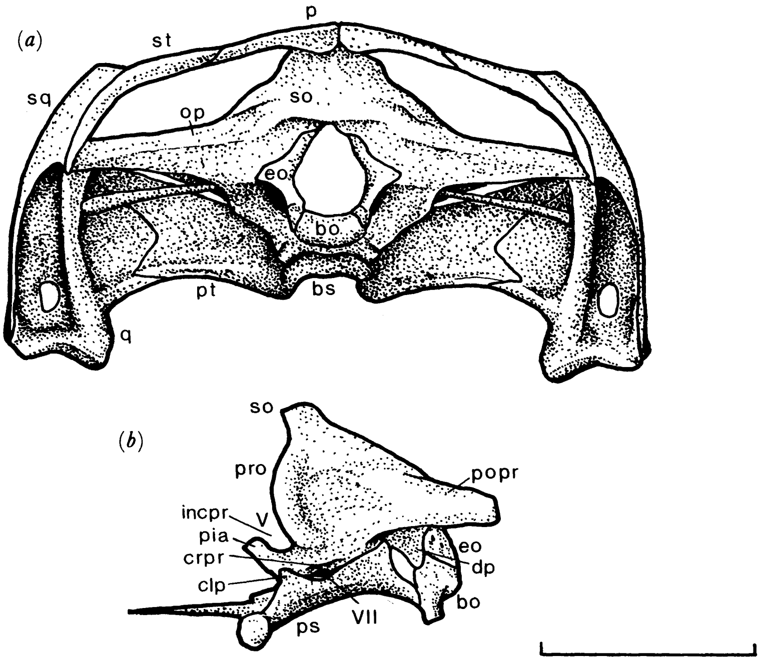


FIGURE 17. *Clevosaurus hudsoni*. Composite restoration of (*a*) the skull in posterior view, and (*b*) the braincase in lateral view. Scale bar 1.0 cm.

(*c*) *The braincase* (*figures* 14 *and* 17)

The floor of the braincase was for the most part formed by three elements; namely the parasphenoid, the basisphenoid and the basioccipital. The parasphenoid and basisphenoid are invariably fused together and in smaller genera, such as *Planocephalosaurus*, they are indistinguishable. However, in *Clevosaurus* a prominent step midway along the dorsal surface of the bone (figure 18), which is partly undercut by a faint horizontal groove, in all probability marks the posterior limit of the basisphenoid. The parasphenoid continues posteriorly towards the basioccipital and extends back as a tongue of bone passing beneath the basioccipital and the basal tubera, stopping just short of the occipital condyle; but essentially the major part of the parasphenoid sheathes the ventral surface of the basisphenoid. Anteriorly the parasphenoid tapers into a slender cultriform process that bisected the interpterygoid vacuity. The well-developed basipterygoid processes, situated either side of the posterior limit of the cultriform process, and directed anterolaterally, are formed by the basisphenoid. Between the basipterygoid processes the carotid foramina separately perforate the parasphenoid and both enter the same chamber, the sella turcica, in the basisphenoid. The dorsum sellae, also formed by the basisphenoid, is a thin wall of bone forming the posterior margin of the sella turcica. Shortly posterior to this is the step which it is believed marks the boundary between the parasphenoid and the basisphenoid. Lateral to the dorsum sellae the parasphenoid (in the form of the clinoid processes, figure 17*b*) curves dorsally to contacts with the prootics. Behind the carotid foramina the parasphenoid extends backwards and outwards into two posterior wings which overlap the anterior margins of the basal tubera. These posterior wings extend a short distance dorsally towards the opisthotics immediately posterior to the fenestrae ovalis. However, in most cases there was apparently only a minimal contact between the parasphenoid and the opisthotic so that an irregularly shaped unossified gap persisted in much the same way as in *Sphenodon* (figure 17*b*). Crocodiles have a similar unossified gap in this region but because the basisphenoid does not extend as far dorsally at this point the gap in crocodiles is essentially between the opisthotic and the prootic. Such openings in the braincase probably mark the position of the lagena.

Anterior to the basal tubera a substantial portion of the basioccipital is sheathed on its ventral surface by the parasphenoid as just described, but the major portion of the prominent basal tubera are formed by the basioccipital. The occipital condyle is situated immediately posterior to, and somewhat above the level of, the basal tubera, and it too is formed for the most part by the basioccipital. Well-defined posterolateral facets on the dorsal surface of the basioccipital received the exoccipitals. Unlike *Planocephalosaurus*, the exoccipitals in *Clevosaurus* rarely, if ever, fuse to the basioccipital. They are essentially columnar structures forming the lateral walls of the foramen magnum, and they are perforated by small foramina that carried branches of the hypoglossal nerve. The anterolateral edges are emarginated by the vagus foramina. Ventrally, each exoccipital is expanded posteriorly and contributes to the extreme lateral margin of the occipital condyle. The dorsal head of the element is expanded mediolaterally where it articulated with the opisthotic, and there is an adjacent facet for the supraoccipital.

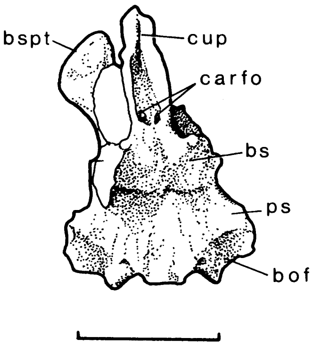


FIGURE 18. *Clevosaurus hudsoni*. A parabasisphenoid, UMZC T1227, in cranial view. Scale bar 5.0 mm.

The supraoccipital, opisthotics and prootics show a marked tendency to fuse together and no delimitating sutures can be differentiated in the preserved specimens. Unfortunately the fenestra ovalis and vagus foramen lend a fragility to the ventral region of the opisthotics and prootics, so that no specimens have been recovered with intact basioccipital and parabasisphenoid facets. A descending process from the opisthotic meets the basioccipital and separates the vagus foramen from the fenestra ovalis, but as noted earlier, this process in turn may have been separated from the parabasisphenoid by an unossified gap. Below the level of the fenestra ovalis the descending process of the opisthotic may have weakly contacted the prootic (figure 17*b*). The paroccipital processes extend laterally and posteriorly to contacts with the supratemporal and possibly also the squamosal. The ventral surfaces of the paroccipital processes are broadly concave, forming a groove leading into the fenestra ovalis. Anterior to the paroccipital processes the prootics extend dorsally towards the supraoccipital and they had additional contacts with the parabasisphenoid in the region of the clinoid processes (figure 17*b*). A foramen close to the articulation between the prootic and the parabasisphenoid defines the exit of nerve VII. Anterior to this foramen the prootic is developed dorsally into the pila antotica forming the anterior border of the open incisura prootica (figure 17*b*).

The supraoccipital forms the median part of the braincase roof. It only contributes a short portion to the margin of the foramen magnum, but it is extended posteriorly into a rudimentary horizontal shelf that partly overhangs the foramen magnum dorsally. Anteriorly the supraoccipital articulated with the parietals in the region immediately behind the pineal foramen.

(*d*) *The lower jaw* (*figure* 19)

The mandible is well represented in both the Cambridge and Aberdeen material and includes several articulated specimens. The lower jaw apparently comprises four bones: the dentary, the angular, the prearticular and the articular complex. The articular complex is formed by the fusion of the surangular and articular but in some instances the prearticular also fuses to this bone. Nevertheless, the degree of fusion of mandibular elements does not attain the level observed in *Planocephalosaurus* (Fraser 1982). No splenials have been identified in the *Clevosaurus* assemblages, but in one or two specimens of the dentary there may be a faint facet on the medial surface situated just below an area of secondary bone growth. This could be interpreted as a splenial facet. On the other hand it could simply be an artefact associated with the ridge formed by the ventral limit of secondary bone growth and the margin of the open meckelian groove. The latter is considered to be the more probable explanation because *Sphenodon* and *Planocephalosaurus* both lack a splenial, the meckelian canal remaining as an open sulcus. There appears to be no discrete coronoid bone, but there is a pronounced coronoid process on the dentary.

The dentary is a deep bone (figure 20, plate 3), slightly expanded anteriorly where it flexes medially and, with its counterpart, formed the entire mandibular symphysis. Behind the coronoid process the dentary is developed into a pronounced posterior process that partly overlaps the surangular portion of the articular complex. The surangular bears a second lateral facet situated below the dentary and which received the posterior half of the angular. In lateral view the reconstructed lower jaw displays a distinct mandibular foramen bounded by the dentary and the surangular (figure 19*c*).

The angular curves from its lateral contact with the surangular, onto the ventral surface of the mandible, and then continues forward below the prearticular and onto the medial surface of the dentary (figure 19*b*).

The prearticular is a long slender element that clasps the ventral surface of the articular. It has a limited exposure in lateral view but it does form much of the retroarticular process (figure 19*b*). It is partly overlapped by the angular both laterally and ventrally. In medial view it runs dorsal to the angular and extends forward and upward towards the base of the coronoid process, thereby forming the ventral margin of the adductor fossa. The dorsal margin of the adductor fossa is formed by a similar extension of the surangular which passes from the dorsal region of the coronoid process back towards the articular (figure 19*b*). The glenoid facet is formed exclusively by the articular, and is positioned immediately posterior to the adductor fossa. The form of its articulation surface corresponds closely to the quadrate condyle. It is in two parts, each part more or less flat but they are set at a slight angle to each other, so that the inner section faces somewhat medially. The more anteriorly disposed lateral portion is

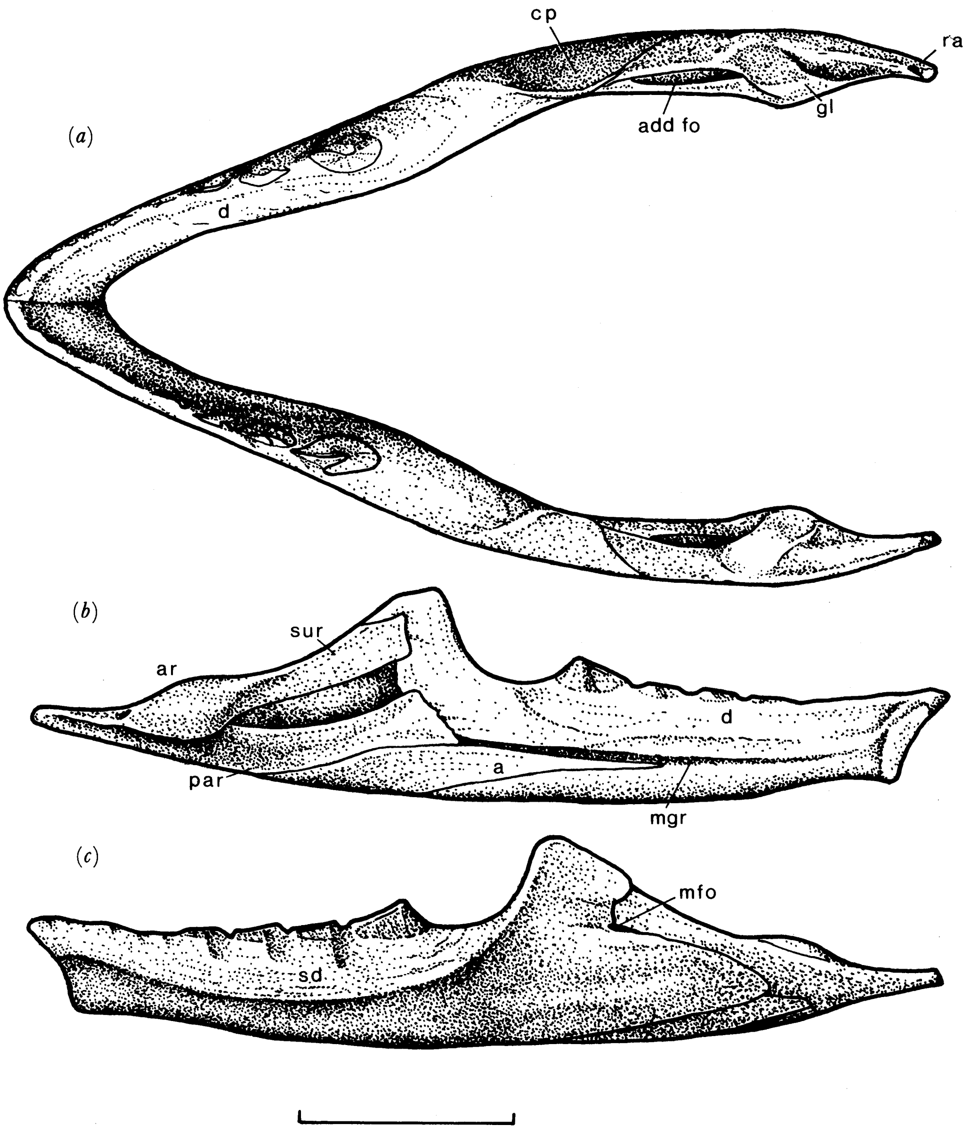
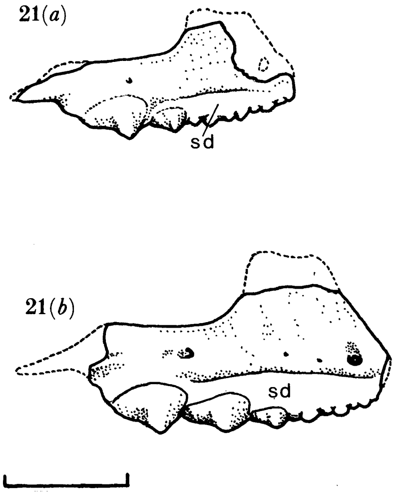


FIGURE 19. *Clevosaurus hudsoni.* Composite restoration of the mandible in (*a*) dorsal, (*b*) medial and (*c*) lateral views. Scale bar 1.0 cm.

orientated more or less horizontally. Behind the glenoid the articular tapers to a process which sits in a dorsomedial groove of the prearticular; both elements contributing to the well-developed retroarticular process.

(*e*) *The dentition*

Of the well-preserved premaxillae available in the Cambridge collections, approximately half bear three 'incisor' teeth and half of them four 'incisors'. This difference cannot be correlated with size or degree of secondary bone growth and there is no evidence of tooth addition or loss in the region. This distinction is unlikely to be a corollary of sexual dimorphism or specific differences because in the Aberdeen collections only two juvenile specimens (from a total of 38) bear four teeth. The remainder all possess just three teeth. The variable numbers in the Cambridge collections are difficult to explain. In both types the posteriormost tooth is distinctly larger than the others, and, with its base situated further dorsally than the remaining teeth, it is more exposed from the underlying bone. It is believed that the larger tooth is a replacement. It may be that where there are normally four teeth in the hatchling individual, either the last one, or in some cases two teeth, are soon replaced, and always by a single large tooth. This would explain the variability in tooth numbers observed in the Cambridge sample but offers no explanation for the lack of mature premaxillae bearing four teeth in the Aberdeen collections. In all the smaller specimens the teeth, whether three or four, are fused to the premaxillary bone at their bases, although their crowns stand clear of bone and are separate from one another. In the larger specimens there is a variable occurrence of secondary bone or dentine growth; the growth tending to be downward so that it filled in the spaces between the tooth crowns and formed a beak-like structure. Ultimately the secondary bone growth almost completely enclosed the teeth to form a single continuous, chisel-like cutting edge on each premaxilla.



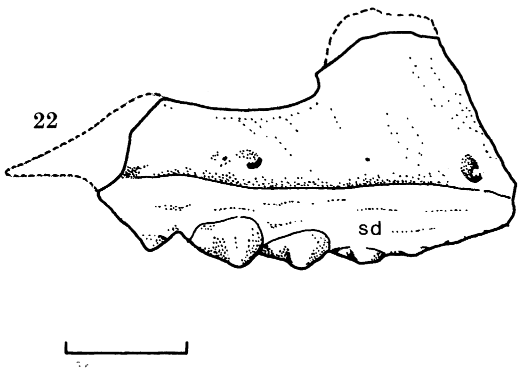


FIGURE 21. *Clevosaurus hudsoni*. Juvenile maxillae in lateral aspect. (*a*) AUP 11146 and (*b*) AUP 11187 (reversed for comparative purposes). Scale bar 4.0 mm.

FIGURE 22. *Clevosaurus hudsoni*. Mature maxilla, AUP 11144, in lateral view. Scale bar 4.0 mm.

The smallest maxilla preserved, AUP 11146, is 10 mm long, and it carries two distinct types of tooth (figure 21). There are eight small conical anterior teeth which together occupy approximately 4.0 mm of the entire tooth row. These teeth alternate in size; the odd-numbered members being slightly larger than the even-numbered members. This series of teeth represents the hatchling dentition and such alternation in size is characteristic of sphenodontids generally. Immediately following the hatchling series is a somewhat larger tooth that bears a distinctive blade-like posterolingual keel. This in turn is followed by a second large tooth carrying a similar posterolingual keel. These two teeth represent the first of the additional series. Subsequent development of the maxillary dentition consists of the addition of still larger flanged teeth one at a time. Thus the next recognizable stage consists of the hatchling series of about eight small teeth occupying the anterior 4 mm of the tooth row, but now followed by three flanged teeth (figure 21*b*). In the mature individual there are four additional teeth successively increasing in size, and in the largest individuals there may be as many as three, although more commonly one or two, smaller subconical teeth added posterior to the flanged series (figure 22). In the assemblages, maxillary specimens have been identified representing various stages of growth and in some, bearing deep excavations at the posterior end of the jaw quadrant, the additional teeth were not fully ankylosed to the bone at the time of death. The final stage in the postnatal development of the maxillary dentition occurs in old individuals in which the teeth have become heavily worn. Secondary bone and dentine growth, similar to that noted in the premaxilla, took place so that ventral downgrowth of the maxilla between and alongside the teeth tended to obliterate them. In the most mature individuals there is a continuous cutting edge of bone along the dental ramus with only the posteriormost few teeth still distinguishable, but nevertheless heavily worn so that even they form part of the cutting blade. However, before the additional teeth become too heavily obscured by secondary bone growth, they display medial wear facets that precisely mirror the form of the mandibular teeth, thereby indicating the occurrence of a precision shear bite of the jaws with no propalinal movements.

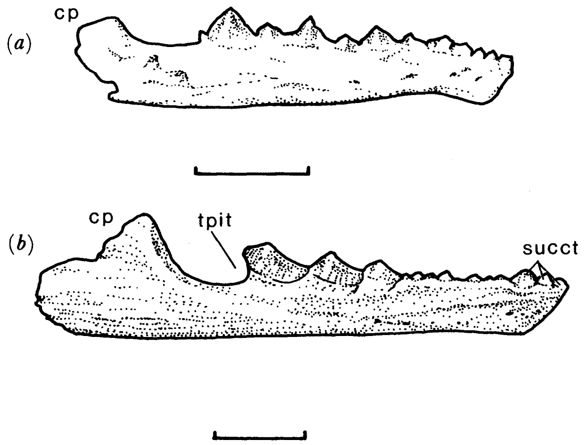


FIGURE 23. *Clevosaurus hudsoni*. (*a*) Juvenile dentary in lateral view. Composite restoration from AUP 11371 and 11372. Scale bar 2.0 mm. (*b*) Immature dentary, AUP 11373, in lateral view showing the empty tooth pit for the fourth additional tooth. Scale bar 2.0 mm.

The dentition of the dentaries show a similar pattern of development to that of the maxilla, but with one or two notable differences. In the earliest growth stages represented in the collections, the dentary exhibits twelve small teeth that alternate in size in much the same fashion as the maxillary hatchling series. Each of these teeth bears an anterior and a posterior flange forming a delicate but sharp razor-like structure (figure 23). There are no other teeth in the hatchling individual. In the next stages available for study the first four or five teeth have been replaced by two or three slightly larger, obtusely conical teeth with their bases positioned further ventrally than the remaining hatchling teeth (figure 23). These represent the successional teeth and they would have occluded against the medial surface of the premaxillary dentition. Posterior to the remnant hatchling series the additional teeth are added one at a time in the same manner as the maxillary additional series, successively increasing in size. Where they differ from the maxillary dentition is in the possession of two flanges: an extensive anterolateral one and a shorter posterior one. In mature individuals the full complement of additional teeth is four. The last tooth is the largest, but it does not possess a posterior flange, and even the anterior flange is relatively less extensive than in the preceding additional teeth. It is apparent that each additional tooth on the maxilla would have occluded against the posterior flange of one dentary tooth and the anterior flange of its neighbour. This precision shear bite produced extensive score lines across the lateral surface of the dentary, which in mature individuals extended into the bone well below the level of the dentition (figure 20). Secondary bone growth also occurs in adult dentaries. This has the tendency to obscure the anterior teeth, but helped to maintain a sharp cutting edge in an animal that has no continuous tooth replacement.

The dentition of *Clevosaurus hudsoni* shows many of the characteristic features associated with sphenodontids generally and typified by *Sphenodon*. These include the reduction of tooth replacement, the acrodont teeth readily categorized into successional, hatchling and additional dentitions, the alternation in tooth size in the hatchling series, the presence of flanges on the additional teeth, and the growth of secondary bone or dentine around the marginal dentition of mature individuals. In *Sphenodon* not only do the hatchling teeth alternate in size but so too do those teeth in the maxillary additional series. The extensive flanges in *Clevosaurus* occupy the spaces between successive additional teeth and as a consequence there is no room for any small teeth. In fact the presence of such flanges in the additional series could be the result of the coalescence of a small tooth with the large tooth preceding it, but there is no evidence for or against this theory, and no mechanism for its development is offered.

(*f*) *The postcranial skeleton*

Like the cranial elements, there are numerous disassociated specimens of most of the postcranial bones that are beautifully preserved. The occurrence of a fairly complete articulated skeleton was of immense value in providing the proportions of the body for restoration. In the absence of articulated specimens for the descriptions of *Planocephalosaurus* (Fraser & Walkden 1984), determination of vertebral numbers necessarily centred upon the abundance of each type of vertebra in the assemblages as well as by comparison with the numbers in the extant genus *Sphenodon*. In the articulated specimen of *Clevosaurus*, UMZC T1272, only the anterior section of the tail is preserved, and the exposed ventral surface of the presacral region is partly obscured by the gastralia. Therefore the assessment of vertebral numbers in *Clevosaurus* is still largely based on those of *Sphenodon*.

(i) *The axial skeleton*

In general terms the axial skeleton of *Clevosaurus hudsoni* is very similar to that of *Planocephalosaurus robinsonae*, although the individual elements are larger and somewhat more massively built. The centra are of the notochordal amphicoelous type throughout and when viewed ventrally have the 'hourglass' outline so familiar of sphenodontids. The zygosphenic articulation is rudimentary and generally not as well pronounced as in *Planocephalosaurus*. The greatest development of the zygosphene–zygantrum is in the cervical series. Accessory articulations situated at the bases of the neural spines take the form of a short posterior spur articulating in a notch on the anterior face of the succeeding vertebra. These accessory articulations are present in the cervical series and occur throughout the vertebral column as far as the anterior members of the caudal series.

The atlas neural arch was formed by paired elements that met in the dorsal midline in the same fashion as *Sphenodon*. No complete specimens of the atlas–axis centrum have been recovered and even in the articulated specimen it is badly damaged so that little information concerning its structure is available, although it is assumed to have been very similar to that of *Planocephalosaurus*.

The cervical vertebrae (figure 24) are relatively short and possess moderately developed elongate neural spines. The diapophysis and parapophysis have fused to form an elliptical synapophysis angled on an anteroventral–posterodorsal slope, and borne partly on the anterior edge of the centrum and partly on the neural arch (figure 24*a*). In *Planocephalosaurus robinsonae* the atlas–axis and the succeeding cervical vertebra possessed separate rib facets associated with a dichocephalous rib (Fraser & Walkden 1984), but there is no evidence for this in *Clevosaurus*. The synapophyses become less elongate in the dorsal series and, in the anterior members, migrate dorsally to become situated entirely on the neural arch (figure 25). However, further posteriorly the synapophyses progressively return to a more ventral position on the neural arch and they exhibit a concomitant reduction in size. The dorsal vertebrae are generally more elongate than the cervical members and their neural spines are lower, yet equally long. In some specimens a distinct suture remains between the centrum and neural arch ossification centres.

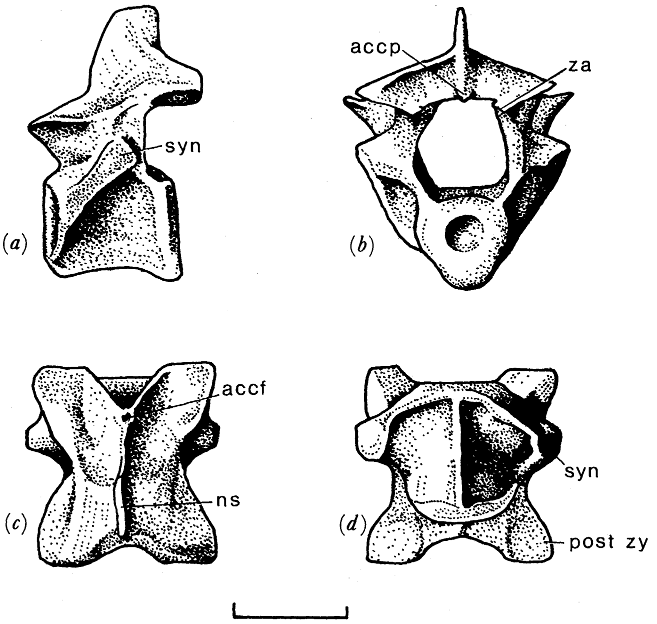


FIGURE 24. *Clevosaurus hudsoni*. Restoration of a cervical vertebra based upon AUP 11171 in (*a*) lateral (*b*) posterior (*c*) dorsal and (*d*) ventral views. Scale bar 3.0 mm.

The two sacral vertebrae are not well represented in the collections and no complete disassociated specimen of the first sacral vertebra had been recovered at the time of writing. The sacrum of the articulated specimen is partly obscured by the puboischiadic plate, but certain features are available for study. A second sacral vertebra housed in the British Museum (BMNH R9266) was one of the original discoveries made by Hudson and listed by Swinton (1939).

Both sacral vertebrae bear low neural spines and stout sacral ribs fused low down on the neural arch and centrum. The ribs of the first sacral are gently inclined downwards and

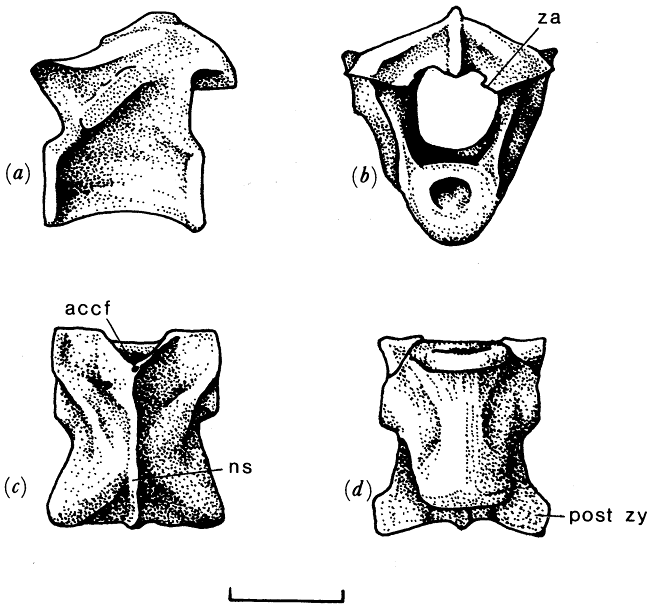


FIGURE 25. *Clevosaurus hudsoni*. Restoration of a dorsal vertebra based upon AUP 11172 in (*a*) lateral, (*b*) posterior (*c*) dorsal and (*d*) ventral views. Scale bar 3.0 mm.

backwards, and, judging from UMZC T1271, the distal end is expanded dorsoventrally where it articulated with the ilium. Like *Kallimodon*, *Homoeosaurus* and *Planocephalosaurus*, the ribs of the second sacral are bifurcated (figure 26). Each rib bears a dorsoventral thickening of the distal extremity where it articulated with the ilium, immediately posterior to the first sacral rib, but it does not appear to have made contact with the first sacral at this point. The posterior process of the second rib is directed posterolaterally and is produced as a slender spur having no contact with the ilium, but presumably forming an extra surface for caudal muscle attachment.

The first three or four caudals are all of approximately equal length to the sacrals and they bear prominent pleurapophyses directed almost at right angles to the long axis (figure 26). These transverse processes are dorsoventrally flattened and have a blunt distal termination. In the first caudal the transverse processes are marked by a shallow groove on the ventral surface which runs the entire length of each process (figure 26*b*). The anterior members of the caudal series bear tall and slender neural spines. Further posteriorly the caudal vertebrae become progressively more elongate and the transverse processes appear progressively shorter and more rounded in cross section (figure 27). The neural spines remain slender but their height is gradually reduced. In addition each pair of zygapophyses move progressively closer together as the neural arch decreases in diameter, until the zygapophyses are lost altogether. In the absence of any complete articulated specimens of the tail, it is impossible to quantify and define exactly where specific changes in the vertebral structure occur. Fracture planes (autotomic septa) are known to occur in the centra of the more posterior vertebrae, but it is difficult to ascertain at what position they begin. None can be observed in the first eight caudal vertebrae preserved in UMZC T1271, but because in *Sphenodon* they begin at V8, it is not unreasonable to suppose that in *Clevosaurus* the autotomic vertebrae begin soon after. In the anteriormost vertebrae bearing fracture planes a small transverse process is still present (figure 27*a*, *d*), but further posteriorly the transverse processes are lost completely and the neural spine becomes

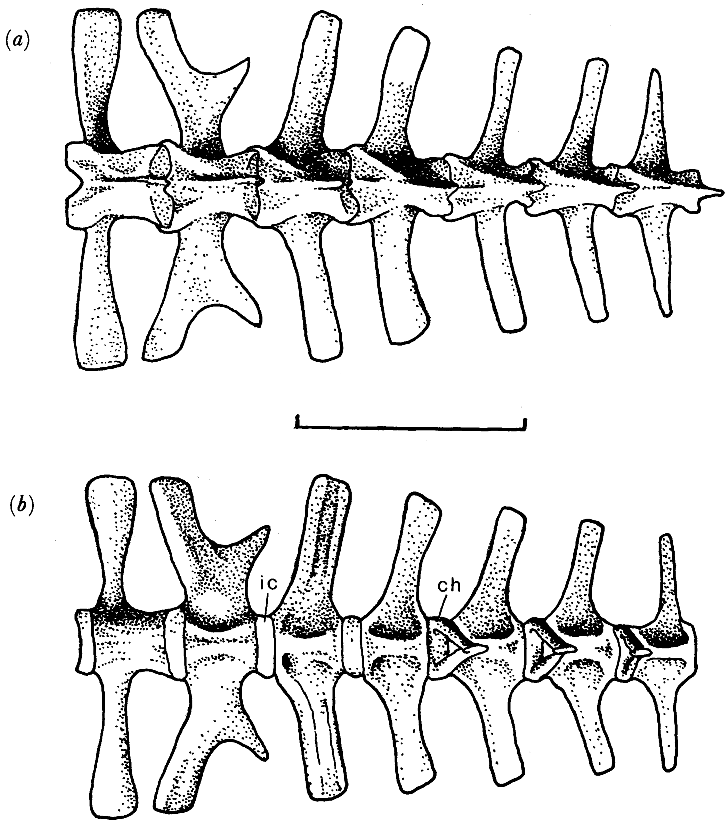


FIGURE 26. *Clevosaurus hudsoni*. Composite restoration of the two sacral vertebrae and the first five caudals in (*a*) dorsal and (*b*) ventral views. Scale bar 12.0 mm.

little more than a small excrescence. On the ventral surface of the autotomic caudals a sagittal groove protected the blood vessels supplying the tail. On each side of the autotomic septa the edges of the groove are raised into small protuberances (figure 27*d*) which Hoffstetter & Gasc (1969) termed 'paraseptal apophyses'.

Separate intercentra were apparently present throughout the entire length of the vertebral column. The precaudal intercentra take the form of simple semicircular bands of bone which in UMZC T1271 are readily visible in ventral aspect, and they are also known from a number of isolated specimens in the collections. Three similar intercentra occur at the base of the tail

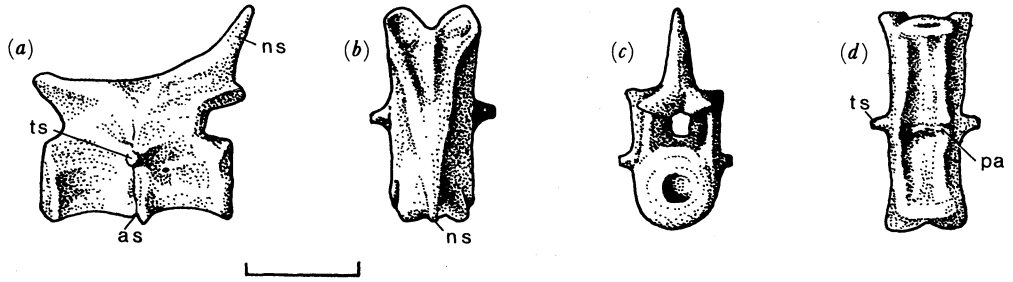


FIGURE 27. *Clevosaurus hudsoni*. Restoration of a mid-caudal vertebra based partially on AUP 11174. (*a*) Lateral (*b*) dorsal (*c*) posterior and (*d*) ventral views. Scale bar 3.0 mm.

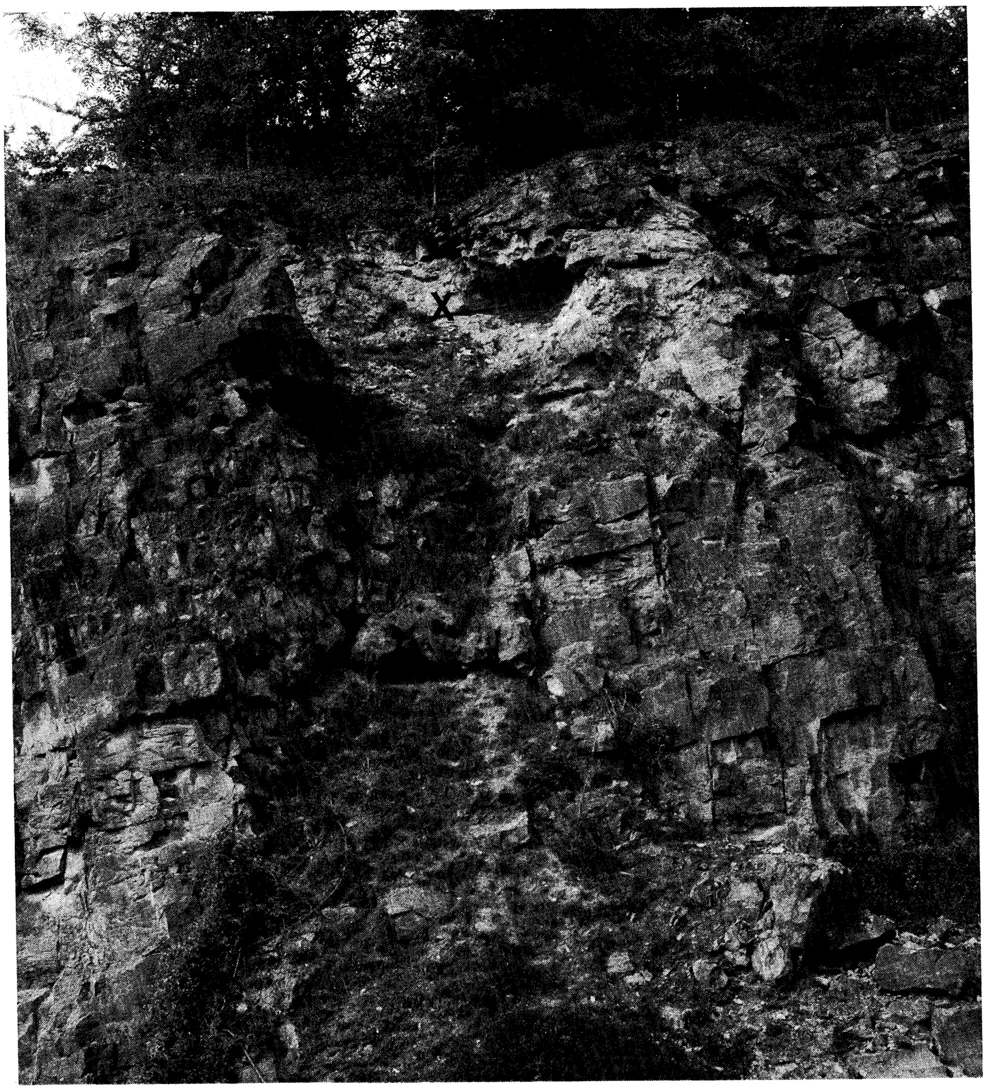


FIGURE 2. Site one, Cromhall Quarry. The main fossiliferous horizon is marked X.

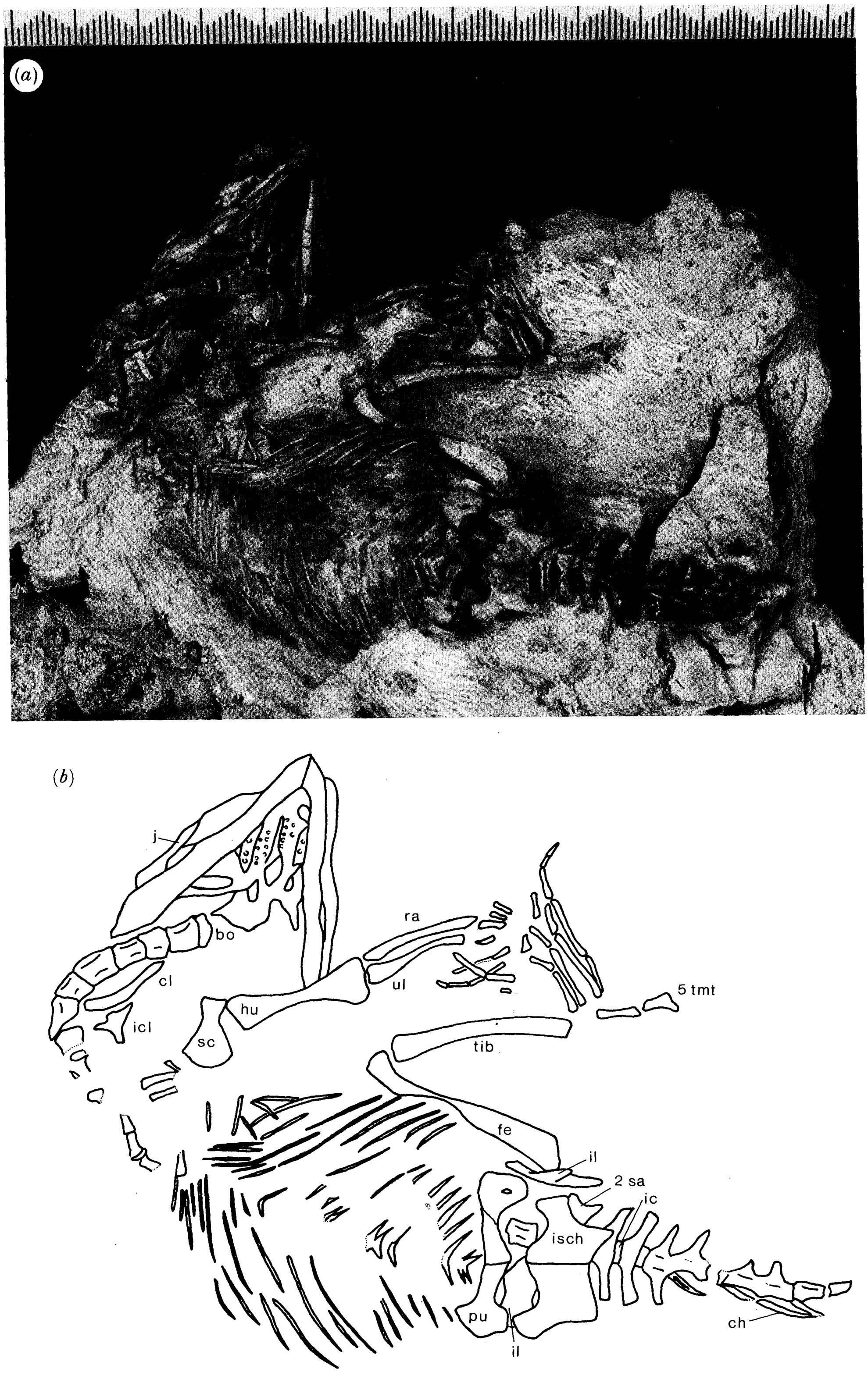
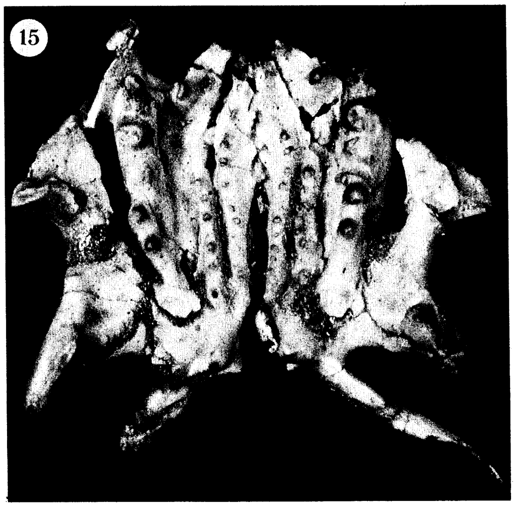


FIGURE 4. *Clevosaurus hudsoni*. (*a*) The articulated skeleton UMZC T1271 in ventral aspect, with (*b*) explanatory diagram.



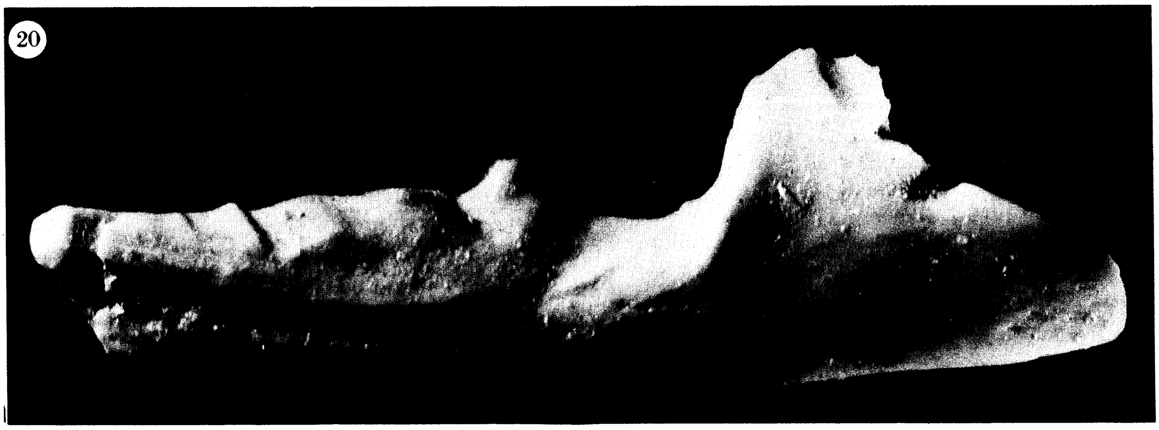


FIGURE 12. *Clevosaurus hudsoni*. AUP 11169, articulated skull exposed in dorsal view and showing the supratemporal, parietal table and interorbital region of the left side. (Magn. × 5.)

FIGURE 15. *Clevosaurus hudsoni*. Partial articulated palate, UMZC T1269, in ventral aspect. (Magn. × 8.)

FIGURE 20. *Clevosaurus hudsoni*. Dentary, UMZC T1276, in lateral view. (Magn. × 3.)

FIGURE 37. *Clevosaurus hudsoni*. A pathological left femur, UMZC T1275, compared with the normal condition, UMZC T1274. (Magn. ×3.)

FIGURE 38. *Clevosaurus minor*. A left maxilla, the holotype AUP 11377, in lateral view. (Magn. ×10.)

but posteriorly the intercentra take the form of chevron bones. The anterior chevrons, as exemplified by the four preserved in UMZC T1271, consist of a basal bar, but in other isolated specimens this bar is replaced by basally widened and contiguous pedicels.

All the isolated ribs in the collections can be described as sub-bicipital; that is each holocephalous rib has resulted from the fusion of the tuberculum with the capitulum. Because of the dorsoventral crushing of the articulated skeleton, and the fact that much of the postcranial skeleton is only exposed in ventral view, no further comment on the arrangement of the ribs is permitted.

In common with *Sphenodon* and the Jurassic genera, *Clevosaurus* possessed rows of gastralia which are well preserved in UMZC T1271. Each row consists of a median V with the apex pointing forward and a pair of slender lateral splints. There are 25 such rows, which conforms to the pattern in *Sphenodon*. *Sphenodon* displays two rows of gastralia per metameric segment, and assuming the same to be true for *Clevosaurus*, it suggests that the number of dorsal vertebrae in *Clevosaurus* is most probably identical to that of *Sphenodon*.

(ii) *The appendicular skeleton*

There are five ossified elements of the pectoral girdle: paired clavicles and scapulocoracoids and a single interclavicle. In addition, there was in all probability a cartilaginous sternum.

The head of the interclavicle is T-shaped and the articulations with the clavicles lie on the anteroventral surface of the cross-bar. There are no complete clavicles in the collections, but judging by the facets on the interclavicle and the general arrangement of the other pectoral elements, it is considered unlikely that they differed greatly from those of *Sphenodon* or *Planocephalosaurus*.

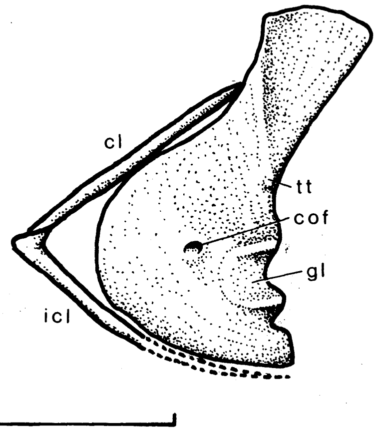


FIGURE 28. *Clevosaurus hudsoni*. Composite restoration of the pectoral girdle. Scale bar 1.0 cm.

There are no growth stages known in which the scapula and coracoid are separated by a complete suture and they will be treated here as a single bone. The dorsal blade appears relatively short (figure 28), although in life it may have been considerably extended by a cartilaginous suprascapula. A ridge running diagonally in an anterodorsal–posteroventral direction ends near the base of the scapula blade in a small tubercle to which the triceps tendon was attached. Below the level of the prominent glenoid, the scapulocoracoid flexes medially and probably met the median ramus of the interclavicle. Behind the glenoid the scapulocoracoid terminates in a blunt process, whereas in *Sphenodon* it extends slightly further posteriorly and tapers to a rounded point. A coracoid foramen is positioned immediately anterior to the glenoid. No fenestration of the anterior margin of the scapulocoracoid of the type reported in *Planocephalosaurus* (Fraser & Walkden 1984) has been observed in any of the specimens collected to date. However, a specimen of *Sphenodon* in the Cambridge University Museum of Zoology (R2582) does exhibit similar rudimentary fenestration, and provides further evidence that fenestration, albeit quite incipient, is not entirely restricted to lizards.

The humerus (figure 29) is very like that of *Planocephalosaurus* but somewhat larger. The expanded proximal head is anteroposteriorly compressed and the posteroventral edge bears a prominent tubercle and ridge (figure 29*a*, *b*) to which the deltopectoralis musculature was attached. As a result of the axial twist of the shaft, the distal head of the humerus is extended at right angles to the plane of compression of the proximal head. The entepicondyle is more extensive than the ectepicondyle and bears a prominent foramen opening out onto the ventral surface, and which penetrates through to the posterior edge of the element (figure 29*a*, *b*). The ectepicondyle foramen is situated on the anterior face of the element and either incomplete ossification or perhaps breakage gives the preserved specimens the appearance of a groove rather than a foramen (figure 29*c*, *d*). The capitellum and trochlea are positioned adjacent to each other on the distal extremity (figure 29*b*).

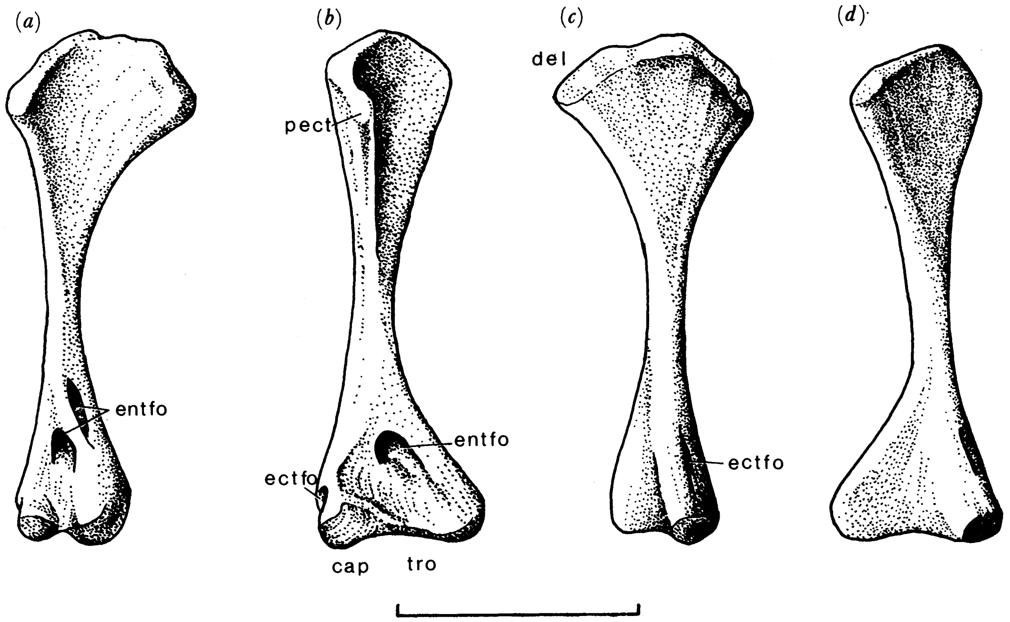


FIGURE 29. *Clevosaurus hudsoni*. Restoration of the right humerus based largely upon AUP 11179. (*a*) Posterior (*b*) ventral (*c*) anterior and (*d*) dorsal views. Scale bar 1.0 cm.

Of the two forelimb epipodials (figure 30), the ulna is the more abundant in the collections. It has an expanded proximal head which is somewhat flattened anteroposteriorly. In the majority of specimens the olecranon process is missing, but in AUP 11178 the olecranon is developed as a prominent spur. This formed part of the sigmoid notch articulating over the trochlea of the humerus. On the anteromedial face, just below the sigmoid notch, there is a small rugosity which presumably apposed a flattened surface on the radius. The shaft of the ulna is slender and subcircular in cross section and the distal head is also somewhat anteroposteriorly flattened where it articulated with the ulnare.

The radius is known from a single isolated specimen and the element in the articulated specimen UMZC T1271. This rarity is presumably a result of its rather delicate structure lending it a fragility that decreases the chances of good preservation. The shaft is slender and bows away from the ulna. Both the proximal and distal heads are expanded very little. From observations on UMZC T1271, the proximal articulation surface appears to have been a shallow oval concavity that was continuous with the sigmoid notch of the ulna. The distal articulation with the radiale took the form of a flattened oval facet.

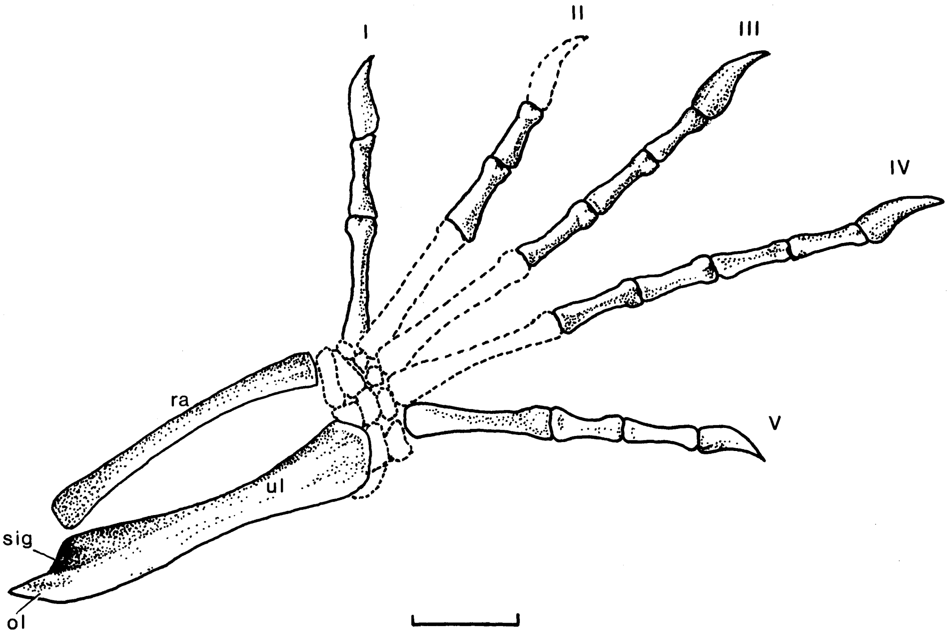
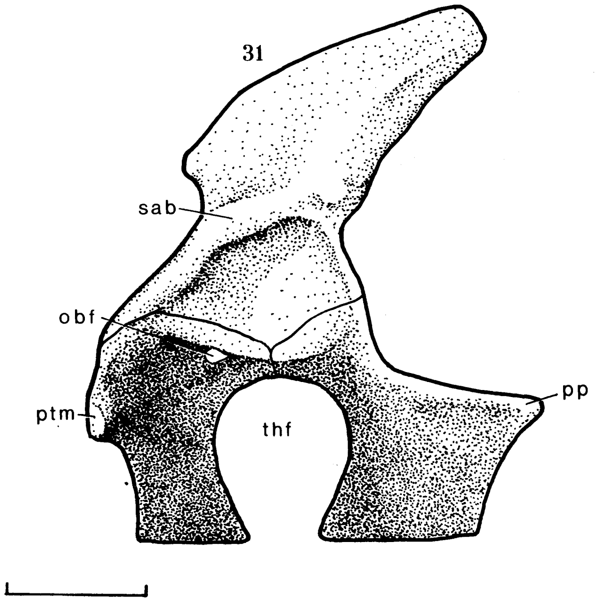


FIGURE 30. *Clevosaurus hudsoni*. Composite restoration of the left forelimb based partly on AUP 11178 and UMZC T1271. Scale bar 5.0 mm.

The pelvic girdle (figure 31) is beautifully exposed in ventral view of UMZC T1271. However, dorsoventral compression has forced it against the ventral surface of the vertebral column, and thereby slightly distorted the relationships of the individual elements. Numerous other isolated specimens of each of the three pelvic elements are available for study, although the distal expansions of both the pubis and ischium are noticeably prone to breakage.

The ilium forms the major part of the acetabulum which is bounded dorsally by a low supracetabular buttress. Above the acetabulum the ilium expands into a broad posterodorsally directed blade, which is relatively broader and blunter than that displayed by *Sphenodon*. At the base of the iliac blade the medial surface bears two articulation facets for the two sacral ribs (figure 32). The facet for the first sacral faces medially and is rather diffuse, although it generally appears oval in outline. It is separated from the facet for the second sacral rib by an extremely narrow bony ridge. The second sacral articulation facet is discrete and elliptical in shape. It lies slightly dorsal to the first facet and it is directed posteromedially. In common with other sphenodontids the anterior edge of the ilium is produced into a slender process that clasps the anterodorsal margin of the pubis.



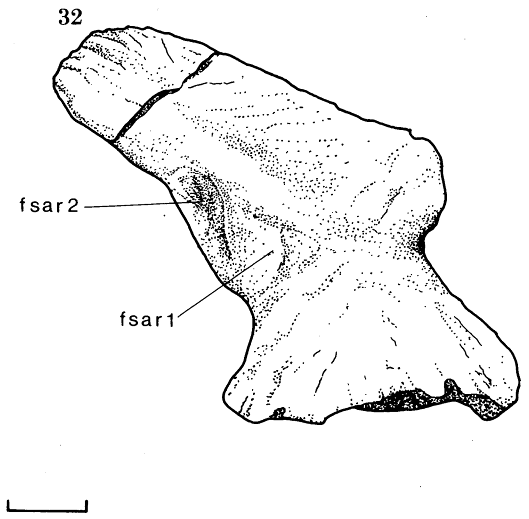


FIGURE 31. *Clevosaurus hudsoni.* Composite restoration of the pelvic girdle in lateral view and based upon AUP 11180 and UMZC T1271. Scale bar 5.0 mm.

FIGURE 32. *Clevosaurus hudsoni.* Ilium, UMZC T1279, in medial view. Scale bar 2.0 mm.

The pubis only contributes a small portion to the acetabulum. The major part of the bone consists of a thin, flat, ventrolaterally directed plate which is emarginated on its posterior side by a large thyroid fenestra. Above the level of this fenestra the pubis had a short contact with the ischium. Positioned immediately in front of this articulation a small obturator foramen perforates the bone. A protuberance on the anterior edge, just beneath the anterior articulation with the ilium, is thought to mark the insertion of the pubotibialis musculature.

The ischium forms the posterior half of the puboischiadic plate and takes the shape of a thin rhomboid which is connected to both the pubis and the ilium by a short thickened neck. The four edges of the rhomboid are formed by the posterior margin of the thyroid fenestra, a straight ventral edge articulating with its counterpart, and a well developed posterior tubercle forming the angle between the remaining two sides. The posterior tubercle appears to be a diagnostic feature of the sphenodontids and was presumably for the attachment of ligaments and tendons associated with the tail musculature.

Several femora representing various ontogenetic stages have been recovered from the deposits. In addition, the left femur in UMZC T1271 is well preserved. It is a long slender element (figure 33) conforming to the generalized sphenodontid pattern displayed by *Sphenodon* and *Planocephalosaurus*. It retains a sigmoid flexure of the shaft and the most prominent feature of the proximal head is the internal trochanter (figure 33*b*, *c*). The distal head is typically divided into a medial (anterior) and a lateral (posterior) condyle (figure 33*c*). The medial condyle articulated exclusively with the tibia, but the lateral condyle, in addition to an articulation with the tibia, also had a sliding contact with the fibula.

The tibia (figure 34) is a stout bone that is well represented in the collections. The proximal head is expanded and partly divided into two condyles (figure 34*b*) corresponding to the medial and lateral condyles of the femur referred to above. The relatively long shaft is

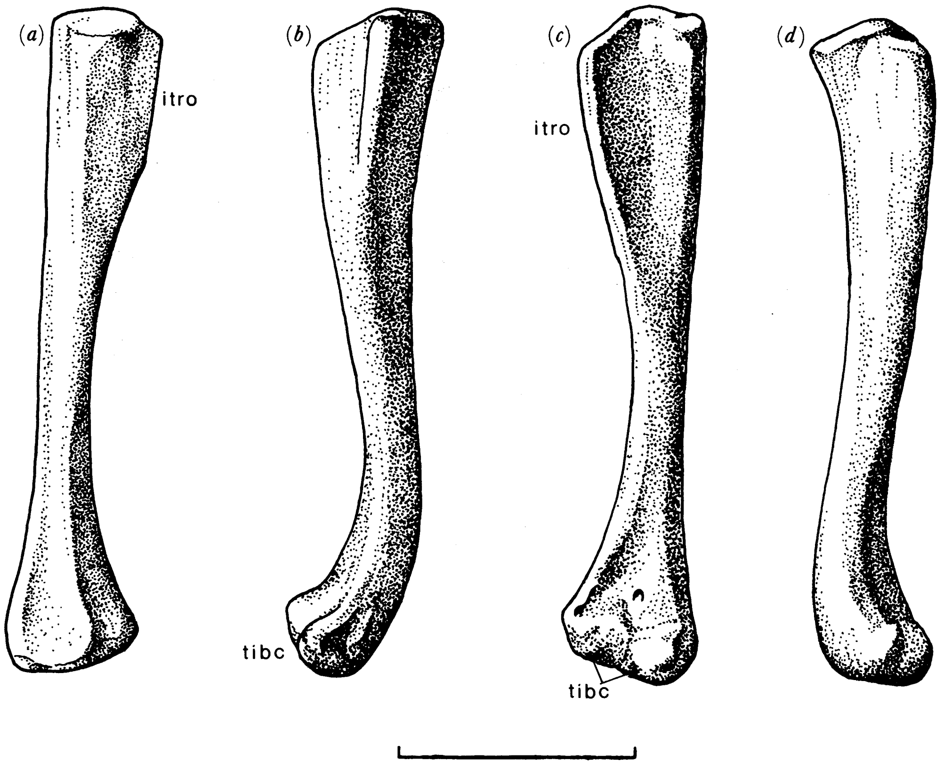


FIGURE 33. *Clevosaurus hudsoni*. Restoration of a right femur based upon UMZC T1274. (*a*) Dorsal (*b*) posterior (*c*) ventral and (*d*) anterior views. Scale bar 1.0 cm.

approximately cylindrical and bows slightly away from the fibula. Towards the proximal end the posterior surface bears a marked groove and rugosity where the iliofibularis musculature had its insertion (figure 34*c*). The distal head is slightly swollen and terminates in a simple, convex articulation surface for the astragalocalcaneum.

The fibula was a very gracile element and for this reason it is poorly represented in the assemblages. It is missing from the articulated specimen and there are no complete disassociated specimens that can be positively identified. There are a few fragments of mediolaterally compressed shafts occurring in both the Aberdeen and Cambridge collections, but they are intermixed with archosaurian remains. Nevertheless they can be more readily identified with *Sphenodon* than with the archosaurian fibula pattern.

The generally flattened, and rugose proximal and distal surfaces observed in many long bone specimens may be attributable to the occurrence of epiphyseal growth in *Clevosaurus hudsoni*.

Several disassociated small carpals, tarsals and metapodials have been collected which on their own would be difficult to assign to an individual species, but the partly preserved left manus and pes in UMZC T1271 considerably aids in their reconstruction.

The small bones of the carpus are missing in UMZC T1271, and, because they are difficult to identify accurately in the disassociated material, the reconstruction (figure 30) has been largely based on *Sphenodon*. The bones of the tarsus (figure 35) are more readily identifiable. The astragalus and calcaneum are fused to form a robust astragalocalcaneum that is anteroposteriorly flattened. The dorsal edge bears discrete facets for the tibia and the fibula. A

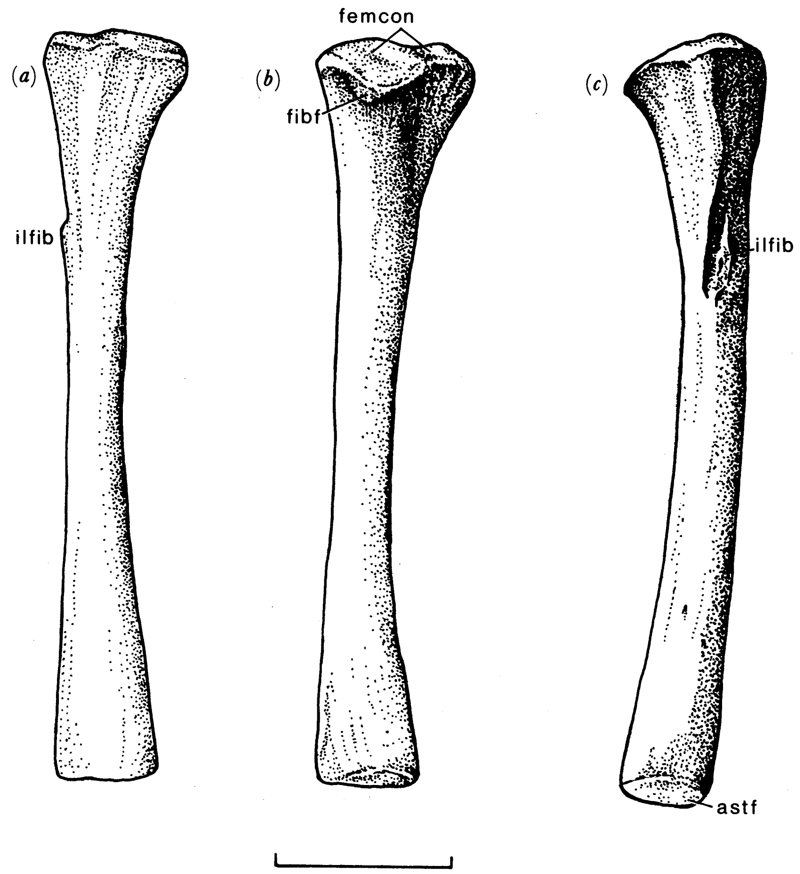


FIGURE 34. *Clevosaurus hudsoni*. Restoration of a left tibia based upon AUP 11184 and 11185. (*a*) Anterior (*b*) lateral and (*c*) posterior views. Scale bar 5.0 mm.

small concavity on the ventral edge received the fourth distal tarsal. The fifth distal tarsal has fused with the fifth metatarsal.

With the exception of the fifth metatarsal (tarsometatarsal), each metapodial has a long slender shaft and a slightly expanded proximal head bearing tuberosities for the attachment of the digital extensor and flexor muscles. The fifth tarsometatarsal is a small compact bone readily preserved in the Cromhall sediments. It is clearly 'hooked' in the fashion described by

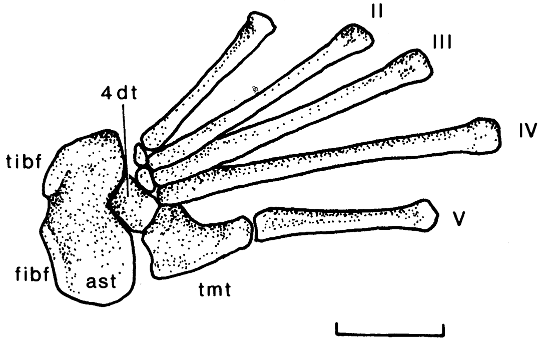


FIGURE 35. *Clevosaurus hudsoni*. Restoration of the left tarsus based upon UMZC T1271. Scale bar 5.0 mm.

Robinson (1975), and as such is comparable with *Sphenodon*. The medial side of the proximal head bears a flattened facet that articulated with the fourth distal tarsal. The plantar surface bears two tuberosities to which the flexor musculature was attached, but the dorsal surface is relatively featureless.

Judging from the remains of the manus and pes in UMZC T1271, the phalangeal formula of *Clevosaurus hudsoni* was almost certainly identical to that of *Sphenodon*, i.e. manus 2:3:4:5:3; pes 2:3:4:5:4.

(*g*) *Reconstruction*

Robinson's initial reconstruction of the skull of *Clevosaurus hudsoni* (Robinson 1973) differs slightly from that indicated by the present material (figure 3). I have restored the skull with a somewhat narrower parietal table and without the lateral bulge of the prefrontals as displayed in dorsal view by Robinson. The new material indicates that the ventral process of the squamosal is rather longer than shown by Robinson, and that, in some instances at least, the jugal overlapped the quadratojugal. Apart from these, there are no significant differences, and the material described here is assigned to *C. hudsoni* without reservation. The differences between Robinson's reconstructions and my own may possibly indicate some phenotypic variation, but more probably result from interpretations of variable states of preservation. The apparent absence of certain slender processes in Robinson's material would seem to be attributable to persistent natural breakage. Similarly it is difficult to assess the degree of compression of articulated material and the extent to which individual elements have moved relative to each other. The dorsal compression and the outward movement of the quadrate condyles in UMZC T1271 give the impression that the skull of *Clevosaurus* is very broad, but the well-preserved skull roof of AUP 11169, with the fused mandibles UMZC T1272, provide a more accurate picture.

The largest jaw bones in the collections are estimated to be from individuals with a skull perhaps a little over 4.0 cm in length. The skull of UMZC T1271 is 3.5 cm long and, despite the presence of a worn marginal dentition, is therefore perhaps not quite representative of a fully grown individual. Nevertheless the postcranial skeleton provides invaluable information concerning the proportions of the body and the various dimensions are given in table 2.

Bipedality has been described in several modern lizards (see, for example, Snyder 1949, 1952, 1954, 1962) and has also been inferred in some small lizard-like fossils (Carroll & Thomson 1982). Snyder (1952) cited various characteristics for bipedality in lizards that might be assumed to be applicable to fossil reptilians. Of particular relevance here are the length ratios of forelimb:hindlimb and hindlimb:trunk. From UMZC T1271, the forelimb:hindlimb ratio can be directly measured from the combined lengths of the humerus and ulna as against the femur and tibia. An independent estimate of this ratio was obtained by taking the mean lengths of all the fully ossified and intact disassociated long bones in the collections (table 3). The proportions so obtained were in reasonable agreement with the articulated skeleton (76 %). In addition the combined length of the femur and tibia in the articulated skeleton was estimated to be approximately 70 % of the total length of the trunk. Bipedal reptiles typically exhibit a great disparity between the lengths of the forelimbs and hindlimbs, although the ratio is highly variable (even among obligate bipedal theropods), and it may be as high as 70 % in *Deinonychus* (Ostrom 1969; Chatterjee 1980). Nevertheless, Ewer (1965) indicates that in facultative bipedal lizards the ratio can be generally expected to be 70 % or less, whereas in

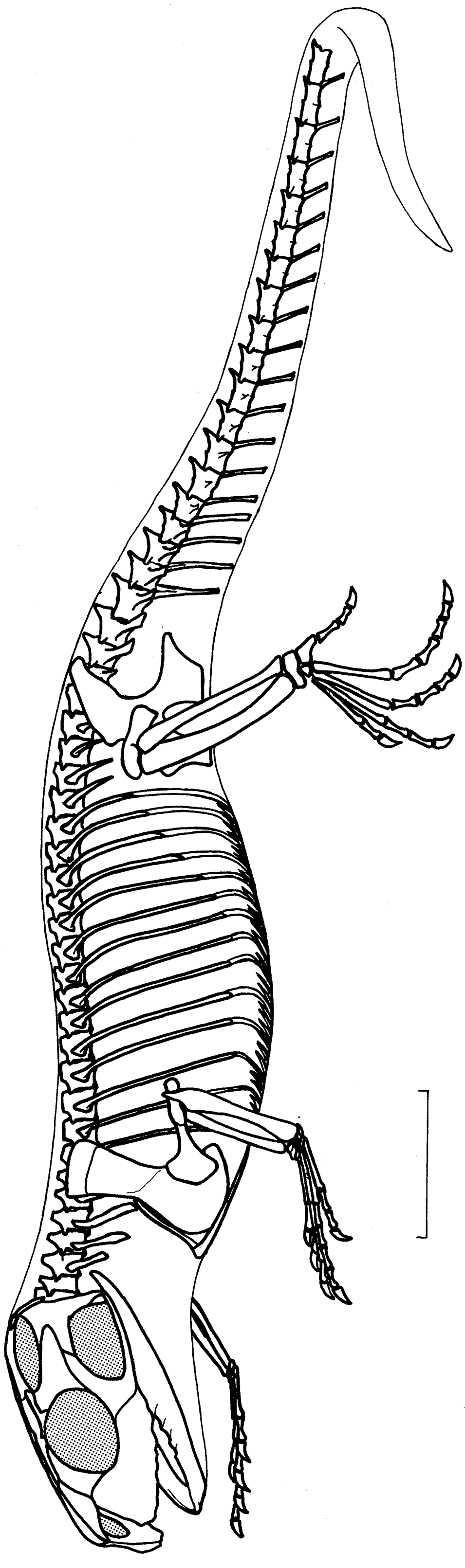


FIGURE 36. *Clevosaurus hudsoni*. Composite restoration of the entire skeleton. Scale bar 2.0 cm.

TABLE 2. DIMENSIONS OF THE ARTICULATED SKELETON OF *C. HUDSONI* UMZC T1271 (FIGURE 4)

	length/mm
skull	35
vertebral column (From atlas to the 8th caudal)	145
vertebral column, between the pectoral and pelvic girdles (trunk)	74
femur	28
tibia	23
humerus	21
ulna	18

quadrupedal forms 75 % or more, is a realistic value. Moreover, although the hindlimb : trunk ratio of *Sphenodon* is approximately 52 %, in fast, agile quadrupedal lizards (such as *Agama*) it is in excess of 70 % and thus closely approaches the estimate for *Clevosaurus*. By comparison in known facultative bipeds, e.g. *Basiliscus*, the hindlimb : trunk ratio attains much higher values, so that 100 % or more is not uncommon (Ewer 1965). The evidence therefore supports the view that *Clevosaurus* was an agile quadrupedal form. It exhibited a 'primitive reptilian sprawling gait' and the gastralia would have afforded some protection to the viscera as the abdomen was held close to the ground.

TABLE 3. LENGTHS (MILLIMETRES) OF COMPLETELY OSSIFIED LONG BONE SPECIMENS OF *C. HUDSONI*

	femur	tibia	humerus	ulna
	31.2	21.2	27.5	19.5
	26.3	23.8	19.6	19.8
	34.8	27.0	22.5	16.3
	23.8	16.5	22.1	—
	—	21.9	20.1	—
	—	—	15.3	—
	—	—	26.0	—
	—		15.1	—
	—	—	15.6	—
mean	29.0	22.1	20.4	18.5

With respect to the proportions and dimensions not directly obtainable from the available material (e.g. the full extent of the tail) the full reconstruction (figure 36) has been largely modelled upon the condition in *Sphenodon*.

(*h*) *Mode of life*

Clevosaurus hudsoni was a lizard-like reptile that, with a maximum length of approximately 25 cm, was somewhat smaller than the extant genus *Sphenodon*. The skull was strongly built and in the adult the jaws and worn dentition formed a powerful shearing mechanism fully capable of crushing the chitin exoskeleton of large insects. It has also been suggested that *Clevosaurus hudsoni* may have been a facultative herbivore (Fraser & Walkden 1983). Certainly the premaxillary 'beak' and anterior 'edentulous' region of the mature individual would have formed an effective cropping implement, and the continuous sharp edge of the jaws would probably have been capable of shredding resistant plant matter. On the other hand the juveniles almost certainly fed exclusively on small insects and soft-bodied invertebrates. The immature jaw bones possess sharp, pointed teeth, and they would have lacked the powerful shearing musculature to have dealt effectively with a tough exoskeleton or cellulose.

Two extreme types of prey capture techniques are widely recognized in modern lizards. These can be broadly defined as 'sit and wait' and 'widely foraging' strategies, but in between these two strategies a whole spectrum of prey capture techniques can be recognized. Schoener (1977) and Stamps (1977) independently recorded aggressive behaviour in lizards that employed the 'sit and wait' feeding strategy. This was manifested by individuals attacking conspecifics that happened to encroach into a guarded feeding territory. Thus it could be expected that in fossil species that employed the 'sit and wait' feeding strategy adults might show a high incidence of fracture damage as a result of territorial aggression. In this respect Evans (1983) recorded a relatively high percentage of mandibular fracture (7%) in the Jurassic insectivorous reptile *Gephyrosaurus*. She therefore postulated that *Gephyrosaurus* may have employed the 'sit and wait' feeding technique, and vigorously guarded a feeding territory. There is some indication of rehealed mandibular fractures in some specimens of *Clevosaurus hudsoni*. One dentary is particularly badly deformed and although the individual obviously survived long enough for the break to be reunited, it may have been that the jaw could not function adequately and the animal ultimately died from its injury. However, fracture damage occurs in less than 1% of the jaw bones and is equally common in juveniles. This may be indicative of injuries arising from unsuccessful predatory attacks, and in turn it perhaps suggests that *Clevosaurus hudsoni* favoured a widely foraging feeding strategy as an insectivore. On the other hand it is also compatible with herbivory because it is highly unlikely that as a herbivore there would be any requirement to defend a feeding territory.

Occasionally other elements, particularly long bones, display thickened rehealed fracture lines. Again these are considered most likely to be the result of unsuccessful predatory attacks or possibly accidental injuries, but they need not have necessarily prevented the individual from leading a reasonably normal existence. By comparison, there is one specimen of femur (UMZC T1273 (figure 37, plate 4)) with a grossly malformed proximal head that cannot be attributed to a simple rehealing process, and more probably represents a pathological condition, for instance bone cancer. Young (1964) noted abundant pathological bones of the pseudosuchian *Fenhosuchus*: these included asymmetrical development of the vertebrae and thickening of the articulated ends of the limb bones. He noted that this might indicate that the genus was not quite fit for the environment, but this explanation cannot be considered applicable in the isolated instances observed in *Clevosaurus hudsoni*.

4. *CLEVOSAURUS MINOR*

A smaller species of *Clevosaurus* has recently been recognized in three different fissures at Cromhall Quarry, and in the Aberdeen collections it is certainly more widespread than *C. hudsoni* (Fraser & Walkden 1983). This small species has only been found in association with *Planocephalosaurus robinsonae*, which is also of a similar size although generally the more abundant of the two species. Because of the apparent homogeneous nature of the sphenodontid postcranial skeleton, there are frequently no unequivocal means of distinguishing between the elements of the two genera. This is particularly enhanced in samples where the fossils are water worn and fragmentary. Consequently it is considered that an attempted reconstruction of the smaller *Clevosaurus* species is infeasible, and in any case it would not be particularly instructive. However, certain diagnostic features of the skull of the new species are evident, and these are described below.

(*a*) *Taxonomy*

Family: SPHENODONTIDAE

Genus: *CLEVOSAURUS*

Species: *C. minor* sp. nov.

Diagnosis

The same as for *C. hudsoni*, except that it is markedly smaller with the skull estimated to be between 2.5 and 3.0 cm long. The anterior vomerine process of the palatine is flat and continuous with the median pterygoid facet. Anteriorly the maxilla bears 2 or 3 prominent successional teeth.

Holotype: AUP 11086, right maxilla.

Paratype: AUP 11087, left palatine.

Type locality: Karstic fissures in Dinantian limestones. Cromhall Quarry, south Gloucestershire.

Horizon: Upper Triassic.

(*b*) *Description*

The premaxillae possess a similar pronged maxillary process to that of *C. hudsoni*, with a dorsal ramus extending behind the external naris. However, all specimens examined bear three acrodont teeth which are commonly of equal size. These tend to become obscured by the growth of secondary bone and dentine in mature individuals.

The majority of the maxillary specimens recovered are from mature individuals exhibiting a full complement of additional teeth, and they display substantial wear facets with growth of secondary bone and dentine. The largest specimens do not exceed 15 mm. long. Unlike *C. hudsoni* the maxilla of *C. minor* invariably possesses two or three successional teeth (figure 38, plate 4). These are instantly distinguishable from the hatchling teeth by their larger size and deeper set bases: this is particularly applicable to the third successional tooth. Following the successional teeth there are normally five or six smaller teeth that alternate in size and together constitute the remnant hatchling series. Additional teeth were added one at a time behind the hatchling series. The first four additional teeth bear pronounced posterolingual flanges, and as a series they increase in size caudad. In addition, either two or three smaller subconical teeth are normally ankylosed behind the flanged series. The relationship of the maxilla of *C. minor* to the adjacent elements is the same as for *C. hudsoni*, and no further details need to be given here.

The structure of the skull roofing elements does not depart noticeably from the condition in *C. hudsoni* (figure 39). The frontals are paired and they possess the same complex interdigitating median articulation illustrated by *C. hudsoni* (figure 39*a*). The parietals are also paired and the rather narrow, but flat, parietal table was pierced by a large pineal foramen (figure 39*b*).

The available material does not permit any comment on the extent of the lower temporal arcade in *C. minor*. Several jugal specimens have been recovered but the posterior process is either incomplete or too polished to reveal any articulation facets that might have been present. Likewise complete quadrates and quadratojugals are unknown. Certainly the better preserved squamosals do not appear to have possessed an anterior spur on the distal end of the ventral process. Therefore in the event that the lower temporal bar was complete it seems improbable

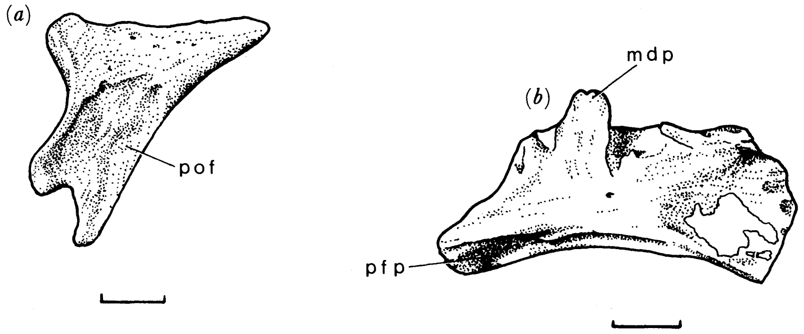


FIGURE 39. Cranial elements of *C. minor*. (*a*) A right postfrontal, AUP 11190, in dorsal view. Scale bar 1.0 mm. (*b*) A left frontal, AUP 11189, in cranial view. Scale bar 1.0 mm.

that the orientation of the jugal, quadratojugal and squamosal conformed to the configuration seen in *Sphenodon* or certain individuals of *Planocephalosaurus*.

With the exception of the palatine morphology, from what is known of the palatal elements, the palate of *C. minor* closely adhered to the pattern exhibited by *C. hudsoni*.

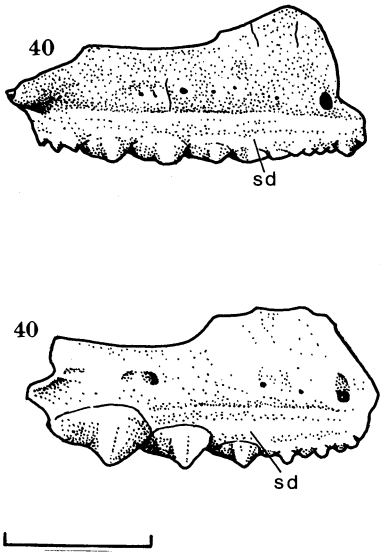
The available palatine fragments are sufficiently complete to indicate that in mature individuals the single lateral tooth row was not elevated on a bony ridge. Likewise, the anterior process, articulating with the vomer, apparently did not flex ventrally, and the overall effect of these differences would have conferred a somewhat flatter palate upon *C. minor*.

Apart from size, the dentaries of *C. minor* are almost indistinguishable from those of *C. hudsoni*. The teeth can be similarly arranged into successional, hatchling and additional categories and they possess similar characteristics. There may be slight differences in the prominence of the successional teeth in the two species. In *C. minor* there appear to be always three quite distinct successional teeth. On the other hand there may be less than three successional teeth in *C. hudsoni* and they are usually less prominent. However, such an apparent specific distinction is difficult to quantify, particularly because variable degrees of tooth wear may be a contributory factor.

(*c*) *A comparison of C. hudsoni with C. minor*

Three basic criteria have been used to justify the separation of *C. minor* from *hudsoni*, and to show that the differences are not purely associated with ontogeny or sexual dimorphism.

Firstly, a comparison of a mature maxilla of *C. minor* with a similar-sized specimen of *C. hudsoni* immediately reveals several differences (figure 40). Whereas the *C. minor* maxilla has a full complement of additional teeth displaying a considerable degree of tooth wear with a substantial layer of secondary bone and dentine, the full complement of additional teeth is invariably absent in *C. hudsoni*. For example, in AUP 11187 two of the flanged series are missing (figure 40). At this stage the *C. hudsoni* maxilla has rather less secondary bone growth, tooth wear is minimal, and, as emphasized earlier, it always lacks successional teeth. Secondly, comparable differences are also revealed between the palatines of the two species. Given a *C. minor* specimen in which the full complement of teeth is preserved in the lateral row, in a similar-sized *C. hudsoni* individual at most only two teeth have been fully ankylosed, and the bone is incompletely ossified (figure 41). In the *C. hudsoni* specimen more teeth could only be added posteriorly with further bone growth. Finally, an examination of the distribution of the various specimens demonstrably indicates that *C. minor* is not a collection of juvenile *C. hudsoni* elements. Occasionally *C. hudsoni* may occur together with *C. minor* in the same deposits but generally they are considered to be mutually exclusive. In the few instances where *C. hudsoni* has been recorded with the smaller form (Fraser & Walkden 1983) it is possible that the *C. hudsoni* material may have been incorrectly identified. In these instances dentaries were attributed to *C. hudsoni*, and the only diagnostic difference between the two species in this element is size. Thus it cannot be discounted that an exceptionally large individual of *C. minor* could be mistakenly assumed to be *C. hudsoni*.



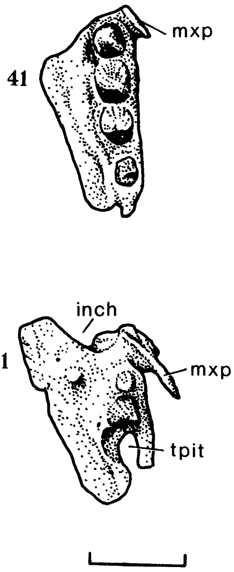


FIGURE 40. Comparison of the lateral aspects of a fully mature *C. minor* right maxilla, AUP 11186 (above), with an immature *C. hudsoni* maxilla, AUP 11187 (below). Scale bar 4.0 mm.

FIGURE 41. Comparison of the ventral aspects of a mature fragmentary palatine of *C. minor*, AUP 11087, (above) with a juvenile palatine of *C. hudsoni*, AUP 11088, (below). Scale bar 2.0 mm.

It would therefore seem that to all intents and purposes *C. hudsoni* and *C. minor* occur in separate deposits, albeit at the same locality. It is implausible to envisage a scenario where one sex of the species is selectively sorted from the other and it is consequently valid to assume that the differences between the two assemblages of *Clevosaurus* are not purely correlates of sexual dimorphism. *C. minor* must therefore represent a separate and quite distinct species, possibly separated in time from *C. hudsoni*.

5. ADDITIONAL SPECIMENS OF *CLEVOSAURUS* SPP.

The most recent excavations at Cromhall Quarry have revealed a new pocket in the fill designated 5A by Fraser (1985). The preliminary work on this fossil assemblage indicates that it is markedly different from the rest of 5 and 5A. Unfortunately, many of the bones have been considerably rolled and polished, and as a result do not permit the desired level of detailed analysis. Incorporated within this deposit are a number of *Clevosaurus* jaw bones that are comparable in size to those of *C. minor*. All the maxillae and dentaries bear anterior successional teeth, and on first inspection do not apparently differ from *C. minor* specimens recovered from elsewhere in the quarry. The palatines are also comparable to *C. minor* material. However, upon closer examination of the additional dentition of the dentaries, a subtle variation in tooth form is revealed. Whereas in lateral aspect the normal *C. minor* additional mandibular tooth exhibits a concave leading edge, the specimens from the new pocket have a much straighter margin (figure 42). A statistical comparison of the height: length ratio for the additional teeth also suggests that the specimens from the new pocket have relatively shorter additional teeth (table 4).

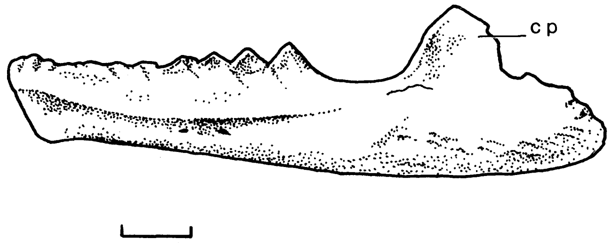


FIGURE 42. *Clevosaurus* sp. Left dentary, AUP 11374, in lateral view (see figure 20 and 23*b*). Scale bar 2.0 mm.

TABLE 4. COMPARISON OF THE DIMENSIONS OF THE MANDIBULAR ADDITIONAL TEETH BETWEEN *C. HUDSONI*, *C. MINOR* AND THE *CLEVOSAURUS* SAMPLE FROM SITE 5A, CROMHALL QUARRY

(In each case there is a good correlation between the length and the height of the teeth. By using Student's t-test to compare the logs of the length: height ratio it can be seen that there is a highly significant difference between the *Clevosaurus* sample from site 5A and the other two species, but not between *C. hudsoni* and *C. minor*.)

	sample size (n)	mean length (x)/mm	mean height (y)/mm	correlation coefficient (r)
C. hudsoni	26	2.361	1.438	0.8994
C. minor	30	2.387	1.537	0.9019
Clevosaurus sp.	30	2.06	1.513	0.9175
	s_x	s_y	mean log	$s_{\log(x/y)}$
C. hudsoni	4.52	3.57	0.2206	0.0489
C. minor	5.42	5.16	0.2037	0.0711
Clevosaurus sp.	5.42	4.13	0.1341	0.0452
		Student's t-test values of t		
C. hudsoni *Clevosaurus* sp.		7.0***		
C. minor *Clevosaurus* sp.		4.523***		
C. hudsoni *C. minor*		1.017		

In the standard *C. minor* maxillae the small additional teeth posterior to the keeled series never number more than three, and often there are only two. By contrast, the *Clevosaurus* maxillae from the new pocket exhibit at least three such teeth, and frequently four, which are packed closely together.

It is difficult to ascertain at present whether these apparent differences in the dental morphology are representative of discrete populations separated by time or space or both, or whether they merely represent some phenotypic variation. For the time being the lack of further evidence necessitates the adoption of a conservative approach and these elements will simply be regarded as *Clevosaurus* sp.

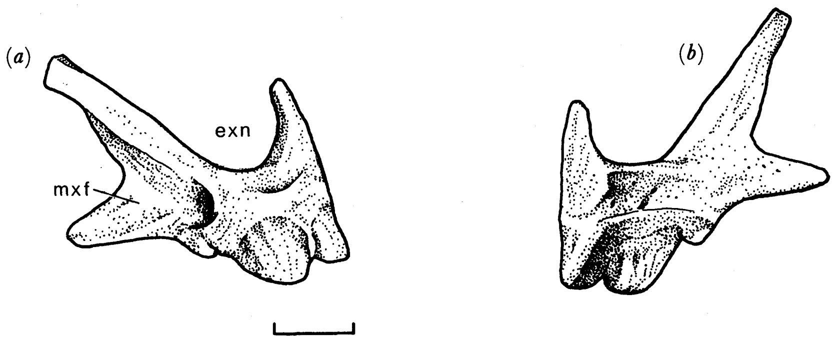


FIGURE 43. *Clevosaurus* sp. Right premaxilla, AUP 11191, in (*a*) lateral and (*b*) medial views. Scale bar 2.0 mm.

In addition, several *Clevosaurus*-like premaxillae have been recovered from the new pocket. The majority are compatible with the structure observed in *C. minor*, and bear three approximately equal-sized teeth. However, there are a few premaxillae that with respect to size are more consistent with those of *C. hudsoni*, but display a quite different tooth arrangement (figure 43). The first two teeth are large and prominently placed, but the third is much smaller and positioned immediately behind the second tooth, ventral to the anterior edge of the maxillary facet. This arrangement of teeth is reminiscent of a premaxilla from Ruthin Quarry described as a probable procolophonid (Fraser 1986*b*). Fragmentary teeth of a little-known procolophonid bearing acrodont teeth are present in the new pocket at Cromhall Quarry; however, it is considered most unlikely that the new premaxillary material is representative of this family. Procolophonids, such as *Procolophon*, *Leptopleuron* and *Hypsognathus*, typically bear large conical premaxillary teeth with posterior wear facets confined largely to the distal portion of the tooth crown. By contrast the teeth in the new material are more obtusely conical, and pronounced wear facets extend over the entire posterior surface of the tooth crowns. In addition, the premaxillary–maxillary articulation is generally less extensive in procolophonids than seen here, and procolophonids also show a marked tendency for the median process to project anteriorly above the level of the dentition. Thus in most respects the new element closely resembles the generalized *Clevosaurus* premaxillary structure, and this extends to the pronged maxillary facet with a posterodorsal lamina of bone separating the maxilla from the posterior boundary of the external naris.

6. A NOTE ON THE GENERAL PALAEOECOLOGY OF THE FISSURE FAUNAE

Judging by the wealth of remains recorded from the Bristol Channel fissure deposits in general, and Cromhall Quarry in particular, it is tempting to suggest that they could form the basis for detailed palaeoecological studies, with analyses of possible effects of interspecific competition and speciation. In the case of Cromhall Quarry, the assemblage in each fissure is normally uniform throughout the fill, but the constituent species and relative abundances of these species are seen to vary from one fissure to the next (Fraser & Walkden 1983), so that theoretically these assemblages could provide potentially good palaeoecological data.

Robinson (1957, 1967*b*, 1971) believed that the assemblages at Cromhall and neighbouring localities related to a unique upland fauna that she believed to be characterized by small, lightly built agile forms. Robinson considered the sediments to be of Norian age and deposited under arid or semi-arid continental conditions. However, Marshall & Whiteside (1980) challenged this viewpoint; arguing for a lowland fauna, but more particularly one inhabiting an island environment. Marshall & Whiteside based their claims on age estimates derived from palynological evidence at one particular locality, namely Tytherington Quarry. They believed that the Tytherington assemblages were contemporaneous with, or even postdated, the initial marine transgression that took place in southwest Britain at the very end of the Triassic. Based on this assumption the fissure faunae are seen as populations inhabiting an island archipelago incorporating rather more equable conditions than the climate envisaged for the upland scenario (Robinson 1957, 1962, 1967*b*; Tarlo 1962; Halstead & Nicoll 1971). However, the situation is probably much more complex than these two diametrically opposed views would suggest. Firstly, although palynological dating indicates that certain fissure sediments are equivalent to the Penarth Group (Westbury Formation), that is they postdate the initial marine incursion, there is strong evidence supporting a pre-transgression age for other localities bearing comparable assemblages (Robinson 1957; Fraser *et al.* 1985). Secondly, the concept that before fully marine influences in southwest Britain there was a topography of rocky outcrops and limestone hills may not be strictly true. Certainly there is evidence for an evaporitic lacustrine environment in parts of what is now Somerset which may have had a distant and possibly periodic marine connection (Mayall 1981), and which is thought to have been very similar to a modern sabkha environment (Tucker 1977, 1978).

Therefore, for the present, it cannot be assumed that the microvertebrate assemblages necessarily represent upland faunae distinct from lowland forms such as those typified by the penecontemporaneous Maleri Formation (Huene 1940*a*, *b*; Jain *et al.* 1964; Roy Chowdhury 1965; Chatterjee 1978, 1980), or the Elgin reptiles (see, for example, Benton & Walker 1985). Likewise we cannot view all the assemblages to be representative of island environments even though by Sinemurian times this was undoubtedly so. Each fissure appears to exhibit its own series of characteristics, and ideally the relative times at which each filled with sediment should be resolved. But this in itself may present an insurmountable problem. Analyses of lithological samples may not be instructive because subaerial erosian may be largely independent of time, provided the climate and source rocks are basically similar. Palynological data are obviously only of limited value when the majority of fissure sediments are devoid of palynomorphs. Early Mesozoic terrestrial faunae are generally too poorly known for use as zonal indices, and in any case many seem to be conservative long-ranging forms. In addition, circular arguments are almost inevitable from such localized fossil occurrences, and direct stratigraphical evidence for dating is rarely available in sediments that do not form a continuous outcrop.

Apart from the lack of robust dating methods for analysing the ages of the assemblages relative to each other, there are also problems concerning aspects of their taphonomy. A fossil sample represents a highly modified relic of the life assemblage of which it is a derivative. Holtzman (1979) has noted the sequence of events leading to the deposition of a fossil assemblage from a life assemblage (figure 44), and Voohries (1969) has outlined the processes that intervene between a living community and the formation of a fossil assemblage. These include factors such as the effect of predation and scavengers, whether the burials are autochthonous or allochthonous, the extent of sorting, the proximity of various habitats to the site of deposition, whether animals died in their preferred habitats, the nature and extent of burial agents, and whether death was attritional or catastrophic. Voohries realized that it might be impossible to recognize the different habitats of ancient animals from analyses of fossil samples simply because original, ecologically significant differences may be obscured by

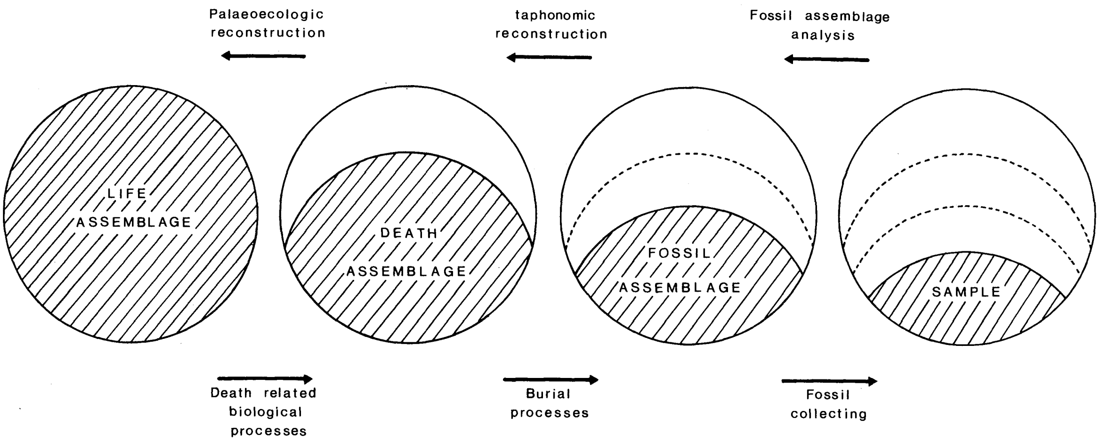


FIGURE 44. A schematic outline of the main processes governing the formation of a fossil assemblage from a life assemblage, and the steps which must be taken into consideration when formulating palaeoecological reconstructions (after Holtzmann (1979)).

secondary differences introduced during taphonomic processes. Voohries's work, as is so much recent taphonomical research (see, for example, Behrensmeyer 1978, 1982; Behrensmeyer *et al.* 1979; Brain 1980; Hill 1980; Van Couvering 1980; Vrba 1980; Western 1980), was directed towards the Cainozoic, particularly mammalian faunae, and the fossils are generally located within continuous bonebeds. The accumulation of fossils and sediments as discrete pockets within crevices and fissures presents its own special constraints on burial. Thus bias resulting from absolute size becomes increasingly important. For instance, some components of the original fauna may be excluded from the fissures by virtue of their large size, and perhaps they were incorporated within a lag deposit elsewhere. In the absence of well-known deposits with comparable taphonomic histories, only broad palaeoecological inferences of the type propounded by Fraser & Walkden (1983) can be made with regard to the Bristol Channel faunae. Statements concerning dietary habits are based upon dental and skeletal morphology, but analyses of the interactions between the various trophic levels are highly speculative and, in the absence of plants, insects, etc., assessments of food chains, biomass and productivity are clearly impossible.

7. DISCUSSION

(*a*) *The affinities of Clevosaurus*

For many years *Sphenodon* was considered to be a close relative of the rhynchosaurs and together they were incorporated within the subclass Lepidosauria (see, for example, Williston 1925; Romer 1956, 1966). Although the link with the rhynchosaurs has now been unequivocally severed (Hughes 1968; Carroll 1976; Brinkman 1981; Benton 1983), *Sphenodon* has been shown to share numerous derived characters with the squamates so that generally they are still grouped together within the Lepidosauria (Carroll 1977; Gardiner 1982; Rage 1982). However, Løvtrup (1977) disputed the monophyly of the Lepidosauria, noting that *Sphenodon* shares several derived characters with turtles plus crocodiles plus birds. Benton (1985) has in turn questioned the polarity, and indeed the significance, of the characters described by Løvtrup (1977). The description of *Clevosaurus* provides another opportunity to assess the status of the sphenodontids.

Since the preliminary description (Swinton 1939), *Clevosaurus* has invariably been referred to as a sphenodontid (see, for example, Robinson 1973, 1976; Carroll 1977; Gow & Raath 1977) but it is interesting to note that *Clevosaurus* shares three characters with proterosuchians. Firstly, the unossified gap between the opisthotic and parasphenoid is analogous to the ventral extension of the fenestra ovalis in *Proterosuchus* (and a similar more pronounced unossified region in *Euparkeria*) (Cruickshank 1972*a*). Secondly, both *Clevosaurus* and *Proterosuchus* possess supratemporals which are also known in prolacertiforms, but interestingly there have been no reliable reports of these elements in any previously described sphenodontid material. Thirdly, bifurcated ribs occur in *Proterosuchus* (Cruickshank 1972*b*) and *Prolacerta* (Gow 1975) as well as *Clevosaurus*, although in *Proterosuchus* at least, it is the first sacral that is bifurcate. In addition the second sacral rib in *Proterosuchus* splits into three rami, which all articulate with the ilium.

The taxonomic position of the proterosuchians is presently somewhat equivocal (Benton 1985). Traditionally they have been placed at the base of the archosaur radiation (see, for example, Hughes 1963; Charig & Sues 1976), but in some other respects they are very like the prolacertiforms. Either way they are far removed from the lepidosauromorph clade and it is consequently surprising to record shared characteristics with *Clevosaurus*. An anomaly enhanced still further by the extension of the premaxilla up behind the naris, a condition normally associated with the archosauromorph clade (Benton 1985). A more formal comparison of *Clevosaurus* with the outgroup consisting of prolacertiforms and archosaurs is therefore required.

Looking first at specific cranial characters, in *Clevosaurus* the snout is short and the skull relatively broad. This contrasts sharply with the condition in *Prolacerta* and *Proterosuchus* where the nasals are longer than the frontals thereby producing a relatively long but narrow snout. The posttemporal fenestrae are much reduced in *Prolacerta* and they are absent altogether in *Proterosuchus*, whereas in *Clevosaurus* they are large and prominent. In both *Prolacerta* and *Proterosuchus* the marginal teeth are recurved in complete contrast to the obtusely conical teeth of *Clevosaurus*, which in the 'cheek' region bear pronounced anteroposteriorly elongated flanges.

In *Clevosaurus* and also *Youngina*, the parasphenoid runs back beneath the basioccipital and almost as far as the occipital condyle, but between the basisphenoid ossification and the basioccipital there is a gap in the braincase floor bridged solely by the parasphenoid. Such a condition also occurs in the millerettids (Gow 1972), but apparently not in the archosauromorphs.

Gow (1975) considers there to be an extensive participation of the parasphenoid in the side wall of the braincase in both *Prolacerta* and *Proterosuchus*, and he believes that such a configuration is a character clearly distinguishing the archosauromorphs from the squamates. The parasphenoid of *Clevosaurus* adheres to the pattern described by Gow (1975) for *Youngina* in which it essentially acts as a flooring plate, albeit with minimally upturned lateral margins. But Evans (1986) does not consider such features to be diagnostic as she was unable to distinguish between *Prolacerta* and *Sphenodon* in this respect. Evans (1986) proposes alternative braincase characters upon which the archosauromorph and lepidosauromorph clades can be separated. In particular, she suggests that in lepidosauromorphs the incisura prootica is positioned well down the anterior edge of the prootic and that the pila antotica contributes to both the prootic and basisphenoid. In addition, the lateral regions of the dorsum sellae, the clinoid processes, are well developed in lepidosauromorphs and form the basal regions of the pilae antoticae. By contrast, the incisurae prooticae of archosauromorphs are positioned further dorsally on the anterior edges of the prootics and in some instances they are closed anteriorly by separate ossifications, the pleurosphenoids. Typically, the clinoid processes are poorly developed in archosauromorphs and the pila antotica is mainly incorporated within the prootic. Evans (1986) also maintains that the archosauromorph clade can be further separated from the lepidosauromorphs on the basis that the prootics of archosauromorphs show a tendency to meet in the midline above the level of the dorsum sellae. *Clevosaurus* supports this observation because the prootics are widely separated in this region. In *Clevosaurus* the incisura prootica is broadly open, and distinct clinoid processes contribute to the bases of the pilae antoticae which are retained well down on the anterior margins of the prootics (figure 17*b*).

Evans (1986) noted that cristae prooticae (figure 17*b*) are absent in younginiforms and *Sphenodon* and that they were probably independently developed within the archosaurs and squamates. It is interesting to note that they occur in both *Clevosaurus* and *Planocephalosaurus* and were therefore presumably derived in more than one lepidosauromorph lineage.

In more general terms *Clevosaurus* exhibits the following typical lepidosauromorph synapomorphies: the postfrontal entering the border of the upper temporal fossa; accessory intervertebral articulations on the midline of the neural arch; cervical centra shorter than the average mid-dorsal centra; and holocephalous dorsal ribs. In addition, despite the premaxilla extending up behind the naris, *Clevosaurus* shows many more characteristics directly opposing archosaur affinities. These include the notochordal vertebrae; absence of elongate transverse processes on the dorsal vertebrae; the occurrence of an entepicondylar foramen in the humerus; the absence of the complex concave–convex articulation between astragalus and calcaneum; and the presence of a fifth metatarsal hooked in two planes rather than a single one.

Clearly the evidence for incorporating *Clevosaurus* within the general boundaries of the Lepidosauromorpha is overwhelming. Consequently it is assumed that the unossified gap in the braincase, the extension of the premaxillae behind the nares and the bifurcation of the second sacral ribs are simply convergent characters shared with the prolacertiforms and proterosuchians. The occurrence of a supratemporal in *Clevosaurus* cannot be satisfactorily explained, and for the present it is best considered as an isolated example of the retention of a primitive character.

Some authors (for example Hoffstetter 1955; Cocude-Michel 1963) chose to treat the Triassic sphenodontians, and *Clevosaurus* is included here, as a group distinct from later forms. Hoffstetter (1955) regarded the Triassic genera as hardly distinguishable from the 'basal eosuchians'. However, more recently Benton (1985) listed fifteen apomorphies that *Sphenodon* possesses when compared with early lepidosauromorphs and the Squamata, and of these *Clevosaurus* possesses ten, thereby supporting its status as a 'true' sphenodontid. These include the absence of a lachrymal, acrodont teeth, a 'beaked' premaxilla, a single row of enlarged teeth on the palatine, a broad mandibular symphysis formed entirely by the dentary, a mandibular foramen bounded by the dentary and surangular, and the dentary produced posteriorly to form much of the lateral wall of the lower jaw. Whiteside (1986) suggested that the Sphenodontidae formed a monophyletic group characterized by eight advanced features. *Clevosaurus* exhibits all eight of these characteristics, which include the occurrence of alternating sized teeth on both the dentary and the maxilla; the presence of flanges on the posterior teeth of each jaw quadrant and the lateral teeth of the palatines; and the presence of chisel structures on the premaxillae which, although initiated by more than one tooth, essentially form one compound tooth per bone.

Clevosaurus, in common with *Sphenodon*, *Homeosaurus* and *Kallimodon*, retains separate frontals and parietals. The frontals of *Clevosaurus* exhibit a complex interdigitating midline articulation which lends rigidity to the paired elements. The parietal table is narrower than either *Planocephalosaurus* or *Homoeosaurus* but, unlike *Sphenodon* or *Kallimodon*, it is not raised into a central ridge and its condition can therefore be regarded as intermediate between the two types.

The structure of the braincase in *Clevosaurus* is quite similar to that observed in *Sphenodon*. Both genera bear strongly developed paroccipital processes extending posterolaterally. In *Clevosaurus* the paroccipital process contacts the supratemporal, but in *Sphenodon*, with the absence of the supratemporal, each paroccipital process articulates directly with the squamosal. Moderately developed ventral processes of the opisthotics in *Clevosaurus* separate the vagus foramen from the fenestra ovalis, but unlike the prolacertids and kuehneosaurids (Robinson 1967*a*), these processes do not descend to partly separate the basioccipital and the basisphenoid.

The lower jaw of *Clevosaurus* is similar to that of *Planocephalosaurus* but with an even greater development of the retroarticular process. However, *Clevosaurus* shows a reduced tendency to fusion of the individual elements, and in this respect it is similar to *Sphenodon*. The dentary is typically developed into a pronounced posterior process so that in lateral aspect it forms the major part of the lower jaw.

The postcranial skeleton of the Sphenodontida appears to have been remarkably uniform throughout the group, and *Clevosaurus* adheres closely to the general pattern. The vertebral column is similar to the Jurassic genera and *Sphenodon*, with the exception of the zygosphenic articulations. In *Sphenodon* the zygosphene and zygantrum are well developed, but they are quite rudimentary in *Clevosaurus*. They have not been reported at all in the Jurassic forms, although this may be a direct result of the preservation of the fossils because in articulated specimens the presence of a zygosphene and zygantrum would probably be obscured. All known sphenodontids have a well-developed thyroid fenestra and a pronounced posterior process on the ischium, and in this respect *Clevosaurus* is no exception. In *Icarosaurus* (Colbert 1966, 1970), *Tanystropheus* (Peyer 1931; Wild 1973), and to a certain degree *Macrocnemus* (Peyer 1937), the ischium is partly developed posteriorly above the level of the median articulation, but in these genera there is no pronounced posterior tubercle.

Other sphenodontid postcranial characteristics displayed by *Clevosaurus* are generally plesiomorphic and have been mentioned already. These include the prominent ent- and ectepicondylar foramina on the humerus and the sigmoid flexure of the femur. The astragalus and calcaneum are fused, although they apparently remain separate in *Homoeosaurus* and *Kallimodon*, and the fifth metatarsal is hooked. Epiphyseal growth, if present, is a derived character shared with squamates.

Robinson (1973) believed that *Clevosaurus* was unusual among sphenodontids in the possession of an incomplete lower temporal arcade. However, the description of *Planocephalosaurus* (Fraser 1982) showed that this character was not unique. On the other hand it also indicated that there were some individuals with a complete arcade, but where the jugal, squamosal and quadratojugal union was incomplete, ligaments might have spanned the gap.

The same situation may also occur in some of the larger *Diphydontosaurus* elements (Whiteside 1986). Similarly, the posterior jugal process in many *Clevosaurus* specimens is produced to such an extent that it undoubtedly overlapped the quadratojugal. However, unlike *Planocephalosaurus*, in those *Clevosaurus* specimens in which the lower temporal arcade was complete, the squamosal evidently did not extend ventrally to meet the jugal.

Rieppel & Gronowski (1981) proposed that changes in the morphology of the external jaw adductor musculature may account for the loss of the lower temporal arcade in some diapsid reptiles. They believed that the development and the expansion of a posteroventral 1b layer of the external adductor muscle, which invaded the lateral surface of the lower jaw, would have to be correlated with the loss of at least the posterior region of the lower temporal arcade. Supposedly, such a development would increase the adductive muscle forces. The occurrence of an incomplete temporal bar in some sphenodontids is certainly not a direct indication of any squamate affinities, and the condition is thought to have been achieved independently in millerettids (Gow 1975) as well as in sphenodontids and squamates. Nevertheless the sphenodontids and squamates may still share a common ancestor; it is perfectly reasonable to suggest that both groups were derived from a form lacking a complete lower arcade, and that a complete lower temporal bar was secondarily achieved in some sphenodontids.

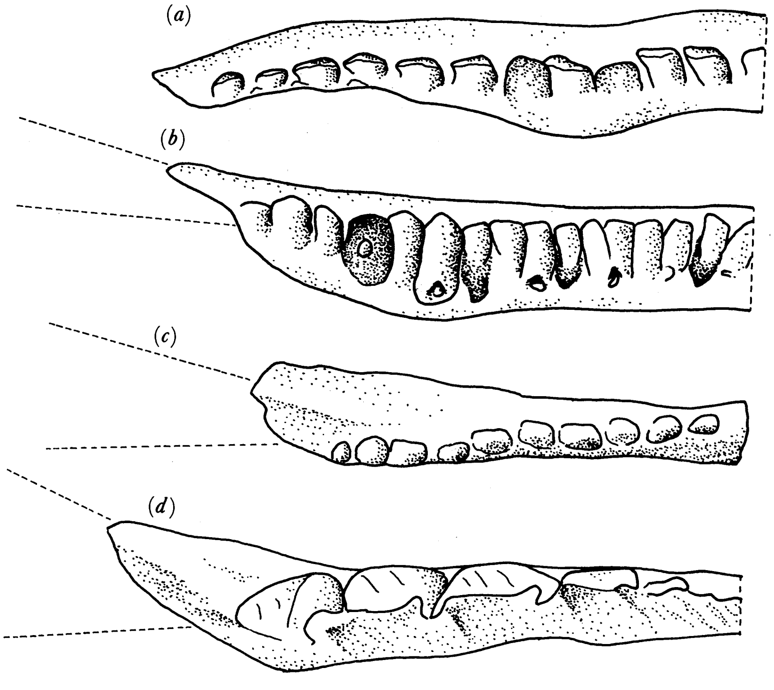


FIGURE 45. Ventral views of the posterior section of the maxilla in (*a*) *Iguana* (*b*) *Lacerta* (*c*) *Gephyrosaurus* sp., UMZC T1278, and (*d*) *Clevosaurus*, showing the degree of lateral bowing from the tooth ramus in each genus.

Within the sphenodontid lineage the initiation of a shearing bite required the strengthening of the lateral walls of the skull. This need may have originally been satisfied by an increased development of the upper temporal arcade. This contention is supported by the interrelationships of the postorbitals, jugals and squamosals of *Clevosaurus*. The rigid and broad upper temporal bar, which is a rather unique feature among diapsids, may have been an adaptation towards the reinforcement of the side of the skull, thereby counteracting the weakness induced by the breakage of the jugal–quadratojugal articulation. The characteristic bowing of the sphenodontid lower temporal bar, whether complete or not, may be correlated with further development and expansion of the jaw adductor musculature. If all sphenodontids did indeed evolve from a form with a well-developed external adductor musculature, any development of a lower temporal bar would necessarily have to pass outside the adductors. The bar would then assume the characteristic lateral bowing that is exhibited to a greater or lesser extent by most, if not all, sphenodontians and also to some degree in *Gephyrosaurus* (figure 45). The significance of the lower temporal bar in *Sphenodon* is not clear, but Whiteside (1986) has reasoned that a torque would develop in a quadrate that is firmly held on the medial side of the pterygoid but only loosely fixed laterally. Such a torque would result in the posterior movement of the lateral side of the quadrate condyle and would effectively disrupt the shearing advantage of a precision shear bite. A complete arcade would rigidly fix the quadrate and thus prevent the twisting of the articular condyles. The functional advantage of an intermediate condition, in which the lower temporal bar has only partly formed, is not apparent but it could have played a strengthening role and provided a point for the attachment of ligaments.

(*b*) *The constitution of the Sphenodontida*

Williston (1925) proposed that *Sphenodon* and its fossil relatives should be incorporated in the Sphenodontia, which he designated subordinal rank. Certain recent authors (McFarland *et al.* 1979; Evans 1984; Benton 1984, 1985) have followed Williston. However, Estes (1983) emended the Sphenodontia to ordinal rank, and within the Sphenodontida he included all sphenodontians. Carroll (1985) has argued that the pleurosaurs were close relatives of the sphenodontids and, if Carroll's view is to be accepted, it might be more appropriate to adopt Estes's emendment because Williston (1925) placed the pleurosaurs in a separate order. By utilizing the term Sphenodontida any doubt that may arise concerning the constitution of the Sphenodontia is removed, and it leaves it free to be used in a more restricted sense should the need arise.

Owing to the incompleteness of much of the sphenodontid material the taxonomy at familial level is still rather speculative, and several different classifications have been published over the past 30 years. Many species have been described solely on the basis of jaw bones and as a result dental morphology has frequently been used as the basic classification criterion. In a recent review of sphenodontid systematics I too (Fraser 1986*a*) relied heavily on dental morphology, but it ought to be pointed out that dental characteristics are also a function of dietary habit and as such may be subject to convergence.

Gephyrosaurus is a Jurassic diapsid that has been described in detail by Evans (1980, 1981) from Welsh fissure deposits. She has cited three synapomorphies which she believes indicate a sister group relationship between *Gephyrosaurus* and the Squamata (Evans 1984). These are namely the occurrence of a pleurodont dentition, the fusion of the frontals and parietals, and the presence of a process on distal tarsal four that fits into a concavity in the astragalocalcaneum.

Fusion of the paired frontals and parietals is known to occur in *Planocephalosaurus* and *Diphydontosaurus* (Whiteside 1986). The former possesses ten of the fifteen characters listed by Benton (1985) as apomorphies of *Sphenodon* when compared with other lepidosuromorphs, and is therefore regarded as a true sphenodontid. *Diphydontosaurus* is slightly more 'primitive' in that only the posterior marginal teeth are said to be acrodont, but nevertheless it too can be considered a sphenodontid in that it possesses nine of Benton's derived character states of *Sphenodon*. As Whiteside (1986) indicates, but for the presence of a rudimentary lachrymal and the entirely pleurodont dentition, *Gephyrosaurus* is strikingly similar to *Diphydontosaurus*, and he referred to *Gephyrosaurus* as a 'near-sphenodontid'. Whiteside (1986) did not consider the wider limits of the Sphenodontida, defining the Sphenodontidae in a more restricted sense. Therefore when he refers to *Gephyrosaurus* as a 'near-sphenodontid' he is presumably using the term sphenodontid in his more limited context.

With regard to the articulation of the tarsal bones, *Clevosaurus* possesses a concavity on the astragalocalcaneum for the reception of distal tarsal four, and so too to a lesser extent does *Planocephalosaurus*. Consequently there is no reason to assume that *Gephyrosaurus* has closer affinities with the squamates than with the sphenodontids, and in fact the reverse would appear to be true (Fraser 1986*a*; Whiteside 1986). I regard the configuration of the dentary and the lower jaw elements, the enlarged tooth row on the palatine and at least a rudimentary lateral bowing of the incomplete lower temporal arcade as derived sphenodontid cranial characteristics shared by *Gephyrosaurus*. In addition, the postcranial skeleton of *Gephyrosaurus* is also very similar to the typical sphenodontid pattern. Although the latter may be largely due to several plesiomorphic characters, the posterior tubercle on the ischium would appear to be a clear synapomorphy shared with sphenodontids. The Sphenodontida is therefore considered to be a valid monophyletic group that includes *Gephyrosaurus*.

I suggest that the fusion of the frontals and parietals in some sphenodontids may be associated with small size, and it is an adaptation towards strengthening of the skull in certain lineages tackling relatively robust prey. This in turn could be correlated with the initiation of a shearing bite in the early sphenodontids. The fusion of certain mandibular elements in *Planocephalosaurus* may be a further development of this phenomenon.

Polysphenodon and *Brachyrhinodon* apparently share with *Planocephalosaurus* the numerous palatal teeth and broad parietal table. Carroll (1985) indicated that there was no fusion of the skull roofing elements in the single specimen of *Polysphenodon*, but the condition in *Brachyrhinodon* is unknown. Kuhn (1969) separated *Brachyrhinodon* from other primitive sphenodontids on the basis of its characteristically short snout, and I tentatively retained this separation (Fraser 1986). However, neither *Polysphenodon* nor *Brachyrhinodon* are completely known and certain details given by previous authors are questionable. For instance the teeth shown by Jaekel (1911) on the ectopterygoid of *Polysphenodon* and the absence of a suborbital fenestra are both incorrect. Research by Fraser & Benton (1989) also suggests that both *Polysphenodon* and *Brachyrhinodon* possess fewer teeth on the palate than either *Diphydontosaurus* and *Planocephalosaurus*, that the premaxillae of the two former genera are produced into ventral chisel-like structures by the fusion of two teeth on each bone, and that in *Polysphenodon* at least the posterior teeth on each jaw quadrant are flanged. So that although these Triassic forms have all been grouped together, further research may show them to be a paraphyletic assemblage. In particular *Gephyrosaurus*, *Diphydontosaurus* and *Planocephalosaurus* may form a single clade characterized by a tendency towards fusion of the frontals and parietals, a relatively elongate nasal region, and a short temporal zone.

Whiteside (1986) described a markedly recessed lingual base in the anterior mandibular teeth of some specimens of *Planocephalosaurus*. He noted that these teeth sit in a remnant shelf and consequently he referred to them as 'semi-acrodont'. In addition, Whiteside refers to the premaxillary teeth of *Planocephalosaurus* as 'semi-pleurodont' because the lingual side of each tooth sits on a shelf, but apparently exhibits no active replacement. Thus a *Gephyrosaurus*, *Diphydontosaurus* and *Planocephalosaurus* grouping might be further characterized by some degree of pleurodonty in the marginal teeth.

The occurrence of a fully acrodont dentition, with an anterior hatchling series alternating in size and additional teeth bearing well-defined keels, is correlated with the attainment of a full precision shear bite as exemplified by *Homoeosaurus*. *Homoeosaurus* also exhibits a marked reduction in the number of palatal teeth, but the overall gross morphology of the skull is similar to the more primitive sphenodontids, and the broad, flat parietal table is retained.

In *Sphenodon*, *Kallimodon* and *Sapheosaurus* the parietal table is much reduced so that it forms a narrow saggital ridge. Fraser (1986*a*) suggested that this may be associated with the greater development of the external jaw adductor musculature. Following on from this, it is postulated that the Eilenodontinae might also have possessed a narrow parietal ridge, but this cannot be tested from the available material.

Palaeopleurosaurus from the Posidonienschiefer, and described as an early pleurosaur by Carroll (1985), retains many features of terrestrial sphenodontids, which led Carroll to suggest that pleurosaurs and sphenodontids may have close affinities. However, on the same grounds it is also possible to argue that *Palaeopleurosaurus* is a true sphenodontid, and that characters it shares with the pleurosaurs are the result of convergence associated with an aquatic habit. It bears many typically sphenodontid properties of the dentition, including the keeled additional teeth, the precision shear bite and the enlarged palatal tooth row. The dentary is produced into a long posterior process, there is a prominent mandibular foramen bounded by the surangular and the dentary, and the lachrymal is absent. By contrast the straight lower temporal arcade of *Palaeopleurosaurus* does not conform to the sphenodontid pattern. With respect to the postcranial skeleton the major departures from the typical sphenodontid are in the proportions of the limbs and the axial skeleton. It shares with sphenodontids the posterior tubercle on the ischium and the bifurcation of the second sacral rib. However, bifurcation of the second sacral rib is also known in *Prolacerta broomi* (Gow 1975), as discussed above, and it is probably a corollary of powerful caudal musculature. But if, as Carroll believes, *Palaeopleurosaurus* does represent an early stage in the evolution of the pleurosaurs, then pleurosaurs represent an offshoot from the sphenodontid stock bearing a narrow parietal table.

The parietal table of *Clevosaurus* can be considered to be intermediate between the narrow type, as exemplified by *Sphenodon*, and the broad form typified by *Homoeosaurus*. Although the parietal foramen has migrated somewhat anteriorly in *Clevosaurus* as a result of the constriction of the parietal table, the paired parietals do not form a median crest and the ventrolateral flanges descending towards the supraoccipital are less steeply angled than in *Sphenodon*. Nevertheless, if a narrow parietal table is indeed a derived character, then *Clevosaurus* can be considered to be more advanced than the Polysphenodontinae and *Homoeosaurus*.

The occurrence of a supratemporal in *Clevosaurus* is not readily reconciled within the framework of previous classifications, although its position may be regarded as quite superficial and as such it might be viewed as a relic of an ancestral stock. The situation is paralleled in squamates, where the presence of a supratemporal is a variable character. In addition the absence of a jugal–squamosal articulation in the complete lower temporal arcade does seem to separate *Clevosaurus* from other sphenodontids possessing two complete temporal arches, and it may be that *Clevosaurus* represents an isolated branch of the Sphenodontida with no known relatives. For the present, on the basis of the narrowing of the parietal table and the anteroposteriorly elongated additional teeth, *Clevosaurus* is here included in an unresolved trichotomy together with *Palaeopleurosaurus* and *Kallimodon* (figure 46).

A single synapomorphy separates *Sphenodon* and the Eilenodontinae from other sphenodontids: namely propalinal jaw movements. Similarly, the Eilenodontinae can be differentiated from *Sphenodon* on the basis of the transversely broadened additional teeth. However, because of the incompleteness of the fossil material future work may change our understanding of the Eilenodontinae.

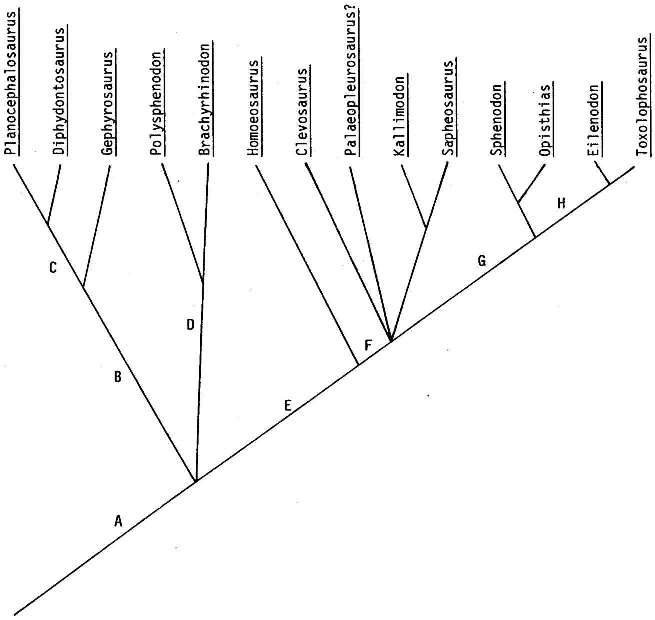


Figure 46. Classification of the Sphenodontida. Shared derived characters are summarized thus: A, enlarged tooth row on the palatine, a broad mandibular symphysis formed entirely by the dentaries, a mandibular foramen bounded by the dentary and the surangular, the dentary produced posteriorly to form much of the lateral wall of the lower jaw, a posteriorly developed tubercle on the ischium; B, frontals and parietals fused; C, dentition at least partly acrodont, lachrymal absent; D, reduction of the antorbital region, the skull almost as broad as it is long; E, acrodont dentition with additional teeth bearing keels, premaxilla developed ventrally into a 'beak', F, reduction of the parietal table; G, development of propalinal jaw movements; H, marginal dentition transversely broadened.

A classification of the sphenodontids, modified somewhat from Fraser (1986*a*), is summarized in figure 46. The majority of subfamilies from that previous classification are still retained, but they cannot be organized at the familial level until some of the uncertainties surrounding the relationships of *Palaeopleurosaurus*, and in particular the Triassic genera, are resolved.

8. Summary

There is evidence to suggest that it may be possible to separate the sphenodontids into forms with a narrow parietal ridge from those with a broad parietal table. If Carroll (1985) is correct in assuming that *Palaeopleurosaurus* is a primitive pleurosaur, then it may be possible to consider the pleurosaurs as an offshoot from those sphenodontids possessing the reduced parietal table.

Some of the most primitive sphenodontids apparently exhibit some degree of pleurodonty in the marginal dentition. If acrodonty is regarded as one of the key synapomorphies of the sphenodontids, then the pleurodont forms, including *Gephyrosaurus* and *Diphydontosaurus*, should perhaps be more strictly regarded as the sister group of all other sphenodontids.

The tendency towards fusion of certain elements of the skull roof in some 'primitive' forms may be associated with the strengthening of the skull in small, relatively lightly built members of the group. This in turn may have been correlated with the initial stages in the development of a shearing jaw action.

Within the Sphenodontida there is apparently a trend for a reduction in tooth numbers, particularly on the palate, and for an increased suppression of tooth replacement.

It is postulated that the Sphenodontida arose from an unknown ancestor in which the lower temporal bar was incomplete. In some sphenodontids the lower temporal bar is secondarily derived and exhibits a lateral bowing where it passed outside an elaboration of the external jaw adductor musculature. This is presumably correlated with a more powerful jaw action. The extent to which the lower temporal bar bulges laterally, and whether it is complete or not, may depend upon the degree to which the external jaw adductor musculature was developed. This in turn would have been dependent upon the mode of life of the particular species. Thus the occurrence of an incomplete lower temporal bar may not necessarily be of taxonomic significance, although it is more likely to be present in the least derived forms in which the precision shear bite was only incipient.

Despite their prevalence in some Mesozoic fissure deposits, as a group sphenodontids are still poorly understood. Detailed analysis of forms such as *Brachyrhinodon* may partly substantiate and resolve the classification, but future work should also be directed towards extending the data base through the collecting of new material.

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LIST OF ABBREVIATIONS USED

a	angular
accf	accessory facet
accp	accessory process
addfo	adductor fossa
ar	articular
arcon	articular condyle
as	autotomic septum
ast	astragalocalcaneum
bo	basioccipital
bof	basioccipital facet
bs	basisphenoid
bspt	basipterygoid process
cap	capitellum
carfo	carotid foramen
ch	chevron
clp	clinoid process
cl	clavicle
cof	coracoid foramen
cp	coronoid process
crpr	crista prootica
cup	cultriform process
d	dentary

LIST OF ABBREVIATIONS USED (*cont.*)

del	deltoid crest
dp	descending process
ect	ectopterygoid
ectf	ectopterygoid facet
ectfo	ectepicondylar foramen
entfo	entepicondylar foramen
f	frontal
fe	femur
femcon	femoral condyle
fibf	fibular facet
fo	fenestra ovalis
fsar 1	facet for the first sacral rib
fsar 2	facet for the second sacral rib
gl	glenoid
hu	humerus
ic	intercentrum
icl	interclavicle
il	ilium
ilfib	insertion for the iliofibularis musculature
inch	internal choana
incpr	incisura prootica
isch	ischium
itro	internal trochanter
j	jugal
jf	facet for the jugal
mdp	median process
mfo	mandibular fossa
mgr	meckelian groove
mx	maxilla
mxf	maxillary facet
mxp	maxillary process
mpr	maxillary prong
n	nasal
nf	nasal facet
ns	neural spine
obf	obturator foramen
ol	olecranon
op	opisthotic
p	parietal
pa	paraseptal apophysis
pal	palatine
palfo	palatal foramen
par	prearticular
pect	insertion for the pectoralis
pf	postfrontal
pfp	postfrontal process
pia	pila antotica
pm	premaxilla
pmf	premaxillary facet
po	postorbital
pof	postorbital facet
popr	paroccipital process
postzy	posterior zygapophysis
pp	posterior process
prf	prefrontal
prff	prefrontal facet
pro	prootic
ps	parasphenoid
pt	pterygoid
ptp	pterygoid process
ptm	insertion for the pubotibialis
pu	pubis
q	quadrate
qj	quadratojugal
qjp	quadratojugal process
ra	radius
rap	retroarticular process
sa	sacral
sab	supracetabular buttress
sc	scapula
sd	secondary dentine
sig	sigmoid notch
so	supraoccipital
sq	squamosal
sqf	squamosal facet
st	supratemporal
stf	supratemporal facet
succt	successional tooth
sur	surangular
sut	suture
syn	synapophysis
thf	thyroid fenestra
tib	tibia
tibc	tibial condyle
tibf	facet for the tibia
tmt	tarsometatarsal
tpit	tooth pit
tro	trochlea
ts	transverse spine
tt	triceps tubercle
ul	ulna
vf	vagus foramen
za	zygantrum
4dt	fourth distal tarsal

FIGURE 2. Site one, Cromhall Quarry. The main fossiliferous horizon is marked X.

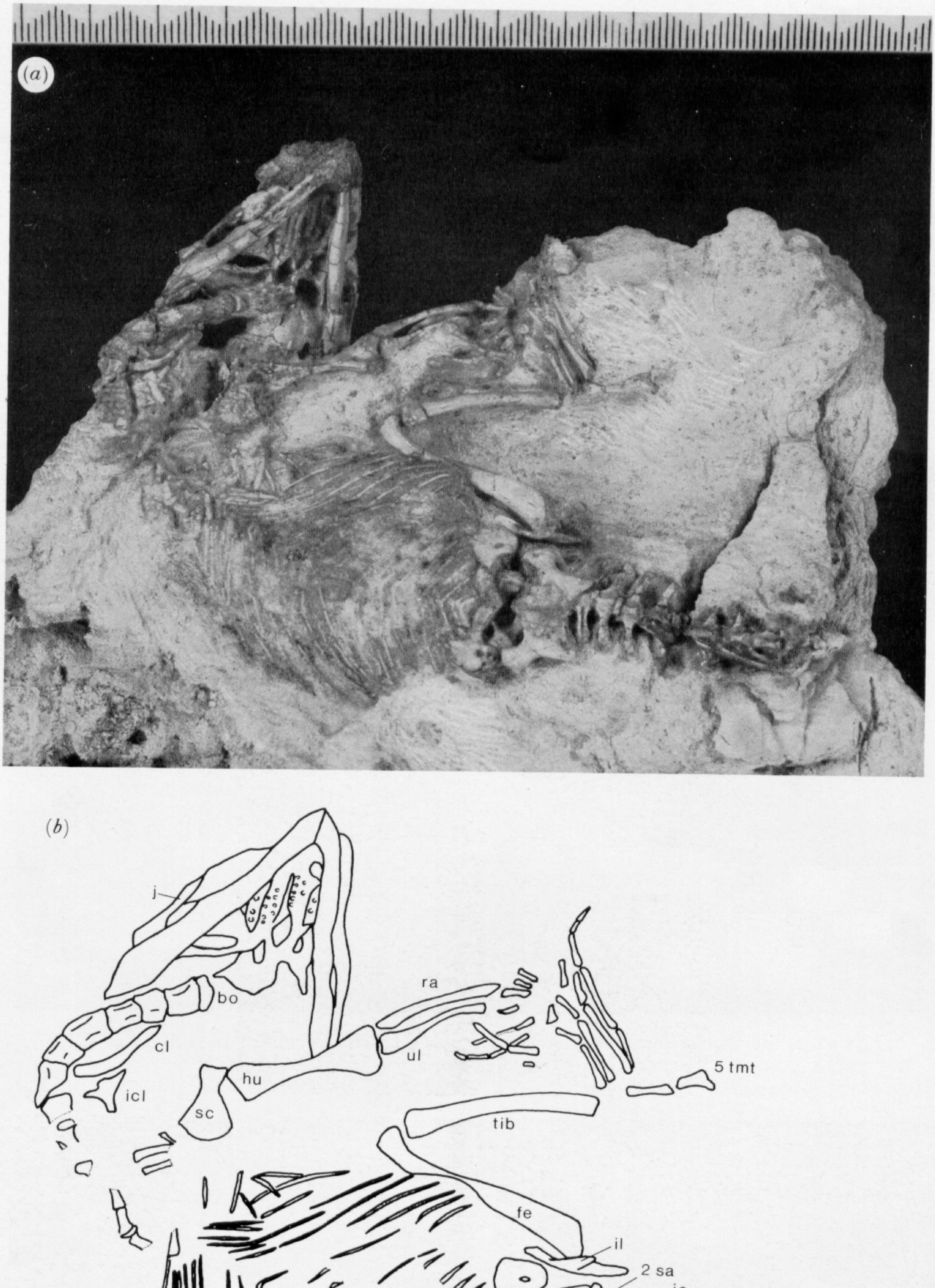
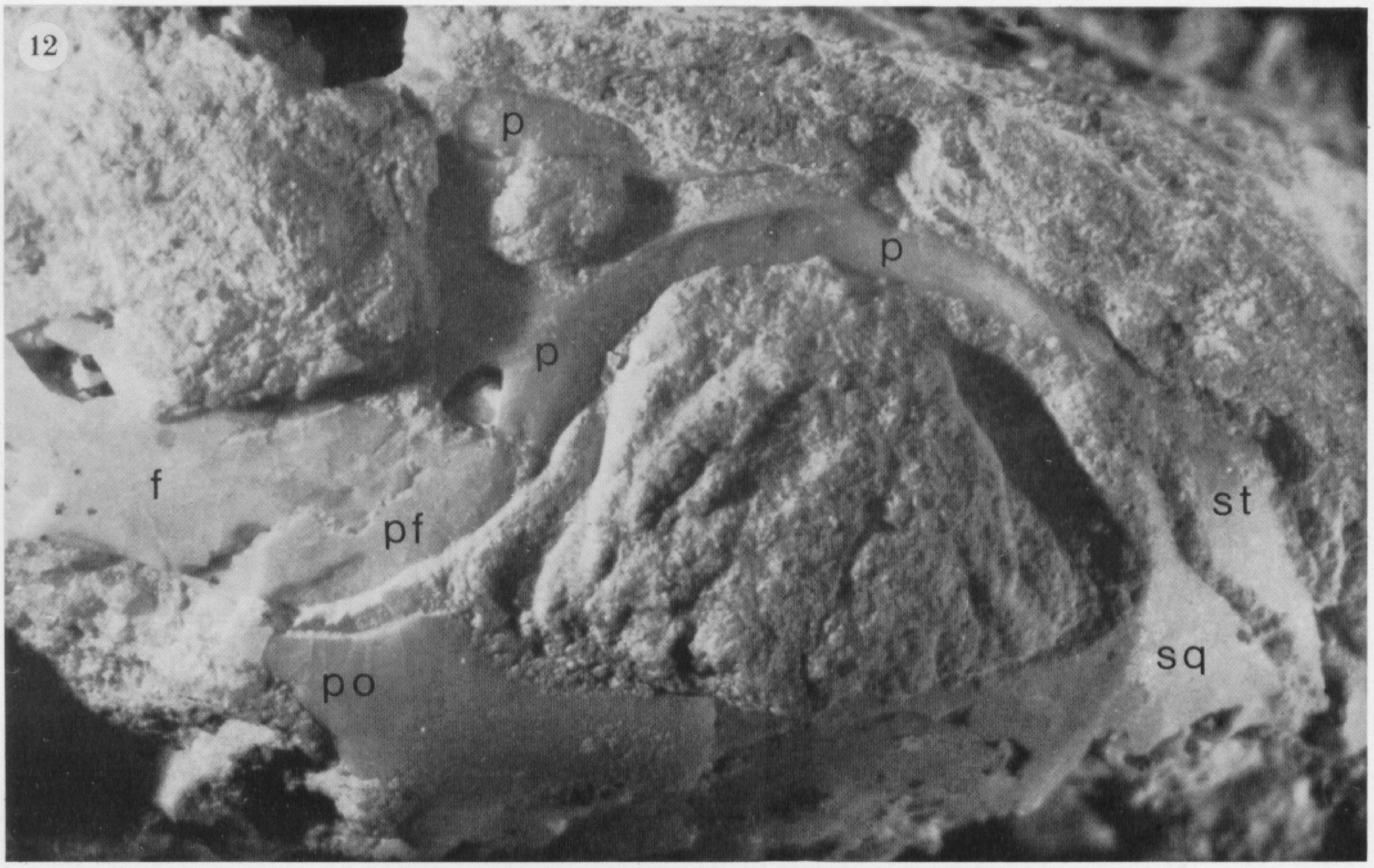
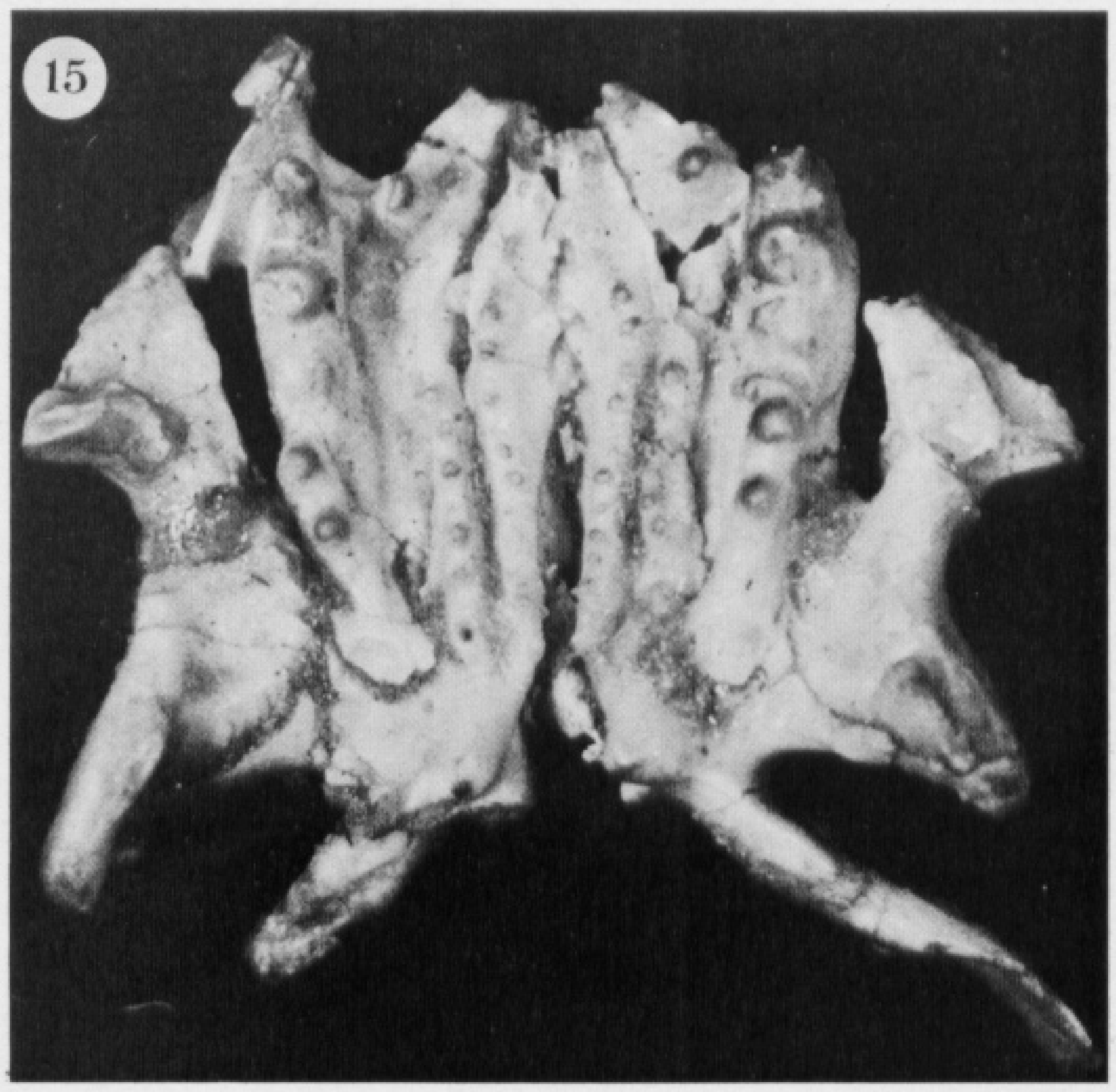


FIGURE 4. *Clevosaurus hudsoni.* (*a*) The articulated skeleton UMZC T1271 in ventral aspect, with (*b*) explanatory diagram.





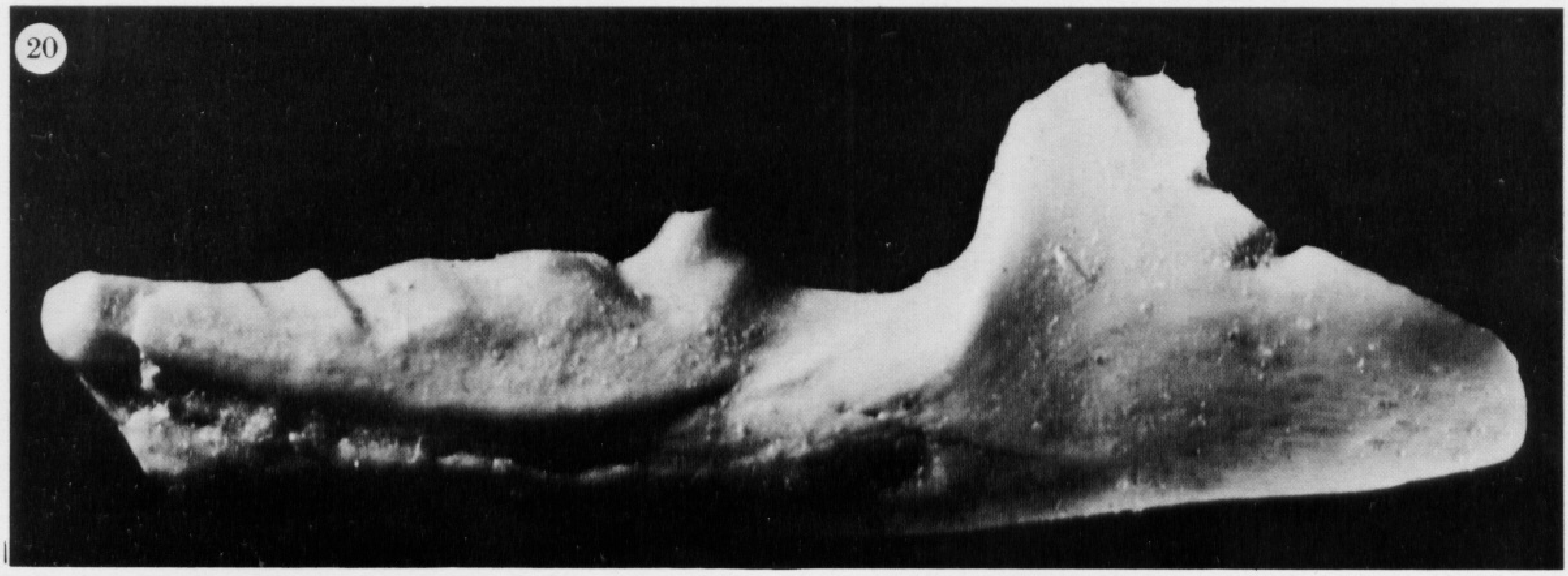


FIGURE 12. *Clevosaurus hudsoni*. AUP 11169, articulated skull exposed in dorsal view and showing the supratemporal, parietal table and interorbital region of the left side. (Magn. ×5.)

FIGURE 15. *Clevosaurus hudsoni*. Partial articulated palate, UMZC T1269, in ventral aspect. (Magn. ×8.)

FIGURE 20. *Clevosaurus hudsoni*. Dentary, UMZC T1276, in lateral view. (Magn. ×3.)

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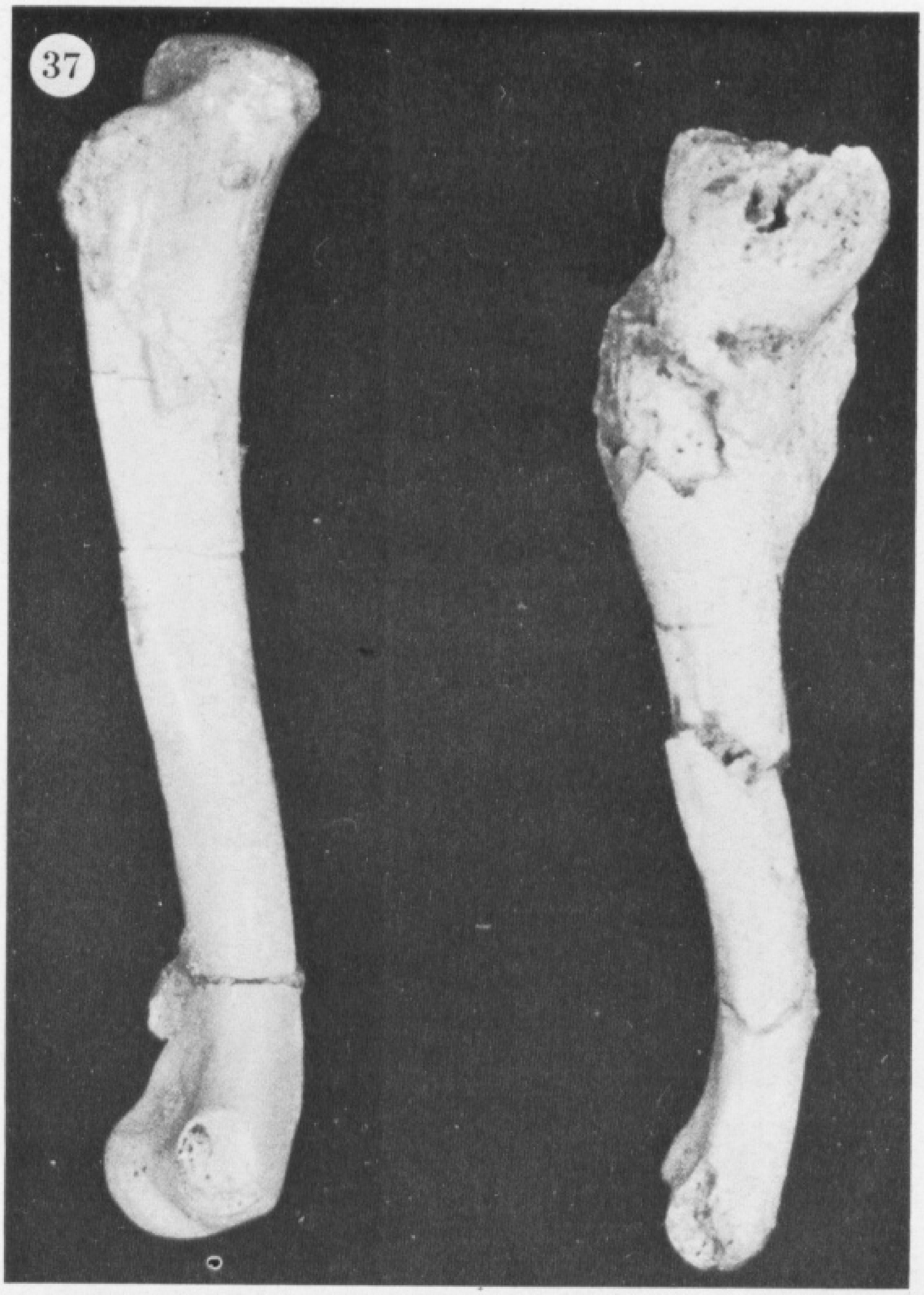

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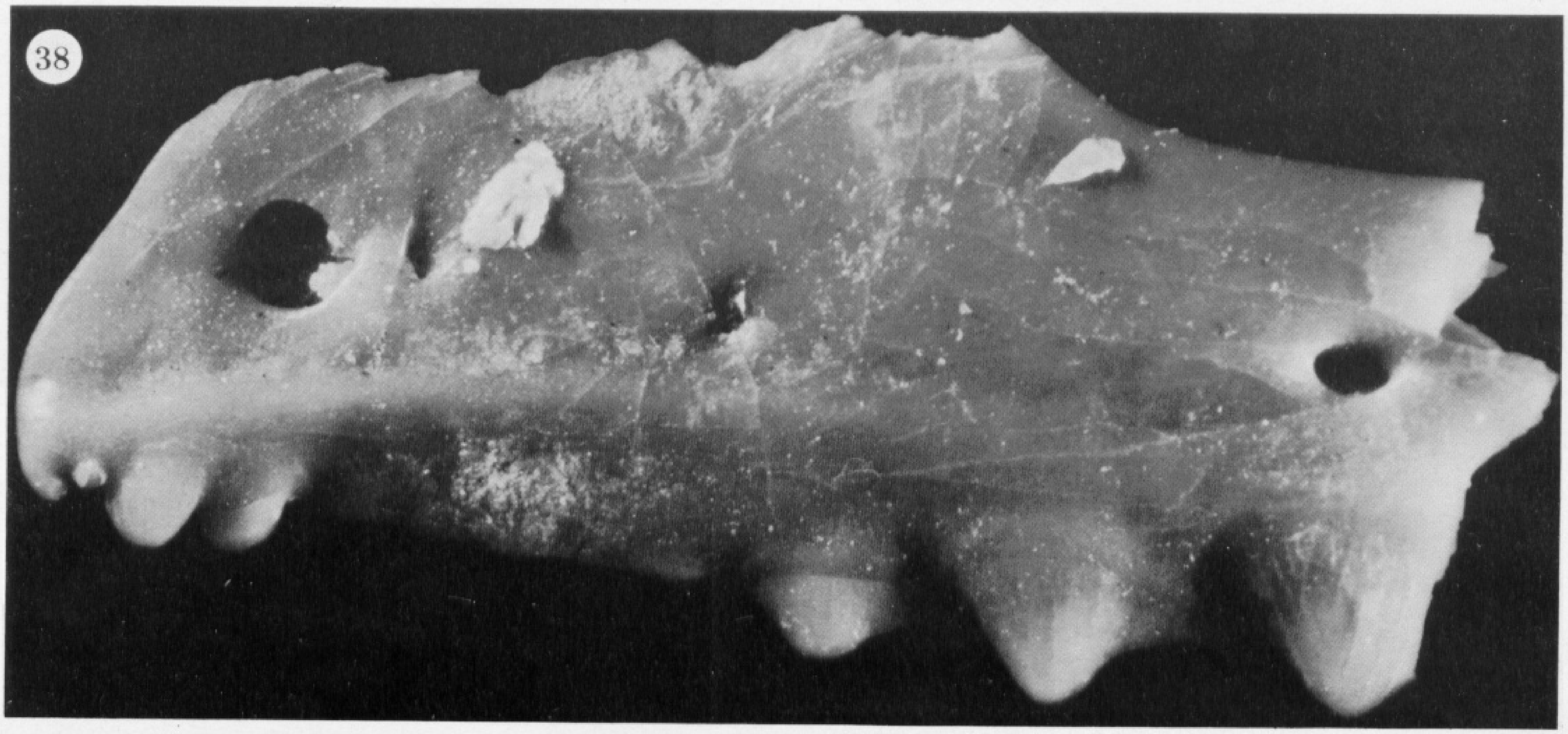

FIGURE 37. *Clevosaurus hudsoni*. A pathological left femur, UMZC T1275, compared with the normal condition, UMZC T1274. (Magn. ×3.)

FIGURE 38. *Clevosaurus minor*. A left maxilla, the holotype AUP 11377, in lateral view. (Magn. ×10.)