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A RHYNCHOSAUR FROM THE UPPER TRIASSIC MALERI FORMATION OF INDIA

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[Plates 5–7]

CONTENTS

Six associated rhynchosaur skeletons, recently discovered by the Geological Studies Unit of the Indian Statistical Institute in the Upper Triassic Maleri Formation, allow an almost complete osteological description and restoration of the species *Paradapedon huxleyi*.

The dentition is highly specialized, ankylothecodont, each tooth firmly fixed with a long root, new teeth added posteriorly in diagonal rows, without tooth replacement. The creatures probably lived in flood-plains or marshy environments, as shell eaters feeding mainly on mussels.

Possible evolutionary trends within the family Rhynchosauridae are outlined. The seven genera of rhynchosaurs are grouped on their morphological characters into three well-defined subfamilies which represent three stages in rhynchosaur evolution, occurring in Lower, Middle and Upper Triassic respectively.

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I. Introduction

Rhynchosaurs were one of the commonest groups of land vertebrates during part of the Triassic period, being recorded from all continents except Australia and Antarctica. They are known from the Karroo Formation of South Africa, from the Manda Beds of East Africa, from the Santa Maria and Ischigualasto Formations of South America, from the Maleri and Tiki Formations of India and from the Lower Keuper and Lossiemouth Beds of Great Britain. Recently rhynchosaurian remains have been discovered for the first time in North America, from the Wolfville Sandstone of Nova Scotia. Their wide geographical distribution and relatively limited geological range make them potentially very useful for Triassic stratigraphic correlation.

The present study describes the rhynchosaurs from the Upper Triassic Maleri Formation of central India. The Maleri Formation was long known to furnish a vertebrate fauna represented by surface fragments; but recently more complete vertebrate specimens have been found *in situ*. The common faunal elements include rhynchosaur, phytosaur, metoposaur, dipnoan and unionid forms. The composition of the Maleri fauna is interesting, especially association of the rhynchosaur with the phytosaur–metoposaur assemblage typical of the continental Upper Trias of the northern hemisphere.

II. Previous work on Indian rhynchosaurs

The earliest record of rhynchosaurs from the Maleri Formation was by Hislop in 1866, when he presented tooth plates, compared by Huxley (1869) with those of *Hyperodapedon gordoni*, to the Geological Society of London. Feistmantel (1880) mentioned the occurrence of rhynchosaurs in the Tiki Formation of the Sone-Mahanadi valley on the evidence of tooth plates collected by Hughes. Lydekker (1881, 1885) gave the name *H. huxleyi* to the Indian forms and described them in detail. Later collections, particularly by Aiyengar in the 1930's, were described by Huene (1938, 1939*a*, 1940, 1942, 1956), who created the genus *Paradapedon* for the species *huxleyi*, and who provided partial reconstruction of his fragmentary material.

Recent expeditions from 1957 onwards, organized by the Geological Studies Unit of the Indian Statistical Institute under the guidance of Dr Pamela Robinson and carried out systematically with improved excavation techniques, have made large collections of metoposaurs, phytosaurs and rhynchosaurs; and knowledge of the stratigraphy of the Maleri Formation is now greatly improved (see Jain, Robinson & Roy Chowdhury 1964; Roy Chowdhury 1965; Sengupta 1966; Chatterjee 1967*a*, *b*; Kutty 1969; Kutty & Roy Chowdhury 1970).

The present paper offers a description of the osteology of *Paradapedon huxleyi* based on the excellent material of these new collections, which allows an almost complete restoration of its form, suggests its mode of life, and allows comparison with other rhynchosaur genera and reference to the distribution of rhynchosaurs in space and time.

III. General geology of the Triassic Formations in the Pranhita–Godavari valley

The Maleri Formation occurs in the Pranhita–Godavari valley of central India, as a member of the wholly continental Indian Gondwana Group, a group of Permian to Cretaceous age that, resting on an eroded surface of Precambrian rocks and overlain by Deccan traps, trends in present outcrop NW–SE for about 480 km (figure 1).

King (1881) recognized six divisions in the group:

Chikiala }
Kota } Upper Gondwana
Maleri }

Kamthi }
Barakar } Lower Gondwana
Talchir }
Precambrian

The Maleri Formation was assigned Upper Triassic age on the basis of the vertebrate fauna (Huene 1940). The underlying Kamthi Formation has a flora of general Palaeozoic affinities, while the unconformably overlying Kota Formation has a fish fauna of Upper Liassic affinities (Pascoe 1959; Fox 1931).

Lithologically, the (original) Maleri Formation is mainly of 'structureless' unlithified clays with subordinate sandstones and 'lime-pellet' rocks. The main exposures are found around the village of Maleri along a belt running 65 km NW–SE, with two other isolated outcrops one to the north, one to the south (figure 1). Recent work has shown that in the (original Maleri Formation a band of barren sandstones (the Bhimaram Sandstone) separates lower clays with a Middle Triassic fauna, from upper clays with an Upper Triassic fauna (Jain *et al.* 1964; Kutty & Roy Chowdhury 1970). Further, Kutty (1969) in demarcating the upper boundary of the Maleri Formation recognized a lithological unit, the Dharmaram Formation, separable on the basis of its late Upper Trias fauna from a restricted Maleri below and the Kota above. In the present paper the term 'Maleri' is used in Kutty's sense, for the rock unit lying between the Bhimaram Sandstone and the Dharmaram Formation (see table 1).

TABLE 1

formation	main lithologies	characteristic fossils	age
Dharmaram	sandstones with red clays	prosauropod dinosaurs	late Upper Triassic (Upper Norian and Rhaetic)
Maleri	sandstones, red clays and lime-pellet rocks	dipnoi, metoposaur, rhynchosaur, phytosaur, aetosaur	early Upper Triassic (Carnian through middle Norian)
Bhimaram sandstone	sandstones with intercalated red clays	none	? (unplaced)
Yerrapalli	red clays and sandstones	capitosaur, ?brachyopid, dicynodonts, erythrosuchid, trirachodont–cynodont	Middle Triassic

The Maleri fossils are more common in the clays than in the sandy layers and the 'lime-pellet' rocks. They show no evidence of appreciable transport before burial. Rhynchosaur bones are common in them, abundantly so in the triangle between the villages Achlapur, Nannial, and Venkatapur (figure 1). The clays are sometimes streaked and mottled green, particularly (but not always) at contact with the bones, a feature especially notable at Venkatapur, where the bones are light-coloured and well preserved.

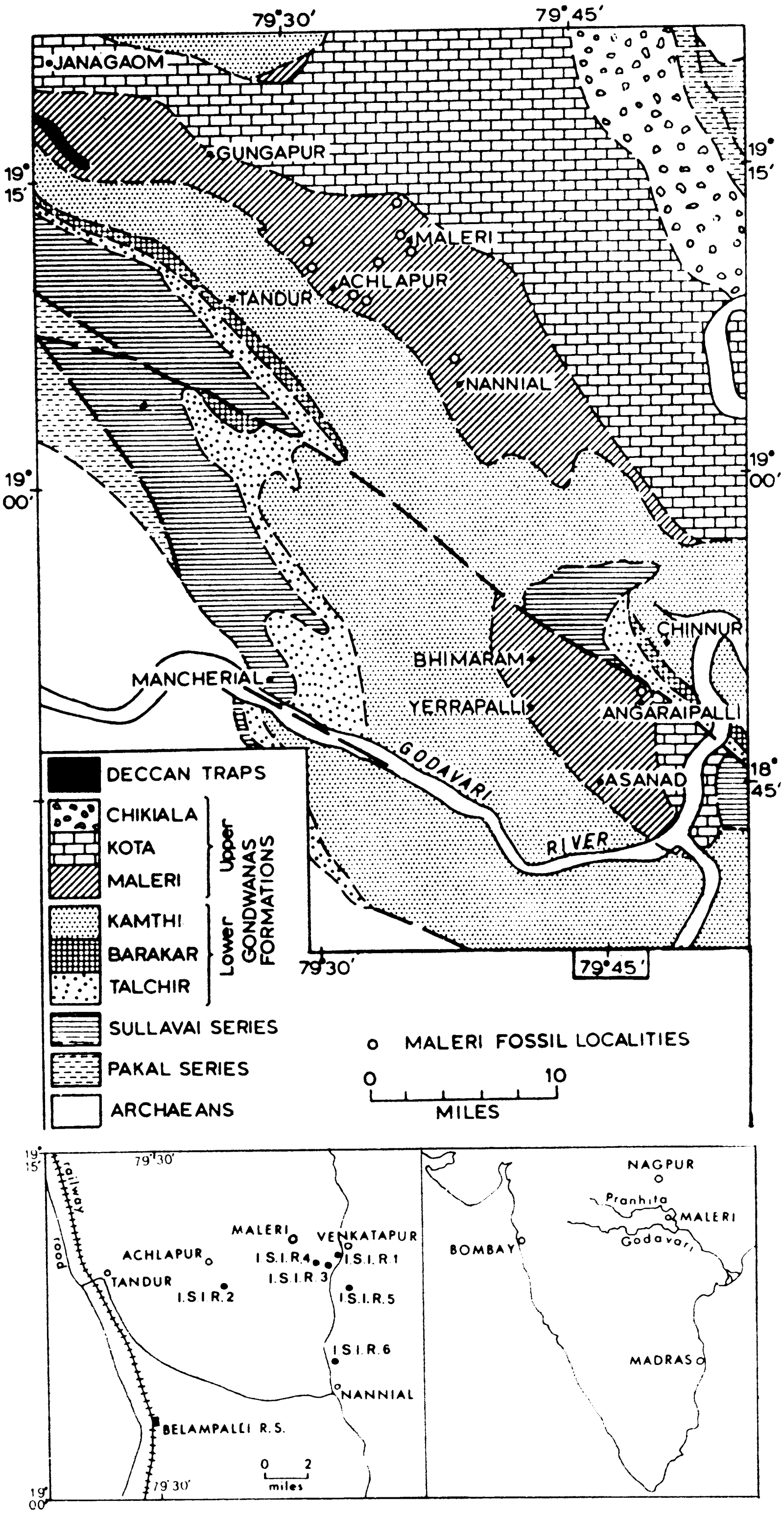

FIGURE 1. Geological map of part of the Pranhita-Godavari valley after King (1881). (Inset, right) Outline map of India showing the Rivers Godavari and Pranhita. (Inset, left) Rhynchosaur fossil localities in the main Maleri outcrop belt.

IV. MATERIAL

The important associations of the newly discovered rhynchosaur materials related to the present study are given below, together with their localities and the type of preservation. Details of the specimens are tabulated in an appendix to a thesis, submitted to the University of Calcutta (Chatterjee 1970), including all the previously described specimens that are housed in the British Museum (Natural History), London, Indian Museum, Calcutta, and I.S.I. Museum, Calcutta.

(1) I.S.I.R. 1: extremely well preserved skull and postcranial materials giving almost complete information about the animal. Estimated skull length 18 cm. Found near Venkatapur (figure 2).

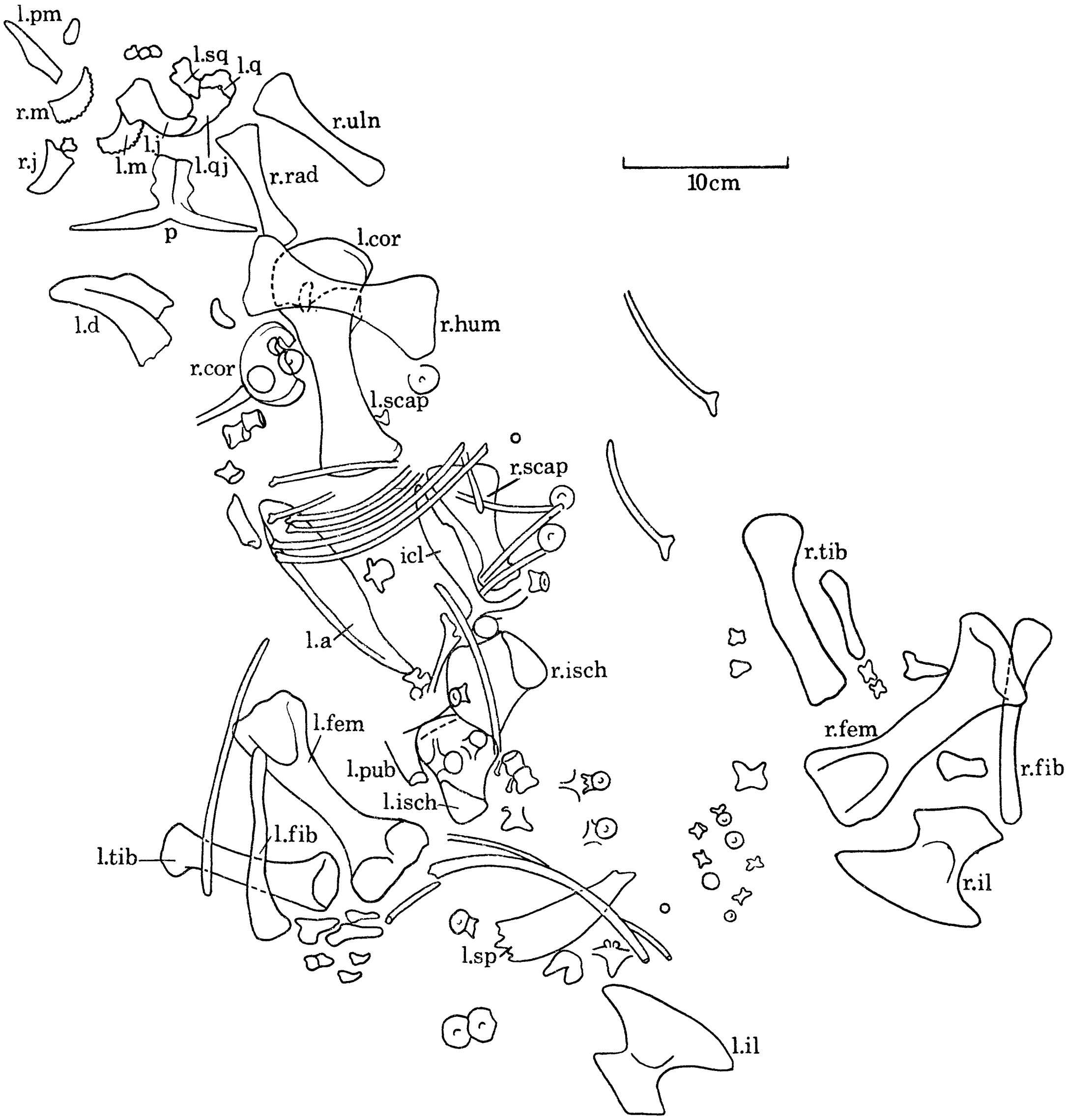

FIGURE 2. *Paradapedon huxleyi* (Lydekker). Associated skeleton (magn. × 0.22), as found in Venkatapur locality. Specimen I.S.I.R. 1; vertebrae, ribs and foot bones are not labelled.

(2) I.S.I.R. 2: part of the skull, a series of vertebrae from 10th presacral to second sacral, associated girdles, limbs and pes. Preservation is fairly good. Estimated skull length 33 cm. Found near Achlapur.

(3) I.S.I.R. 3: showing greater part of the skull, 46 vertebrae, a femur and phalanges. Smallest individual in the collection, and well preserved. Estimated skull length 11 cm. Found near Venkatapur.

(4) I.S.I.R. 4: a large partial skull including endocranium, excellently preserved girdles, a series of seven vertebrae including sacrum. Largest known rhynchosaur, estimated skull length 42 cm. Found near Venkatapur.

(5) I.S.I.R. 5: mainly skull, occiput is well represented. Estimated skull length 26 cm. Found near Wigaon.

(6) I.S.I.R. 6: part of left side of a skull, compressed dorsolaterally; preservation is good. Estimated skull length 23 cm. Found near Nannial.

V. Description of *Paradapedon*

1. *Paradapedon huxleyi* (Lydekker)

(Figures 2–26; plates 5–6)

Lectotype. A right maxillary tooth plate; specimen no. G.S.I. 281/1a, housed in the Indian Museum, Calcutta. Figured by Lydekker, 1885, Plate 1, Figure 2. Shown here in figure 29*b*, *c*, *d*.

Type locality. Maleri village in the Adilabad district, Andhra Pradesh.

Horizon. Maleri Formation of the Gondwana Group in the Pranhita–Godavari valley; Upper Triassic.

Generic diagnosis. Unusually broad skull, the width being greater than the length. Dentition is distinctive. Multiple rows of teeth are present in the maxilla on either side of a longitudinal groove. The dentigerous space lateral to the longitudinal groove is always greater and bears a greater number of rows of teeth than that medial to the groove. A single row of teeth is found on the occlusal surface of the dentary. In addition, the medial surface of the dentary shows extra rows of teeth.

All the rhynchosaur material from the Maleri Formation is considered here as *Paradapedon huxleyi*. The nomenclature is discussed separately in §VIII.

2. *Skull*

There are remains of six skulls in our collections, showing collectively all the cranial features in detail. A wide range of size exists between the different individuals. Usually the skulls are found in association with the postcranial materials and show no sign of compression or shearing except the specimen I.S.I.R. 6.

A table of main measurements of *Paradapedon* follows (see table 2).

Dermal bones of the skull-roof (*figure* 3)

The converging *premaxillae* curve down antero-ventrally from the skull table to form the edentulous beak. Each bone is triangular in cross-section, swells in thickness at the middle, but tapers at either end. In the anterior half of each bone the pair run alongside one another at the midline. The contact seems to be loose without any suture. Behind this contact the two bones gradually separate to flank the median naris. Posteriorly each bone fits into an elongate notch provided by the prefrontal, nasal and maxilla.

The *maxillae* are better considered as part of the palate, described later.

The *nasals* are incompletely preserved. The anterior margin borders the naris and ends in a short process lapping the postero-medial corner of the premaxilla. Behind this, each nasal makes a brief contact with the prefrontal by its lateral edge. Posteriorly the bone articulates with the frontal by a strong serrate suture.

TABLE 2. MAIN MEASUREMENTS/cm OF *PARADAPEDON HUXLEYI*

	specimen I.S.I.R. 1
skull length in mid-line	18
skull width across quadratojugal	27
skull height	12.5
mandible length in mid-line	19
presacral column length	64
scapulocoracoid height	16.2
scapula height	11.9
breadth apex of scapula	7.2
coracoid length	4.9
coracoid breadth	8.2
interclavicle length	11
humerus length	14.5
humerus, least diameter of the shaft	2
radius length	10
radius, least diameter of the shaft	1.1
ulna length	10.6
ulna, least diameter of the shaft	1
metacarpal II length	2.8
ilium, crest length	10.5
ilium, breadth of the neck	4
ilium, height	9
pubis length	6†
pubis height	9†
ischium length	9.4
ischium height	10
femur length	14.3
femur, least diameter of the shaft	2.3
tibia length	12.3
tibia, least diameter of the shaft	1.7
fibula length	12.7
fibula, least diameter of the shaft	1.2
metatarsal II length	5
pes length including tarsus	17
estimated total length	140

† Estimated.

The *frontals* are rather elongate and form the central part of the skull roof. Antero-laterally and postero-laterally they receive the pre- and postfrontals by practically straight sutures. The short free lateral margin is included in the border of the orbit. The two frontals meet along their longest, medial, borders. A transverse suture separates them from the nasals, another from the parietals. The dorsal surface is somethat depressed on either side of the midline. On their ventral surface a pair of strong ridges bound a medial shallow concavity which probably formed the roof of the olfactory tracts.

The *parietals* are co-ossified to form a T-shaped structure, with a long median branch and a posterior crossbar. The median branch bears a prominent sagittal crest, and proceeds forward

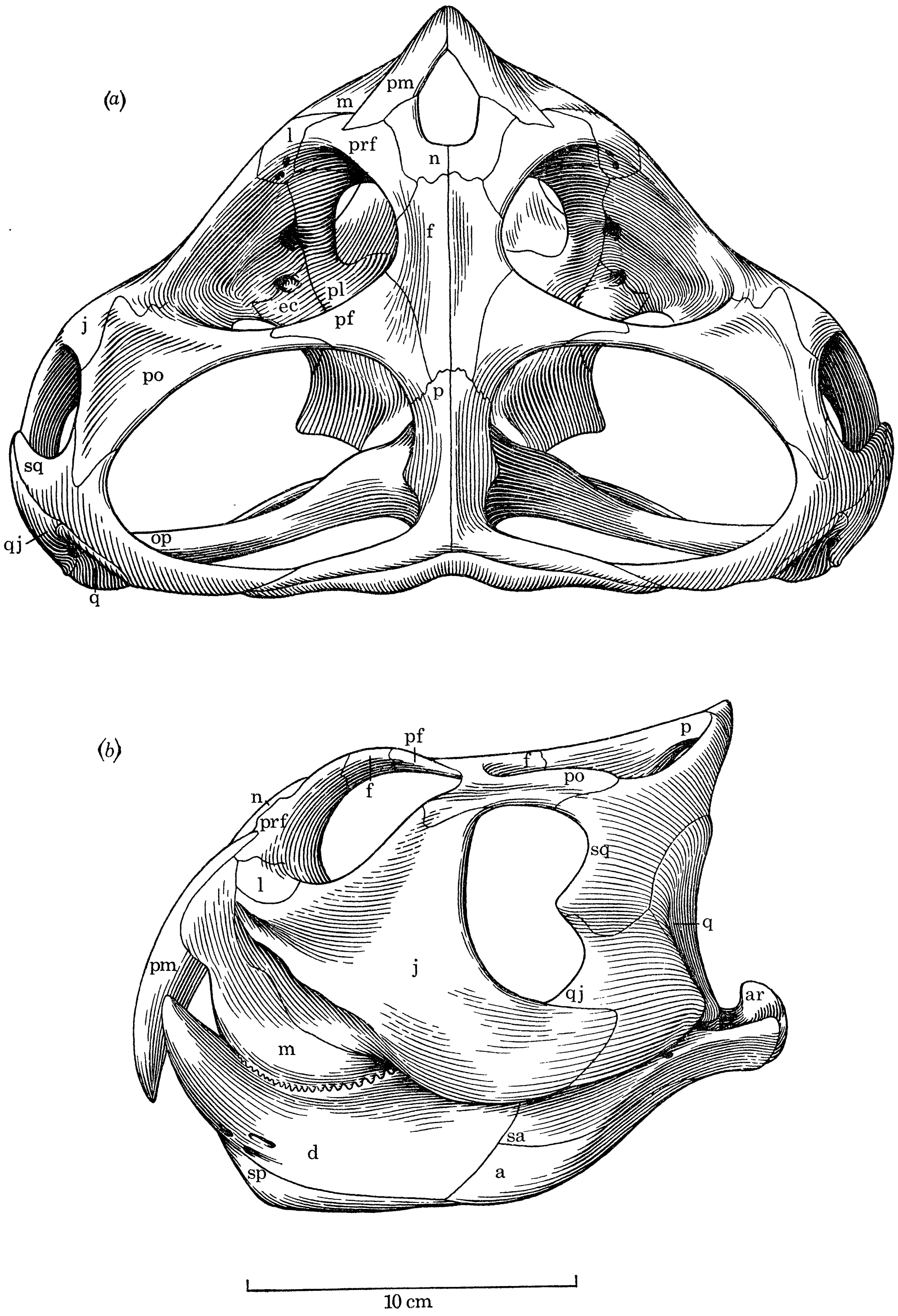

Figure 3. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Composite restoration of the skull. (*a*) Dorsal view; (*b*) lateral view with mandible in place.

to meet the frontal and postfrontal. The crossbar extends considerably laterally on either side to receive a dorsal branch of the squamosal behind the supratemporal fenestra.

Ventrally the median branch is deeply excavated to accommodate the supraoccipital. This excavation becomes shallow anteriorly and continues beneath the frontals.

The *lacrimal* is a little crescent fixed among the maxilla, jugal, prefrontal and palatine. Ventrally the external surface of the bone laps over the junction of the jugal and the maxilla for a short distance. The inner surface of the bone penetrates farther downward and meets an ascending process of the palatine in a long irregular suture. Two canals are visible on the inner surface at the border of the orbit and are probably related to the lacrimal duct.

The *prefrontal* is marked dorsally by a strong curved ridge which forms the antero-medial edge of the orbit. It is appreciably thickened at its lateral edge. Here it rides over an ascending process of the palatine internally and the lacrimal externally, partly concealing the latter, and barely touches the maxilla farther forward. Anteriorly, it is excavated into a notch for the reception of the premaxilla. The medial edge meets the nasal, while the posterior end passes below the frontal as a tapering process.

The *postfrontal* is a small triangular element on the postero-medial edge of the orbit. A short lateral process overlaps the postorbital to form a bar between the orbit and the supratemporal fenestra. Medially it meets the frontal by a long straight suture, but has a short contact with the parietal posteriorly.

The *postorbital* lies at the junction of the three skull openings. It is a triradiate bone whose three apices are firmly tied with the jugal, postfrontal and squamosal respectively. The dorsal surface is slightly depressed at the centre and in one juvenile specimen (I.S.I.R. 3), bears a small foramen.

The *jugal* is a large three-pronged bone in the cheek region, radiating anteriorly, dorsally and postero-ventrally. The anterior prong articulates firmly with the lacrimal. Below this articulation, the jugal overlaps the maxilla by its long sinuous anterior edge. Dorsally a strong ridge follows the contour of the maxillary/jugal suture for some distance and then continues on to the maxilla near the anterior branch. A row of foramina is excavated below this ridge. On the inner surface of the anterior branch, a prominent flange is buttressed against an ascending process of the palatine. Here a large canal is shared between the palatine and the jugal.

The dorsal prong interfingers with the postorbital. Internally a second flange is seen here projecting almost vertically from the inner surface of the jugal. This flange forms a steep wall behind the maxillary tooth plate and joins the ectopterygoid by a serrate suture which is pierced dorsally by a foramen.

The postero-ventral prong of the jugal descends a little below the jaw margin as a tongue-like process, and ends in a sheath of the quadratojugal.

The *quadratojugal* is an L-shaped structure. The lower leg of the L proceeds forward along the ventral and inner surface of the jugal. The upper leg of the L is broad and convex on its outer surface. Dorsally it is appreciably thickened and bifurcated to receive the descending process of the squamosal. Postero-medially it has an interfingering suture with the quadrate.

The *squamosal* is a triradiate bone. The anterior branch is short but broad and underlaps the postorbital. The dorsal branch is narrow and elongate and curves around the anterior margin of the cross-bar of the parietal. The third branch runs downward and forward and fits into a cleft of the quadratojugal. The posterior margin of this branch rides over the antero-dorsal edge of the quadrate and receives the head of the quadrate into a shallow ventral notch. Medial to the quadrate articulation, the bone shows a depressed surface for the reception of the paroccipital process.

Dermal bones of the palate (*figure* 4)

The *maxillae* are well exposed on the palatal and lateral aspects of the skull, but are nearly hidden in dorsal view. Each bone has two distinct divisions; a lateral ascending process, and a palatal tooth-bearing surface. The dental border, as seen laterally, is convex ventrally (figure 3*b*). From this border the thin ascending process forms a vertical narrow sheet which does not reach up to the orbit, but is separated from the latter by the jugal and the lacrimal. The long posterior margin of the ascending process of the maxilla is braced by the jugal, and above the latter by the lacrimal. Anteriorly, the ascending process forks to receive the postero-ventral surface of the premaxilla.

In palatal view, the maxillae are represented by a pair of long narrow triangular tooth plates thickly and heavily built, and converging towards one another anteriorly. Each is crowded with a number of longitudinal rows of the small projecting teeth, and is traversed by a longitudinal groove for the reception of the dentary. The medial wall of the tooth plate is convex, the lateral wall is concave. On the lateral wall, just above the dental margin, lies a row of foramina which probably served as exits for branches of the superior alveolar nerve and small blood vessels. The tooth plate is strongly clamped by the vomer, palatine, ectopterygoid and the jugal. A V-shaped channel is seen between the posterior extremity of the tooth plate and the ectopterygoid.

The tooth plate was regarded by earlier workers (Huxley 1869; Lydekker 1885) as a palato-maxilla, as they considered the median longitudinal groove to be the line of junction between the palatine and the maxilla. The fact that the tooth plate is a single bone, a maxilla, is confirmed by sectioning the bone. Moreover, the palatine is recognized as a separate element in all rhynchosaurs (Huene 1938, 1942); it is applied on the medial surface of the maxilla and does not form part of the dentigerous surface.

The *vomers* terminate anteriorly as short tapering processes behind the premaxillae. Posteriorly each bone forks to flank the anterior rim of the choana. The medial branch is a thin vertical plate, closely appressed against the similar branch of the opposite side along the midline to form a bar between the choanae, and then continues farther backward to wedge between the palatine and the pterygoid. The lateral branch is strongly fixed to the antero-medial corner of the tooth plate and then barely touches the palatine posteriorly.

The *palatines* have two well-marked divisions – a medial, and a dorsal segment. The medial segment is curved to form the major part of the palatal channel. The inner edge of this segment articulates with the vomer and the outer surface of the palatal ramus of the pterygoid by a long suture which curves towards the postpalatine fenestra behind the palatal channel. Here the palatine makes a brief contact with the ectopterygoid. The outer edge of the medial segment coats the postero-medial wall of the maxillary tooth plate posterior to the vomerine contact and bends towards the dorsal segment.

The dorsal segment roofs over the maxillary tooth plate. Posteriorly it has a strong flange across the width of the tooth plate which is concealed laterally by the jugal. Anteriorly the bone sends up a long ascending process which successively joins on its course the inner anterior ridge of the jugal, a small medial edge of the lacrimal, and a ventral process of the prefrontal. A big canal partially separates the jugal from the palatine.

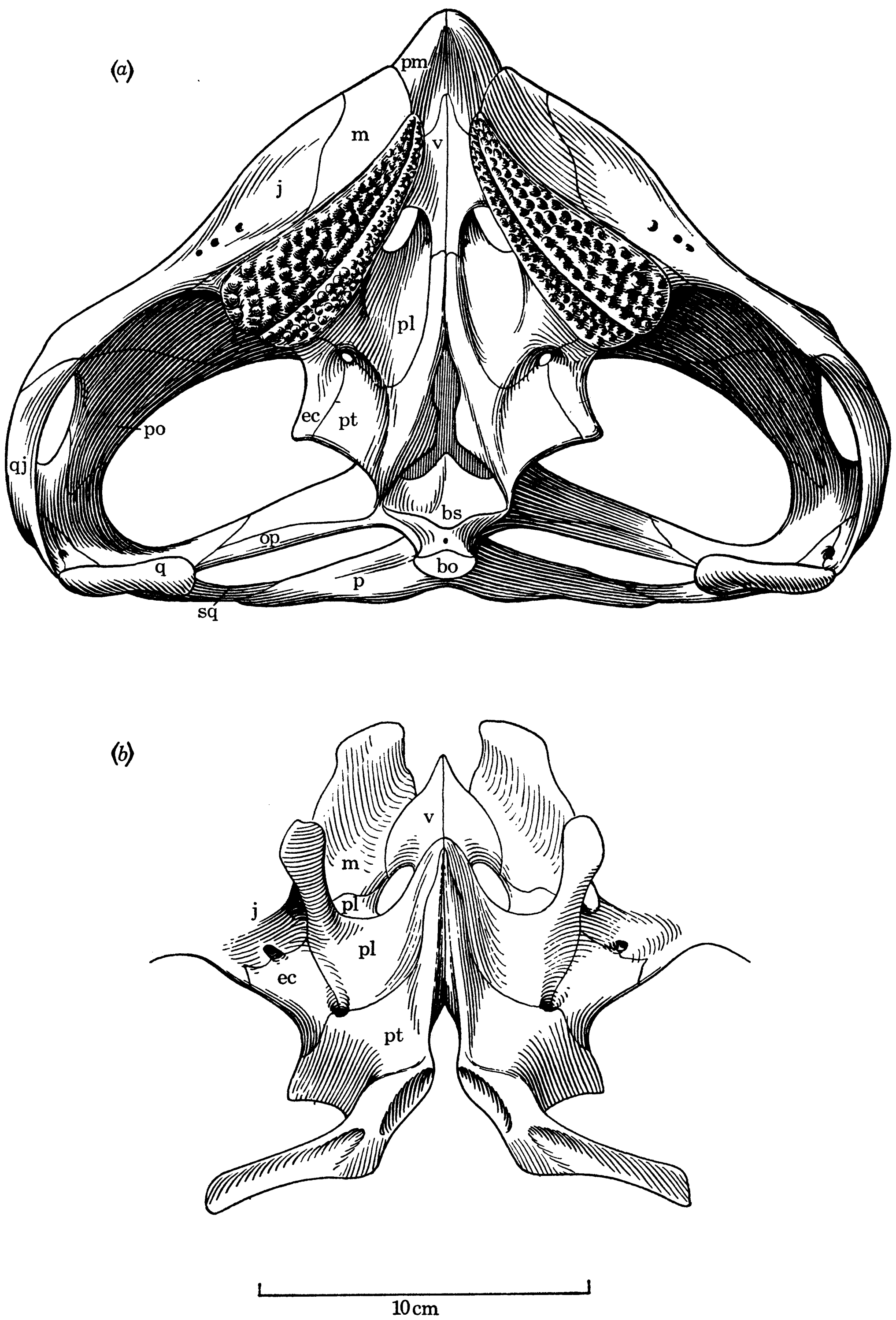

FIGURE 4. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). (*a*) Composite restoration of the skull in palatal view; (*b*) composite restoration of the palate in dorsal view (skull roof and endocranium omitted).

The *ectopterygoid* is a small inverted L-shaped bone. The upper leg of the L lies dorsally to form a prominent buttress behind the maxillary tooth plate and extends farther forward over the roof of the tooth plate. This buttress meets the palatine anteriorly but is overlapped by the jugal on the lateral side. The suture between the ectopterygoid and the jugal is excavated into a large canal on the roof of the tooth plate. The lower leg of the L is directed posteriorly and overlaps the lateral edge of the pterygoid flange on the ventral aspect.

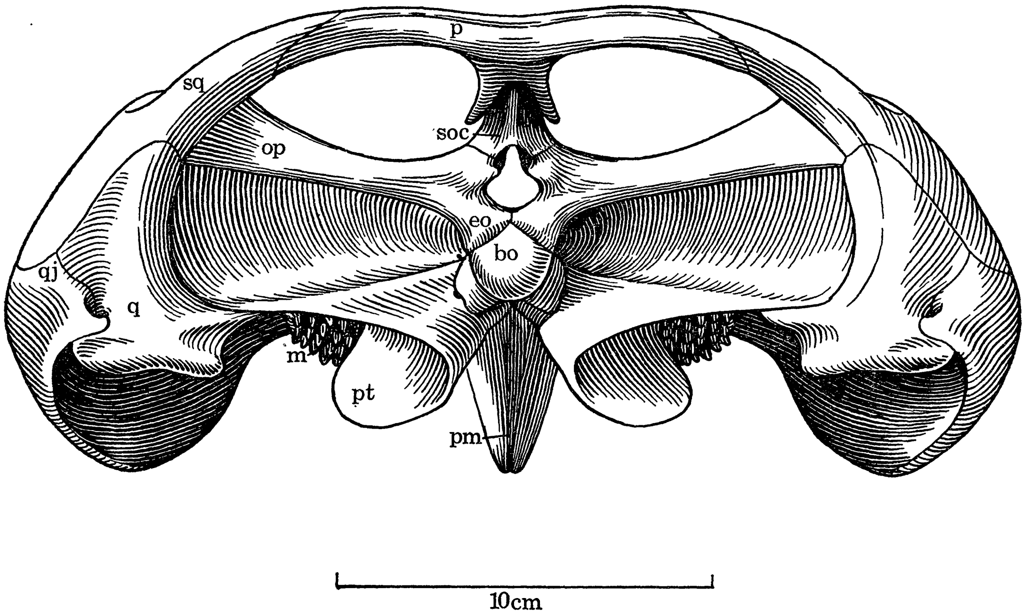

Figure 5. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Composite restoration of the skull in occipital view.

The *pterygoid* is a long triradiate structure, differentiating into a medial palatal ramus, a lateral wing in the form of a cone, and a nearly transverse quadrate ramus. At the junction of the three rami, on the medial aspect of the bone, lies the articular facet for the basisphenoid.

The palatal ramus extends forward as a long vertical plate to overlap the medial surface of the vomer. Behind the vomer the lateral edge of the plate forms the steep medial wall of the palatal channel and meets the palatine for a long distance. Medially the vertical plates press against each other along the ventral margin. Passing farther backwards the medial plates tend to diverge gradually in front of the brain-case to form the narrow interpterygoid vacuity. Behind the beginning of the vacuity the medial plate contains a shallow elliptical facet facing upward and backward. This facet is prolonged antero-posteriorly and receives the whole antero-ventral surface of the basipterygoid process. Here the palatal ramus passes to the deep conical pterygoid flange behind the maxillary tooth plate. The ventral surface of the flange curves laterally and is sheathed by a small overlap of the ectopterygoid. The dorsal surface of the flange passes laterally towards the quadrate.

The quadrate ramus is a thin sheet of bone, relatively deep, and extends laterally as a steep sloping wall. Anteriorly at the confluence of the lateral and quadrate rami lies the base of the epipterygoid. The posterior surface is marked by a deep channel. The thin lateral edge is strongly applied to a postero-medial shelf of the quadrate.

Quadrate and epipterygoid

The *quadrate* forms a vertical pillar in the plane of the occiput (figure 5). Dorsally the bone is produced into a tapering head which fits into a socket of the squamosal. More ventrally the lateral edge of the quadrate makes a sinuous contact with the quadratojugal, pierced by the quadrate foramen. The mesial extension of the quadrate, below the head, bears a strong semicircular depression for the reception of the quadrate ramus of the pterygoid.

The basal articular condyle is slightly convex, and lies transverse to the sagittal plane of the skull. It maintains an almost uniform antero-posterior width.

The *epipterygoid* is incompletely known. It has a broad triangular base, closely applied to the anterior surface of the pterygoid. Dorsally it becomes slender and narrow. The relation of epipterygoid with the braincase is not shown in any of the Maleri specimens.

Endocranium (figures 6 and 7)

Nine specimens display portions of endocranium of which I.S.I.R. 1, I.S.I.R. 4 and I.S.I.R. 5 are fairly complete and are important for interpreting the detailed structures. A fine disarticulated basisphenoid is represented by specimen I.S.I.R. 25 (figure 7*a*). The rest of the material is in the form of specimens of co-ossified basioccipital/basisphenoid, these robust bones being commonly found as isolated specimens in Maleri clay. A little variability in the endocranial structure is seen among the different individuals, presumably at least partly related to small changes occurring during the growth of the animal.

The ossified parts of the endocranium include the median basioccipital, basisphenoid and supraoccipital, and paired exoccipitals, pro-otics and opisthotics. The basisphenoid is so intimately fused with the dermal parasphenoid that demarcation is not possible. The exoccipital and opisthotic are usually co-ossified. The articulations between the median and paired elements tend to be loose. No cultriform process is found preserved.

The *basioccipital* contributes the major portion to the single hemispherical occipital condyle. Dorsally it is almost excluded from the formation of the floor of the endocranial cavity by the overlying exoccipitals. Ventrally, anterior to the hemispherical condyle, the bone contracts to a neck and then swells again to form a pair of rugose tubera, in conjunction with the basisphenoid, for the attachment of neck muscles.

The *basisphenoid* is a thick compact bone, triangular in shape, and lies in front of the basioccipital. Ventrally the two tubera, mentioned above, are widely spaced and separated by a shallow depression which continues farther forward to become a very narrow furrow between the two basipterygoid processes. The basipterygoid processes are directed postero-ventrally and somewhat laterally from the antero-ventral portion of the basisphenoid. The ventral tip of each process reaches farther ventrally than the adjacent tubera.

The anterior face of the basisphenoid closely resembles that of *Sphenodon* in a general way, although the basisphenoid of *Paradapedon* is enormously thick. As in *Sphenodon*, the vertical wall of the dorsum sellae contains a pair of shallow fossae at the base, separated by a median ridge which is pierced by a common foramen for the internal carotid arteries (figure 6*c*). Save-Soderbergh (1946) interpreted these fossae in *Sphenodon* as 'retractor fossae' for the attachment of the retractor bulbi group of eye muscles. He further suggested that due to the invasion of the retractor bulbi group of eye muscles at this position, the pituitary body is uplifted and is well separated from the wall of the dorsum sellae by a membraneous septum. In *Paradapedon*, no

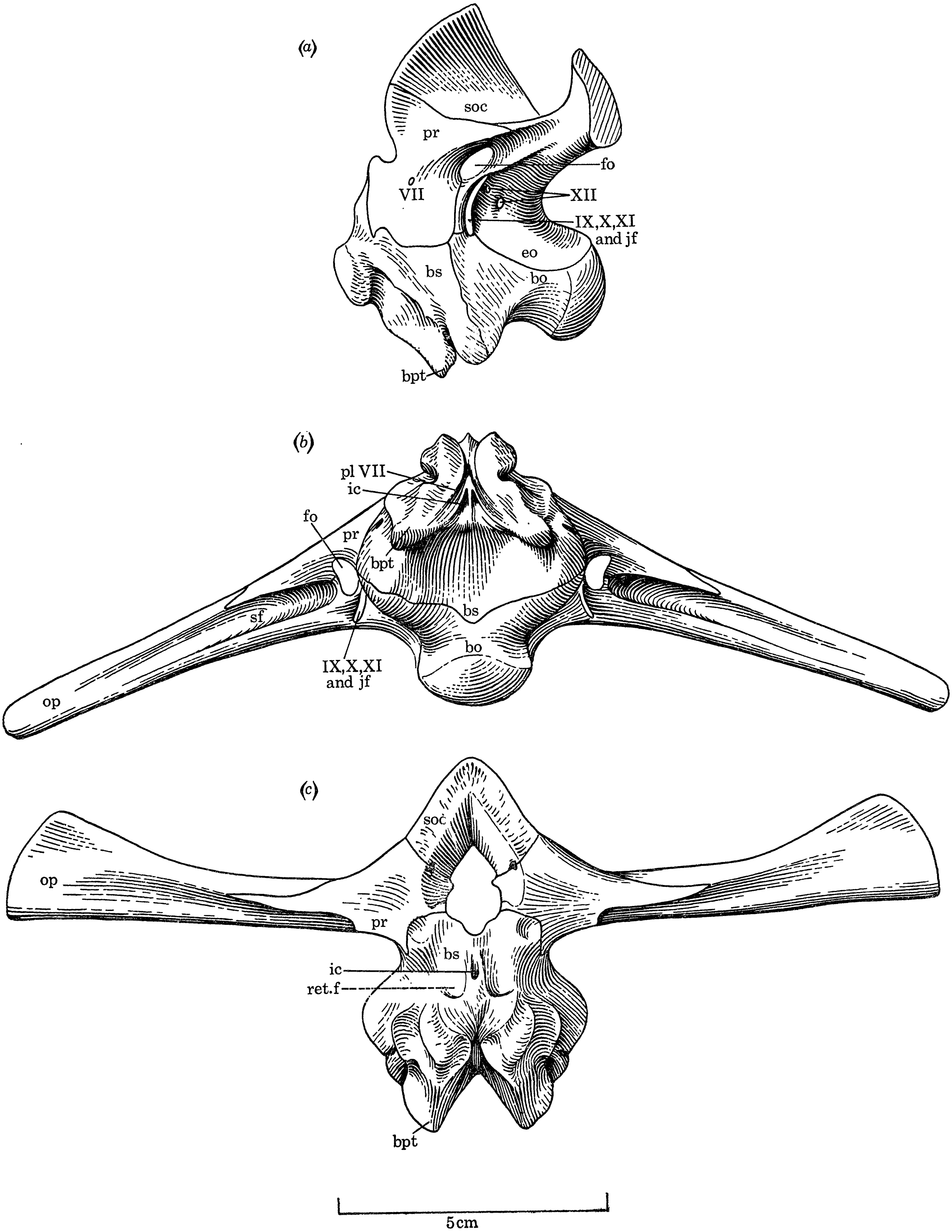

Figure 6. *Paradapedon huxleyi* (Lydekker) (magn. × 1). Composite restoration of the endocranium. (*a*) Left lateral view; (*b*) ventral view; (*c*) anterior view.

sella turcica is present, and the pituitary body was presumably separated from the dorsum sellae by a fairly wide interspace and would possibly be enclosed in a separate membraneous sac. Below the retractor fossae, a small unfinished surface probably represents the site of the delicate cultriform process of the parasphenoid. Dorsally the basisphenoid forms a small part of the floor of the endocranial cavity. Here an unusual longitudinal groove is seen at the midline especially in the disarticulated specimen (figure 7*a*). That this groove would be closed above by the basioccipital is shown by the presence of a long median tunnel reaching the surface of the endocranial floor just behind the dorsum sellae in associated specimens of basisphenoid and basioccipital. This tunnel passes postero-ventrally through the junction of the basisphenoid and basioccipital for a considerable distance, but seems to end blindly before reaching the ventral surface of the endocranium. Probably this median tunnel may represent a remnant of the endocranial fenestra. The lateral portions of the dorsal surface of the basisphenoid form rugose sutural facets for the reception of the pro-otics. The isolated basisphenoid well displays the large, complex, and rugose facet for the reception of the basioccipital.

The paired *exoccipitals* are placed on the dorso-lateral surface of the basioccipital, each is indistinguishably fused with the opisthotic of its own side. Each exoccipital is a small bone, differentiating into a broad basal region and a narrow ascending process. The basal region bears an elliptical facet for the articulation with the basioccipital. The basal rami of the two exoccipitals meet each other at the midline and, conjoined, conceal the dorsal part of the basioccipital. From its basal portion, each bone curves upward and backward to form a tapering ascending process which braces the opisthotic. The ascending process bears a postero-ventrally directed projection for the reception of the pro-atlas.

The *opisthotics* are dominated by the prominent paroccipital processes projecting laterally far beyond the otic region to form the lower boundary of the post-temporal fenestrae. Each process becomes spatulate at the lateral termination and abuts against the descending process of the squamosal. The antero-ventral face of each process encloses the longitudinal stapedial fossa which probably served to accommodate the stapes. However, no stapes is found in the collection. Medially each opisthotic forms the posterior part of the otic capsule. Here it is adjoined by three bones: the supraoccipital lies dorsally, the pro-otic at the anterior border, and the exoccipital at the ventro-medial region.

The *pro-otic* forms the anterior and antero-ventral parts of the otic capsule. Dorsally it articulates with the supraoccipital and then passes laterally to the opisthotic extending for a short distance along the anterior surface of the paroccipital process. Its antero-mesial border contains the pro-otic or trigeminal incisure. Ventrally it overlies the basisphenoid. Postero-ventrally it has a sutural contact with the opisthotic just below the fenestra ovale.

The *supraoccipital* forms the arched roof of the foramen magnum and fits into a socket under the median branch of the parietal. The bone has two symmetrical lateral flanges that slope ventro-laterally to meet the pro-otic in front and opisthotic behind. The antero-dorsal surface is unfinished indicating the cartilaginous extension of the synotic tectum and taeniae marginales.

The position and relationships of the various endocranial foramina preserved in the Maleri specimen can be interpreted by comparing them with those of present day reptiles. Nerves I–IV evidently emerged from the anterior unossified portion of the endocranium and thus cannot be located accurately. The trigeminal left the endocranial cavity through the pro-otic incisure which was presumably closed in life by the taenia marginalis. The dorsum sellae does not show any visible foramen for the abducens. Below and behind the trigeminal incisure, a

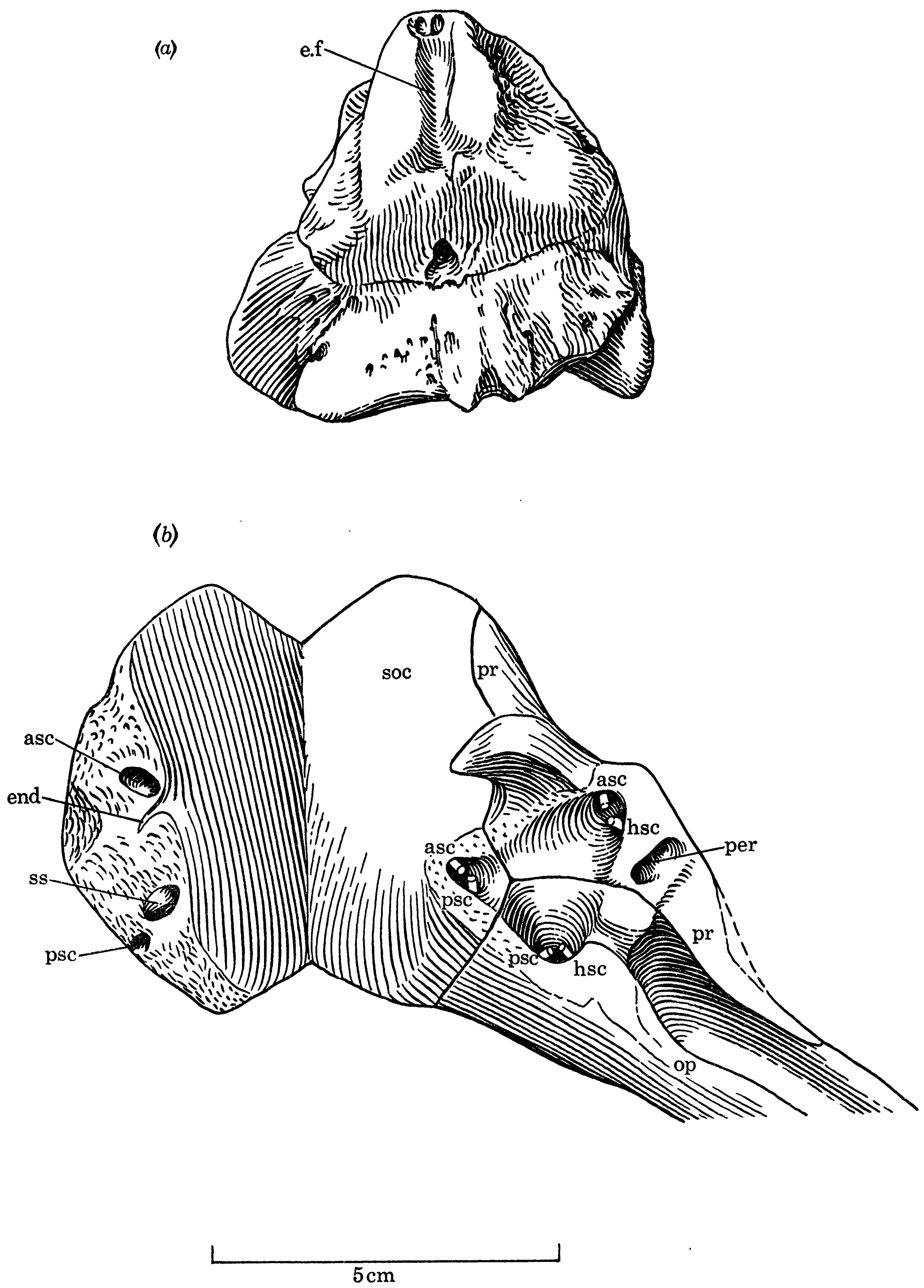

Figure 7. *Paradapedon huxleyi* (Lydekker) (magn. × 1). Endocranium. (*a*) Dorsal view of a disarticulated basisphenoid (specimen I.S.I.R. 25) showing endocranial fenestra and the articular facets for pro-otic (lateral) and basioccipital (posterior); (*b*) postero-ventral view of the conjoined pro-otic, opisthotic and supraoccipital showing the vestibular cavity and the canalicular system of the inner ear. The positions of the different semicircular canals are shown by wires; specimen I.S.I.R. 6.

small foramen in the pro-otic conveyed the facialis nerve. A palatine branch of the facialis probably ran ventral to the basipterygoid process, as a well-defined groove is present there leading in an anterior direction. No vidian canal is present. A pair of foramina is seen at the midline, on the ventral surface of the basisphenoid, between the roofs of the two basipterygoid processes. These foramina tunnel through the bone and make their anterior exits through a common passage at the base of the dorsum sellae, indicating the course of the internal carotid arteries. The foramina for acoustic nerves are not represented in the ossified portion of the otic capsule. A thin bridge of opisthotic separates the fenestra ovalis from the jugular foramen. The fenestra ovalis lies fairly high and is enclosed by the pro-otic and opisthotic, and would receive the stapes. Behind the fenestra ovalis lies the deep narrow jugular foramen, surrounded by pro-otic, opisthotic and the basioccipital, and which probably transmitted nerves IX, X, XI and the posterior branch of the jugular vein. Behind this, the exoccipital is pierced in its basal portion by two foramina for the hypoglossal nerves.

The internal contours of the *inner ear* cavity, unusually well preserved in specimen I.S.I. 4/6, give fairly complete information about the topography of the endolymphatic system of the inner ear (figure 7*b*). The canalicular system exhibits the normal trio of semicircular canals which are completely enclosed in separate bony tunnels. The courses of these tunnels are followed by putting fine wires inside them. The anterior vertical semicircular canal is shared between the pro-otic and supraoccipital, the posterior vertical semicircular canal passes through opisthotic and supraoccipital, whereas the exterior horizontal semicircular canal tunnels through pro-otic and opisthotic.

The upper portion of the bony cavity in which the vestibule lay is triangular in shape, formed mainly by the pro-otic and opisthotic with a little contribution from supraoccipital, and is surrounded by the canalicular system. The three apices of the vestibular cavity are placed anteriorly, posteriorly and dorsally respectively, and each apex is connected with the two of the semicircular canals. At the anterior apex lies the anterior ampullary recess that lodged the ampullae of the anterior vertical and exterior horizontal canals. The posterior apex forms the similar ampullary recess for the posterior vertical and exterior horizontal semicircular canals. The dorsal apex lies in the supraoccipital and contained the sinus superior of the utriculus. It leads into the channel for the posterior semicircular canal in front and the channel for the posterior semicircular canal behind. Here a tunnel is seen, shared between the supraoccipital and the pro-otic for the passage of the endolymphatic duct. The perilymphatic system probably ended blindly in a small cavity in the pro-otic, postero-lateral to the vestibular cavity, which is pierced by two foramina.

The slope of the vestibular cavity indicates the irregular triradiate structure of the utriculus, but the shape of the sacculus is merely a speculation, probably rounded. A pair of pockets is seen at the junction of the dorsal surface of the basioccipital and basisphenoid, probably for the reception of the ventral stem of the lagena. Each pocket lies well away from the fenestra ovalis of its own side, suggesting that the lagena was probably elongate.

Restoration of the skull

The restoration of the skull is mainly based on specimen I.S.I.R. 1, which is fairly complete and undistorted. Supplementary characters are taken from other skull materials in the collection. Figures are drawn by engineering projection method permitting a constant check on accuracy in different views.

The skull belonging to specimen I.S.I.R. 1 was not found intact in the enclosing matrix. It was broken into four main pieces, consisting of the median roofing bones, endocranium, and the two lateral portions of the skull with palate. The breaks were mainly across the bars between the various skull openings. A lot of care has been taken to reconstruct the correct proportions of the skull. The two lateral portions of the skull were put together along the median bars of the pterygoid, which show interlocking facets for articulation, thus fixing the width of the skull. The endocranium was then placed behind the interpterygoid vacuity in such a fashion that the basipterygoid process could fit into the corresponding facets of the pterygoid medially, and the paroccipital process could touch the corresponding facets of squamosal laterally. The latter articulation provides a check on the width of the skull. Finally the median roofing bones are joined together to the two sides of the skull, keeping the undersurface of the parietal over the supraoccipital. The width and the height of the skull are thus verified. The broken pieces of the skull, when assembled together, exhibited a symmetrical form. An undistorted and almost complete skull of *Hyperodapedon*, housed in the University of Newcastle-upon-Tyne, was very helpful during this reconstruction process.

In skull restoration (figures 3–5), the plane joining the tip of the premaxilla and free ventral projection of the jugal is kept horizontal and is taken as the reference plane. Dorsal and palatal features are well exhibited in specimens I.S.I.R. 1, 3 and 6. The pterygoquadrate articulation is taken from I.S.I.R. 5. The endocranium is restored from I.S.I.R. 1, 4 and 5. Details of the cranial sutures in the skull roof are well shown in a juvenile specimen I.S.I.R. 3.

3. *Mandible*

The *mandibles* (figure 8) are set somewhat inside the antero-lateral skull boundaries. The dorsal profile of the jaw ramus is a gently sigmoid curvature. It is concave laterally in its more anterior half, which is dominated by the dentary, then curves into a convexity in its posterior half, which contains the adductor fossa. The latter opens dorsally, but leads anteriorly into the blindly ending meckelian canal. Seen in lateral view, the dorsal margin of the dentary and the coronoid is concave. The splenials form the entire jaw symphysis. The dentaries remain free and diverge antero-dorsally above the symphysis level to receive downwardly curving premaxillae.

The *dentary* is a large crescent. It tapers antero-dorsally into an edentulous beak-like rostrum. Behind the rostrum the sharp dorsal margin bears a single row of marginal teeth which fits into the longitudinal groove of the maxilla. The teeth continue posteriorly throughout the dorsal margin and the most posterior teeth lie lateral to the coronoid. Additional tooth rows are encountered on the medial surface slightly ventral to the main dental margin. These teeth are fewer in count and more irregularly spaced than those on the summit of the jaw. Below these additional tooth rows, a shallow longitudinal groove runs subparallel to the dental margin and in life probably lodged a prehensile tongue. Ventrally the dentary divides into two flanges, one lateral and one mesial, which form the roof of the meckelian canal. The lateral flange projects farther ventrally than the mesial, and is pierced anteriorly by scattered foramina. Internally the lateral flange sits on a cleft of the splenial and conceals the anterior part of the angular. The medial flange is partly overlapped by the splenial. The postero-medial surface receives the coronoid. Posteriorly the bone ends in a narrow process which connects with the surangular.

The *splenial* is a flat bone applied to the inner surface of the dentary. It is narrow anteriorly where there is a strong rugose facet to form the symphysis. Anterior to the symphysial facet it curves upward and is freed from contact with its fellow of the opposite side. Posteriorly the bone

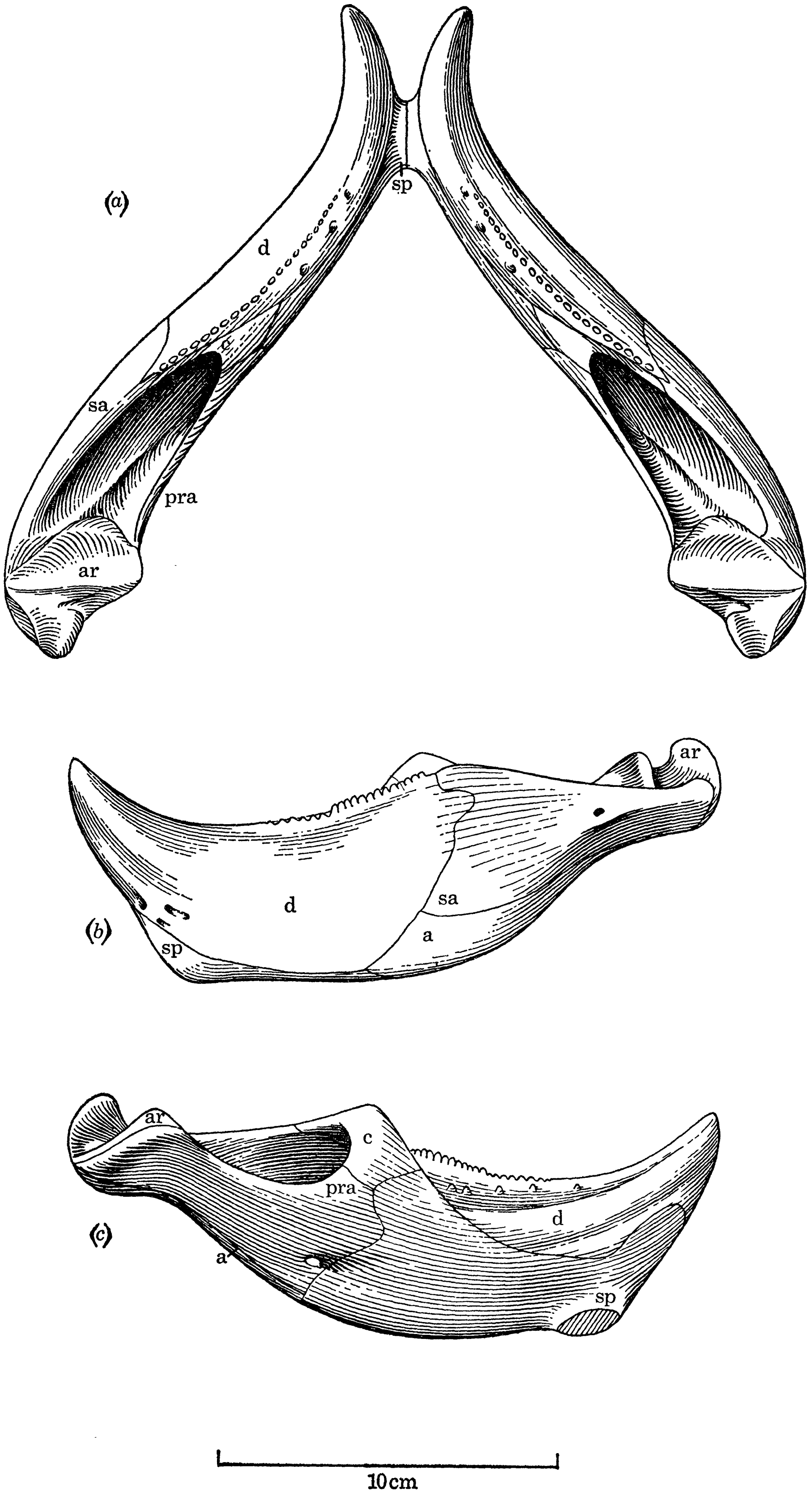

FIGURE 8. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Composite restoration of the mandible: (*a*) occlusal; (*b*) lateral; (*c*) medial.

becomes thin and diverges away from the medial wall of the dentary to accommodate the angular, the prearticular, and the antero-ventral part of the coronoid between itself and the dentary.

The *coronoid* is single and forms the anterior rim of the adductor fossa. It coats the medial wall of the dentary and more postero-ventrally, it passes beneath the splenial. Posteriorly the bone is curved and fits in a slot of the prearticular.

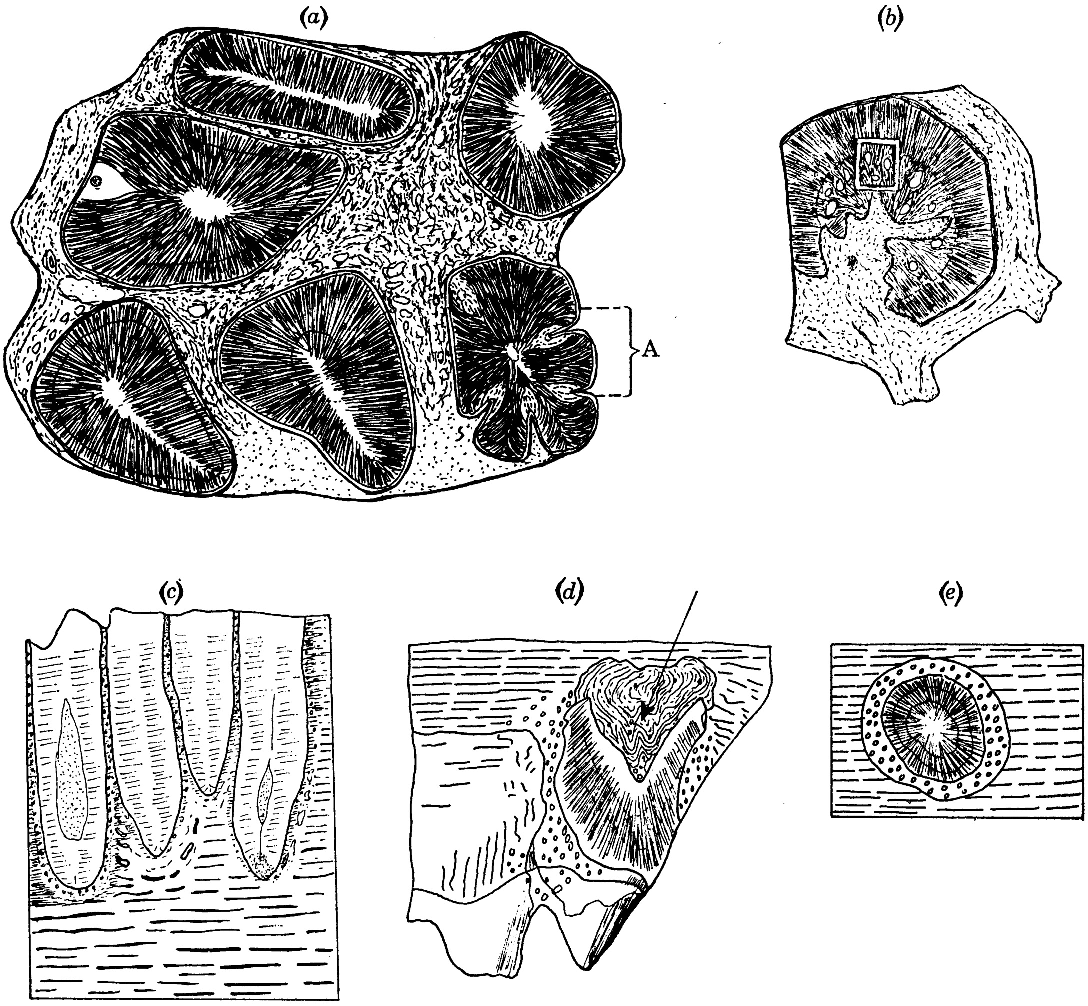

Figure 9. *Paradapedon huxleyi* (Lydekker). Dentition. (*a*) Transverse section of the maxillary teeth showing the minute variation of tooth structure (magn. × 12). The right bottom one shows the flutings; the portion labelled A is shown in figure 10*a*, plate 5, in enlarged view. (*b*) Tranverse section of a maxillary tooth showing the canalicular system (magn. × 12). The white rectangular area is shown in figure 10*b*, plate 5, in enlarged view. (*c*) Vertical section of the dentary showing ankylothecodont type of tooth implantation (magn. × 6). (*d*) Vertical section of maxillary teeth; the arrow indicates the curious layered bone of attachment encroaching on the pulp cavity of a tooth (magn. × 6). (*e*) Natural transverse section of a maxillary tooth showing the foamy bone of attachment (magn. × 6). All semi-diagrammatic.

The *angular* is an elongate, canoe-shaped bone, highly excavated dorsally and forms part of the floor of the meckelian canal. Anteriorly, the bone is wedged between the splenial and dentary and remains practically hidden. Posteriorly it wraps the ventral surfaces of both the prearticular and surangular and visibly becomes the base of the mandible.

The *surangular* becomes thin anteriorly and slips between the dentary and the coronoid. Posteriorly it takes a small role in the formation of the glenoid. At the level of the floor of the adductor fossa, the surangular divides into two concave surfaces by a strong ventro-lateral longitudinal ridge. The medial one wraps the whole lateral surface of the articular posteriorly as well as the ventral surface of much of the prearticular. The lateral one is pierced by two foramina.

The *prearticular* extends up to the mid-length of the mandible and is overlapped by the splenial where it is pierced by the meckelian foramen. Above the splenial it receives the coronoid. Ventrally it fits into the longitudinal groove of the angular and then gently curves inward on its posterior course to lap around a strong ridge of the surangular. Father backwards the bone gradually tapers and wraps strongly the medial and lower surface of the articular.

The *articular* is a small posterior element which accommodates the major part of the glenoid fossa. The bone is widest at the glenoid and is sheathed by the prearticular medially, the surangular at the outer surface and the conjoined prearticular and surangular at the ventral surface. The glenoid is a shallow concavity, bounded anteriorly and posteriorly by a projection and a strong ridge respectively, and these structures restrict the antero-posterior movements of the condyle in the glenoid. Behind the glenoid, the medial wall of the articular is deeply notched leaving a strip of compact dorsal surface which rolls down ventrally to form the strong retro-articular process. Anterior to the glenoid the bone terminates in the adductor fossa as a roughened surface, which probably indicates the presence of the meckelian cartilage in life.

4. *Dentition*

Introduction

The dental specializations of rhynchosaurs include three peculiarities. First, the anterior part of the jaws are edentulous, with the development of a beak-like premaxilla and anterior end of dentary (Huxley 1869). The edentulous regions are entirely bony, lacking enamel or dentine, as is evident from their microscopic structure. Secondly, tooth implantation on maxilla and dentary is not of acrodont type, as was previously thought by, for example, Huene (1939*b*) and Romer (1956); the teeth have long roots which are firmly fixed to sockets by bone of attachment. Thirdly, the ventral surface of the maxilla bears multiple rows of tiny teeth running subparallel to the jaw margin. This last feature raises questions regarding the way in which the teeth are added as size increases, and, when considered in conjunction with the ankylosed type of tooth implantation, whether tooth replacement occurs, and if so how.

Tooth structure and form

The teeth are small and exclusively confined to the maxilla and the dentary. In the maxilla several longitudinal tooth rows are closely packed in a tooth plate; each plate is elongate, acutely triangular, broad posteriorly and is dissected by a longitudinal groove. In the dentary, a single row of teeth is set along the dorsal edge, and this row bites into the longitudinal groove of the maxilla like a 'knife blade fitting into its handle' (Huxley 1869). A few additional teeth are found on the lingual surface of the dentary.

The maxillary teeth are pyramidal or conical in shape, pointed and straight at their tips, but broad at the base, often with the development of a few irregular longitudinal flutings. The flutings reflect the infolding of the enamel and dentine layer of the tooth (figure 9*a*; figure 10*a*, plate 5). In transverse section the teeth are not uniform in shape but vary in minute detail from each other. Mandibular teeth are cylindrical, and compressed medio-laterally to a chisel-shape. Lingual teeth on the dentary are widely spaced and resemble those of the maxilla in shape. In vertical section, each tooth shows an enamel-capped crown, a long dentinal root, and an axial pulp cavity. The crown is partly submerged by the growth of secondary smooth-textured bone which occurs superficially on the jaw surface around the bases of the teeth after they have fixed to the jaw, as also seen in *Sphenodon* (Harrison 1901). Successive layers of dentine at the bases of some teeth indicate appositional growth encroaching on the pulp cavity, the latter thus gradually diminishing as the tooth becomes older (figure 9*e*). The pulp cavity is often surrounded by a series of tiny parallel canaliculi. These canaliculi in horizontal section show concentric arrangement and the dentinal tubules swirl around each of them (figure 9*b*; figure 10*b*, plate 5). They probably served in life for the passage of the blood vessels.

Tooth arrangement on the maxilla (*figure* 12)

The teeth are not haphazardly set on the maxilla, but tend to arrange in regular patterns. It is possible to resolve the array of small teeth into two alternative patterns, oriented in rows, either a longitudinal (figure 12*a*) or a diagonal (figure 12*b*) pattern of rows. On either side of the longitudinal groove, several longitudinal rows of teeth tend to lie parallel to the median groove and to one another, but *en echelon* to the labial and lingual margins of the tooth plate. Since the tooth plate is acutely triangular, and broad posteriorly, and tooth rows lie parallel to the longitudinal groove, there is always a higher count in the number of longitudinal tooth rows in the posterior part of the tooth plate. In *Paradapedon*, the number of tooth rows which occur lateral to the longitudinal groove is usually slightly greater than those occurring medial to it (Lydekker 1885). For ease of description, the successive tooth rows lateral to the longitudinal groove are labelled as L1, L2, L3, . . . , respectively, L1 being the row lying nearest to the groove. Similarly, medial rows are numbered as M1, M2, M3,. . . .

The pattern of diagonal rows is more prominent in larger individuals, particularly in the posterior part of the maxilla, on either side of the longitudinal groove. The posterior free margin at the extremity of the maxilla is V-shaped in occlusal view, the longitudinal groove terminating near the apex of the V. Diagonal rows of teeth tend to lie parallel to this V-shaped posterior margin on either side of the longitudinal groove. Thus each diagonal row begins at the longitudinal groove, and the lateral rows slant antero-labially, the medial rows slant antero-lingually.

Implantation (*figure* 9*c–e; figure* 10*c*, *d*, *plate* 5)

The roots of all the teeth are firmly ankylosed by bone of attachment to well-developed sockets. This type of implantation is termed here ‘ankylothecodont’. The bone of attachment is spongy in appearance resembling a foam of very small bubbles and it entirely surrounds the socketed portion of each tooth anchoring it firmly to the bony wall of the alveolus. A curious bony layered structure is seen at the base of some teeth, invading the pulp cavity. Possibly this structure represents bone of attachment which thus not only bound the outer perimeter of the tooth to the alveolar wall but also anchored the tooth’s hollow base to the bottom of the alveolus.

Longitudinal groove and tooth wear

The lateral and medial dentigerous surfaces both slope towards the longitudinal groove, present in all maxillae, into which the dentary always fits. The position in the tooth plate in relation to the tooth rows, the continuity of the groove along the whole length of the maxilla, the lack of wear on the posterior part, and the complete absence of teeth centrally along it combine to show that the groove is an inherent character, not simply the result of wear. A comparable

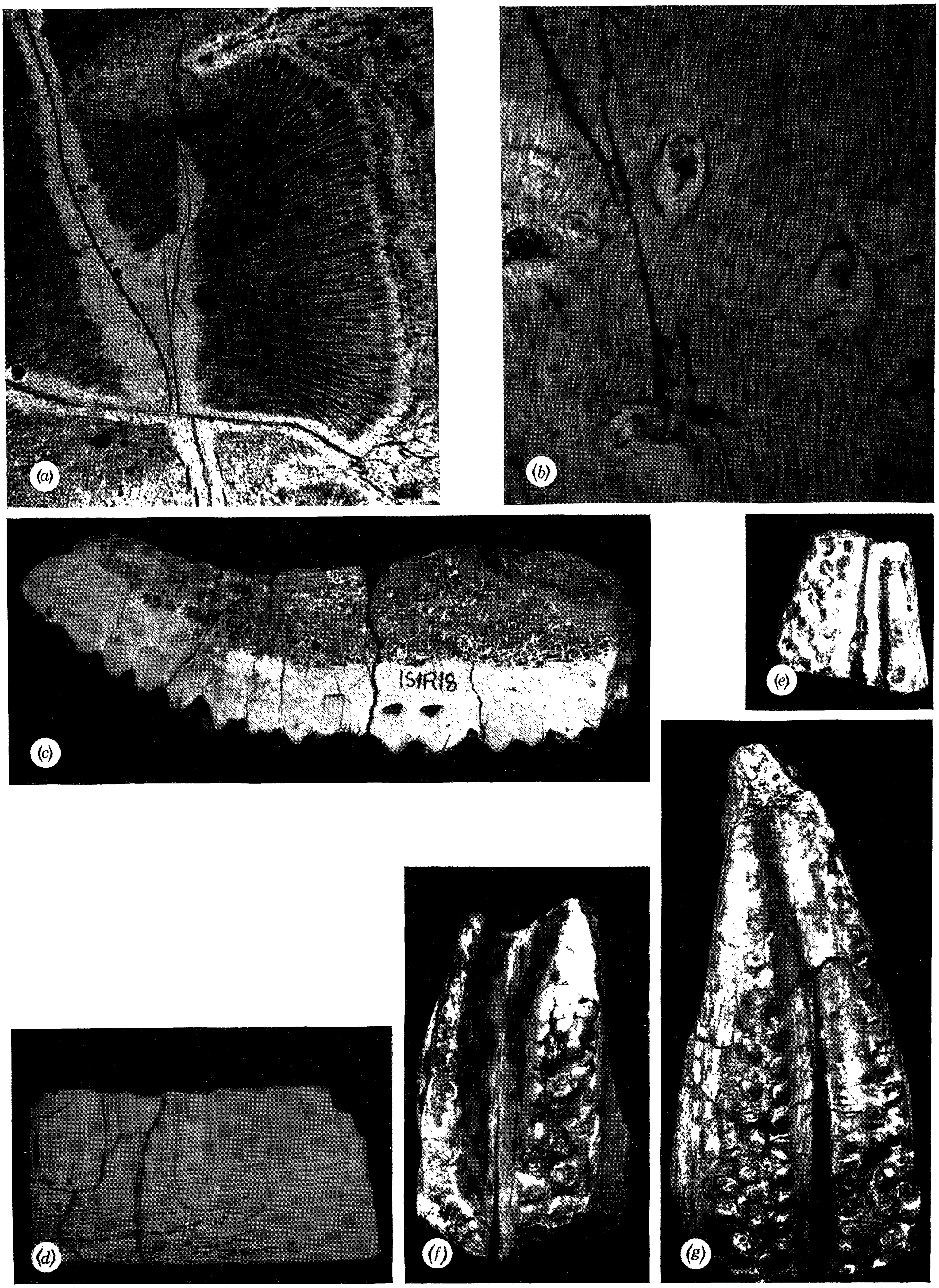

FIGURE 10. *Paradapedon huxleyi* (Lydekker). Dentition. (*a*) Photomicrograph of maxillary dentition showing enlarged view of the portion of the fluting mentioned in figure 9 (magn. × 20). (*b*) Photomicrograph of maxillary dentition showing the enlarged view of the portion of the canalicular system mentioned in figure 9*b* (magn. × 20). (*c*) Vertical section of the maxillary tooth plate showing ankylothecodont type of tooth implantation (natural size). (*d*) Vertical section of the dentary showing ankylothecodont type of tooth implantation (natural size). (*e*, *f*, *g*) Occlusal views of three isolated maxillary tooth plates showing the wear of the longitudinal groove (natural size).

FIGURE 11. *Paradapedon huxleyi* (Lydekker). Three views of the skull (magn. × 0.5). (*a*) Right lateral; (*b*) left lateral; (*c*) occipital. Specimen I.S.I.R. 1.

groove for the reception of the dentary is to be seen in *Sphenodon*, but here the groove lies between the single row of teeth on the maxilla and a similar row on the palatine.

The jaw is ginglymic, the wear concentrated in the anterior region. Wear facets are found, directed dorso-ventrally, on the lateral surface of the premaxilla as on the medial surface of the dentary. They are a product of the repeated contact of the premaxillae as they hooked down between the diverging ends of the dentaries. In lateral aspect the dentigerous upper and lower jaw margins are curved, the dentary comparatively shallowly so that in occlusion the dentary comes into contact only with the anterior part of the longitudinal groove of the maxilla. In several specimens (I.S.I.R. 21, I.S.I.R. 23) the longitudinal groove is widened anteriorly by the dorso-ventral chisel action of the dentary, where not only the crowns of the maxillary teeth but also the anterior part of the bony apex of the maxillary tooth plate are smoothly worn to expose cross-sections of a few teeth, the roots remaining embedded in the alveoli (figure 9*d*, figure 10*e*, *f*, *g* plate 5). With increasing growth of the animal, the longitudinal groove was deepened and widened anteriorly, the dentary gradually coming into contact with the posterior part of the groove.

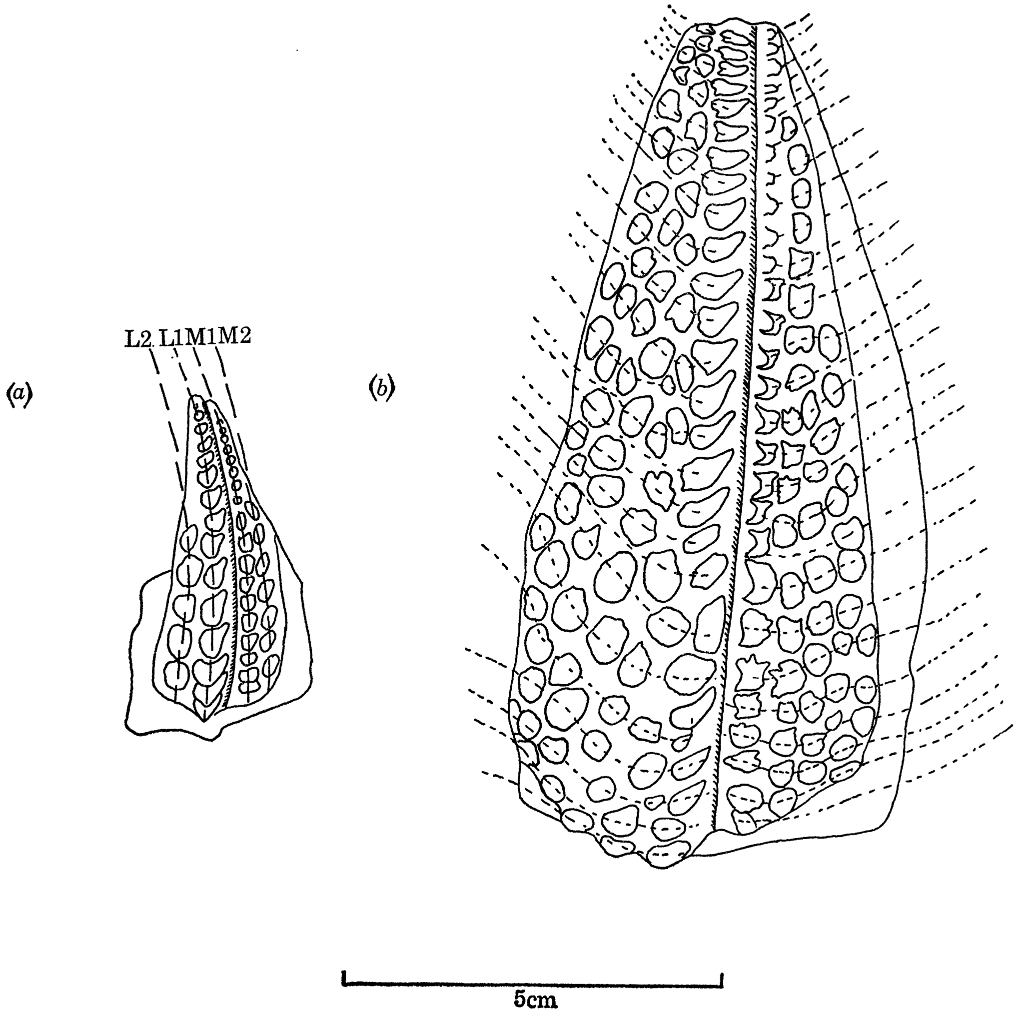

FIGURE 12. *Paradapedon huxleyi* (Lydekker) (magn. × 1). Maxillary dentition. The two methods of describing orientation of the teeth into rows: (*a*) longitudinal rows (specimen I.S.I.R. 11); (*b*) diagonal rows (specimen I.S.I.R. 17).

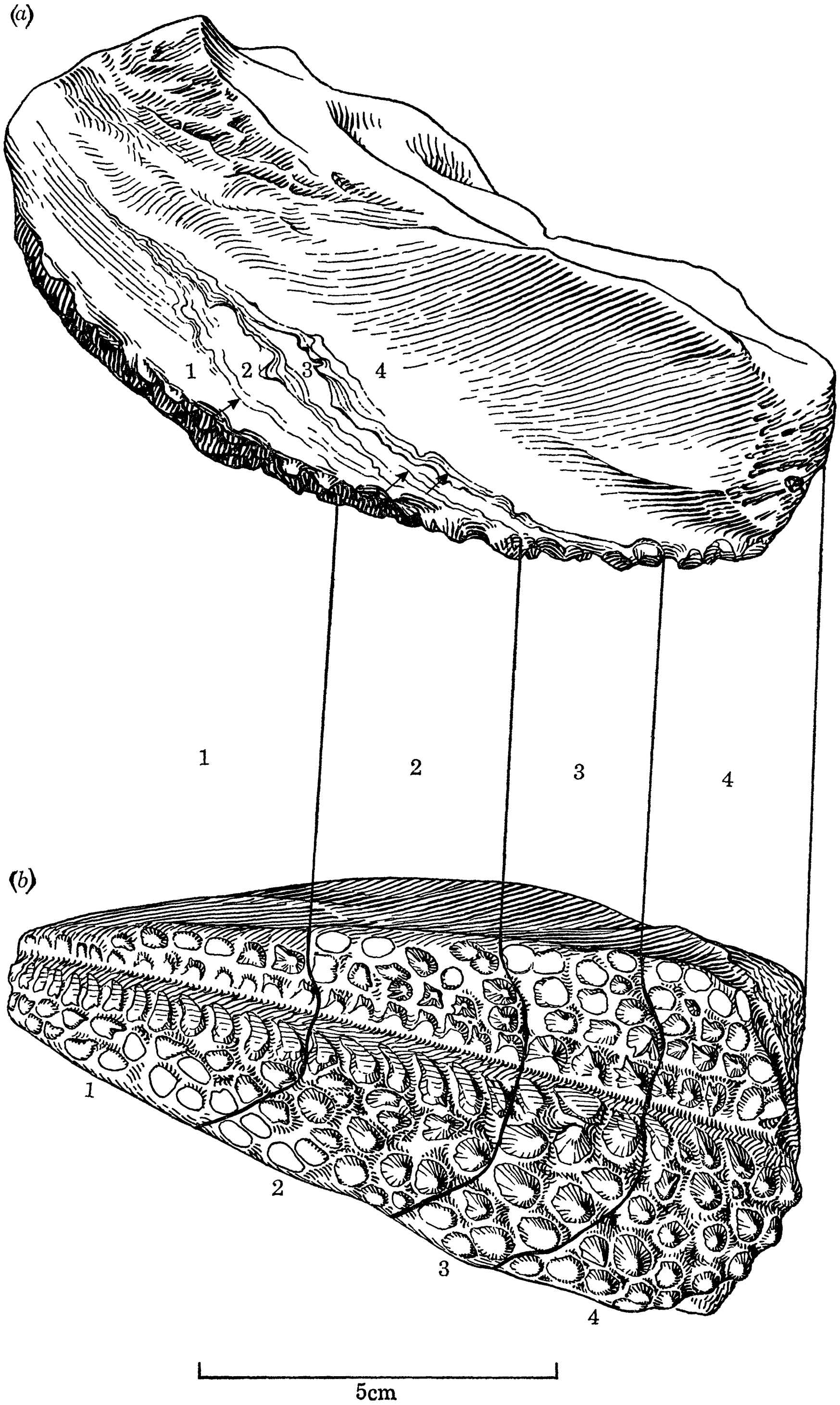

FIGURE 13. *Paradapedon huxleyi* (Lydekker). Maxillary dentition, specimen I.S.I.R. 17 (magn. × 1). To show the appositional growth of the tooth plate. (*a*) Medial view of maxilla, showing the indications of the mode of addition of bone in layers seen as oblique lines on the medial surface. For simplicity four of the growth lines have been selected for indication by arrows and represent four arbitarily chosen stages of bone accretion. (*b*) Occlusal view of the maxilla, the same four growth lines are indicated showing the serial growth of bone and teeth in a posterior direction.

The dorsal edge of the dentary gradually was blunted as the anterior teeth became worn away; and the lateral wall of the dentary, below the dental border, shows prominent dorso-ventral wear, formed by its sliding against maxillary teeth.

Tooth wear is also seen medially and laterally, not therefore the product of dentary friction; it confirms a diet of hard food.

Tooth replacement

The teeth are ankylosed to the jaw, without evidence of replacement even of the deeply worn teeth in larger individuals; with growth the first-formed (anterior) teeth are supplemented by the eruption of posterior teeth.

Growth of the tooth plate

Variation in maxillary size indicates that the tooth plate grew in size by the accretion of bone without much change in the ratio of breadth to length but with a proportionate increase in height; but there was insignificant deposition of bone on the occlusal face. Tooth wear being accentuated in the anterior region, and newer teeth erupting in the posterior part of the plate, the increase in length of the plate with growth of the animal was maintained by accretion of bone posteriorly. In specimen I.S.I.R. 17 (figure 13*a*) this appositional growth is well displayed: successional bony layers lie well above the dental border anteriorly but they gradually converge towards the dental border posteriorly, the layers overlapping like roof shingles, the most anterior layer meeting the dental border at the mid-length of the tooth plate, the most posterior meeting the border at its hinder limit. The relationship is well brought out in occlusal view (figure 13*b*).

Table 3

			longitudinal tooth rows									
			lateral					medial				total number of
specimen number	length cm	width cm	L5	L4	L3	L2	L1	M1	M2	M3	M4	M5	teeth
I.S.I.R. 11	1.6	5	—	—	—	5	17	21	7	—	—	—	48
I.S.I.R. 13/1	2	6.7	—	3	5	10	20	20	9	1	—	—	68
I.S.I.R. 1	3.1	8.7	2	5	7	20	26	31	26	15	4	—	136
I.S.I.R. 17	4.6	12.2	5	9	13	21	30	28	19	11	8	3	150

Tooth addition

In the monophyodont development of *Paradapedon* the addition of teeth complements increasing size. The tooth plate of specimen I.S.I.R. 11 is about 5 cm long and carries four longitudinal rows of teeth: L1 and M1 run along the whole length of the plate, but L2 and M2 are present only in the posterior half (figure 14*a*). Specimen I.S.I.R. 13 is about 6.7 cm long, with seven rows of teeth, four laterals and three medials, M3 being represented by a single tooth (figure 14*c*). Specimen I.S.I.R. 1 is 8.7 cm long, with nine rows of teeth, five laterals and four medials (figure 4*a*); of the medials, M1, M2 and M3 consist of teeth in regular linear rows, but the incipient M4 contains a few irregularly arranged teeth; the teeth in the lateral rows are regularly arranged anteriorly, but are irregularly crowded posteriorly; and anteriorly the longitudinal groove is widened by wear which also affects the adjacent teeth of L1, L2 and M1. Specimen I.S.I.R. 17 is 12.2 cm long: it has ten tooth rows, five laterals and five medials (figure 13*b*); the anterior teeth are heavily worn; the continuity of the tooth rows is difficult to trace posteriorly.

There being no tooth replacement with growth, the anterior teeth, formed by the young animal, are in the adult smaller than the posterior, and the size of a tooth in its particular place in the jaw is a reflexion of the size of the animal at the time of eruption; in specimen I.S.I.R. 10 empty alveoli in the most posterior parts of L1, L2 and M1 indicate that ankylosis was not complete as the latest teeth were being formed (figure 14*b*); and in I.S.I.R. 11 the last tooth of L1 is about to erupt and is not cemented by secondary bone.

In polyphyodont reptiles the dental lamina usually lies in a shallow longitudinal groove lingual to the single longitudinal row of marginal teeth; but the rhynchosaur maxilla does not show such a groove and in all probability the site of the dental lamina with its tooth germs lies in the V-shaped channel between the posterior extremity of the tooth plate and the ectopterygoid (figure 14*a*). The diagonal arrangement of the tooth rows, conforming with the V-shaped posterior channel, is then primary in nature and reflects the successive 'Zahnreihen' (Woerdeman 1921; Edmund 1960) incorporated into the jaw. Presumably each diagonal row forms a separate Zahnreihe, each Zahnreihe constituting a series of teeth of a single generation, with each tooth derived from a single tooth germ; but it should be noticed that the mesial diagonal rows do not always form a perfect V with the lateral rows, but a row may lie between flanking rows (figure 12*b*).

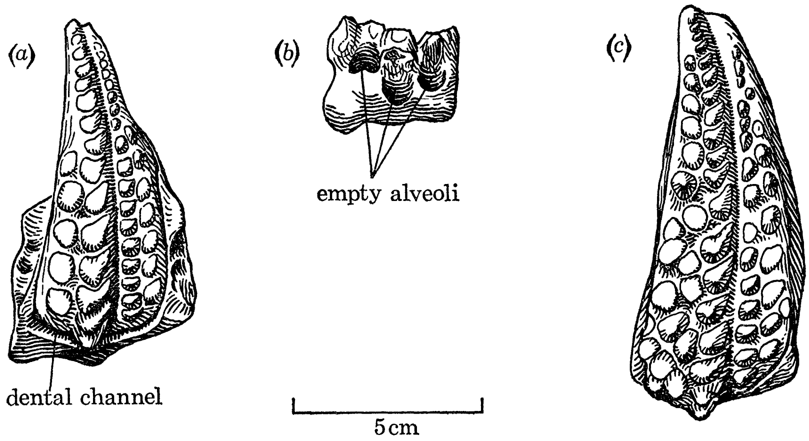

Figure 14. *Paradapedon huxleyi* (Lydekker). Maxillary dentition. Specimens to show the addition of teeth, and increase in number of tooth rows in both modes of orientation, with increase in size. (*a*) Occlusal view of the right maxilla showing the position and nature of the channel for the dental lamina (specimen I.S.I.R. 11). (*b*) Posterior view of a right maxilla showing empty alveoli (specimen I.S.I.R. 10). (*c*) Occlusal view of the right maxilla (specimen I.S.I.R. 13/1). All natural size. For the occlusal views of the maxillae of specimens I.S.I.R. 1 and I.S.I.R. 17, see figures 4*a* and 13*b* respectively.

As in other reptiles (Woerdeman 1921), when one Zahnreihe in *Paradapedon* is complete, another is initiated immediately behind, and diagonal row after diagonal row is thus formed to match the growth of the jaw. All the teeth in a Zahnreihe did not form simultaneously; in specimen I.S.I.R. 11 the last lateral Zahnreihe has a single tooth on L1, the preceding Zahnreihe has five. In specimen I.S.I.R. 17 the last lateral Zahnreihe is complete. It is likely that the teeth in a Zahnreihe were erupted alternately from the median longitudinal groove to the labial and lingual margins of the tooth plate.

The number of teeth in the single dorsal row of the dentary also increases with increase in size of the dentary, the teeth being added posteriorly in sequence. A longitudinal channel

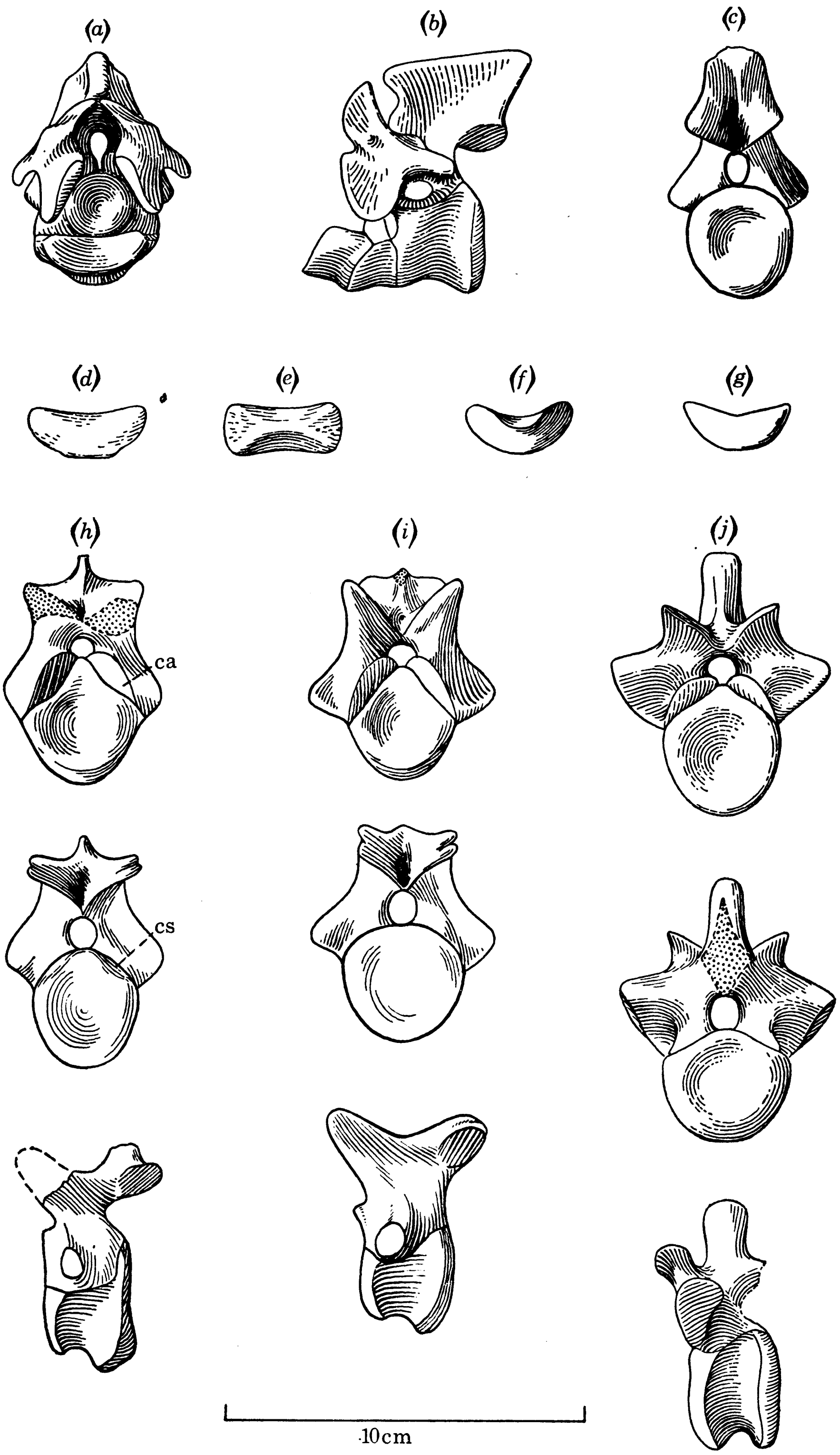

Figure 15. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Cervical vertebrae. (*a*, *b*) Atlas-axis complex, anterior and lateral views; (*c*) axis, posterior view; (*d*, *e*) atlas intercentrum, posterior and dorsal views; (*f*, *g*) axis intercentrum, anterior and posterior views; (*h*, *i*, *j*) third, fourth and eighth vertebrae. The three views of each vertebra are, from top to bottom, anterior, posterior and lateral.

formed between the postero-lingual extremity of the dentary and the coronoid opens dorsally and indicates the possible site of the dorsal lamina. The channel slopes antero-ventrally, and the extra lingual rows of teeth also tend to have an antero-ventral diagonal distribution.

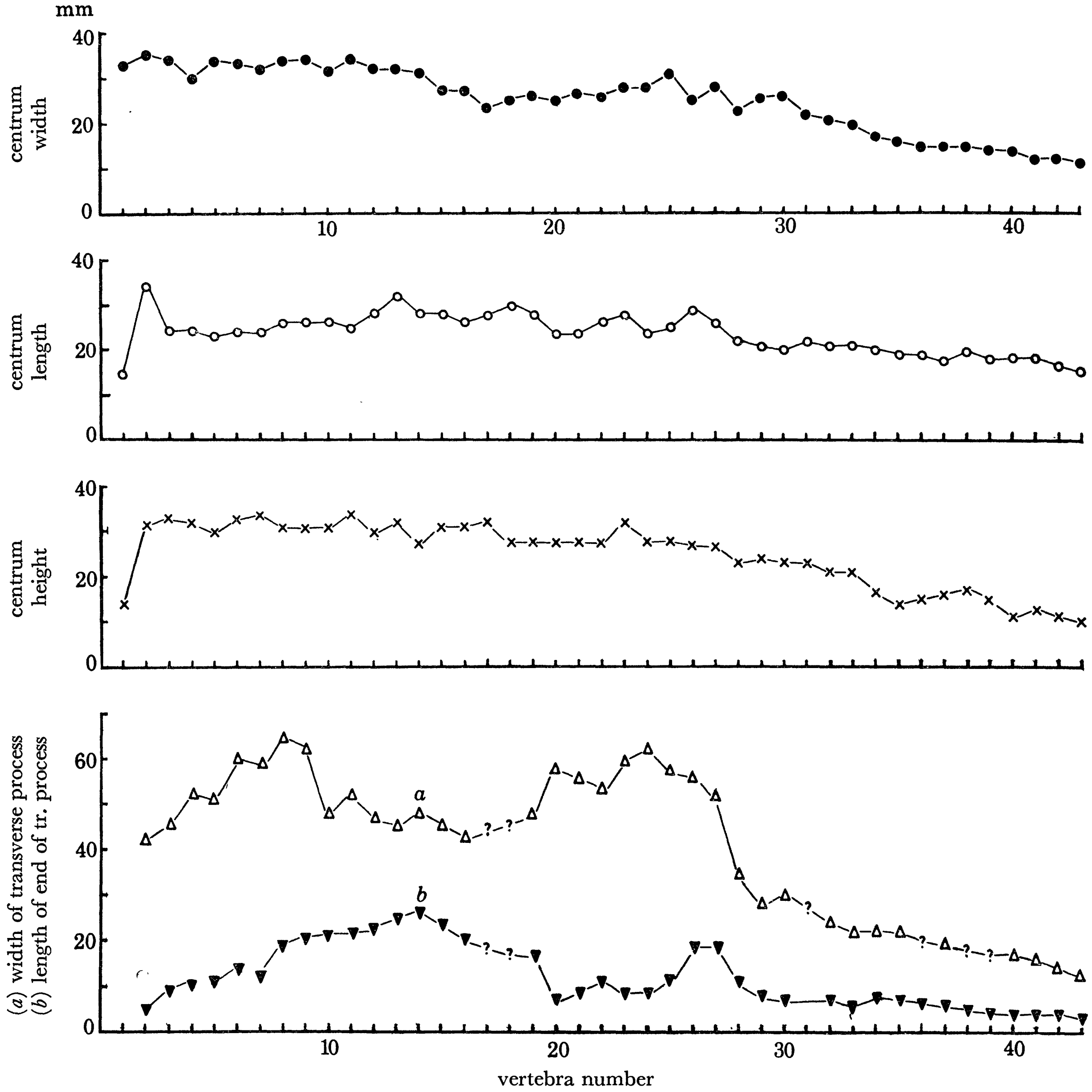

FIGURE 16. *Paradapedon huxleyi* (Lydekker). Chart of vertebral measurements showing regional variation throughout the series.

5. *The vertebral column*

A well-preserved association of 43 vertebrae, from atlas to 16th caudal in specimen I.S.I.R. 1, and of at least 25 caudal vertebrae in specimen I.S.I.R. 3, indicates a vertebral column of 25 presacrals, two sacrals, and more than 25 caudals.

Atlas-axis complex

A pro-atlas has not been found, but a pronounced facet on the roof of the atlantal arch points to its existence. Crescentic intercentra of the atlas (the larger) and the axis are preserved, but no other. The atlas intercentrum and the paired neural arches form a ring with a cupped depression for the single hemispherical occipital condyle (figure 15*a*).

Presacral series

In the remainder of the presacral vertebrae a gradual change of form in the centra is less useful than rib facets, seen as weakly concave articular surfaces and present throughout the series (figures 15, 17), in differentiating eight cervicals from 16 dorsals (figure 16). A mid-ventral keel runs the whole length of the anterior cervicals but progressively diminishes in the posterior. The length of the centrum ranges from 2.5 to 3.1 cm in specimen I.S.I.R. 1.

The cervical vertebrae, with dichocephalous ribs, have separate diapophyses and parapophyses, but the parapophyseal facet is not readily discernible, being represented only by the anterior edge of the centrum below the neurocentral arch suture. The parapophysis gradually rises upwards in the cervicals and ultimately disappears from the centrum, becoming confluent with the diapophysis in the second dorsal. A serial change in the position and the nature of the diapophysis is seen throughout the column. In the third presacral, the diapophyseal facet is small and rounded, projects a little laterally, and is placed well above the centrum. Farther backwards, the diapophysis gradually increases in size, comes closer to the parapophysis and becomes oval shaped in the posterior cervicals. The beginning of the dorsal series can be recognized by the presence of the greatly increased diapophysis, prolonged progressively as a narrow band in the dorso-ventral direction. The lower part of the facet approaches nearly to the anterior edge of the centrum. The dorsal edge of the diapophysis rises more and more obliquely upwards so that a deeper excavation is seen in 'end view' on the lateral wing of the neural arch. From the mid-dorsal region posteriorly, the facet for rib articulation gradually diminishes in size, and the parapophysis loses its identity. In the last six to seven presacrals the rib facet becomes appreciably smaller and oval shaped. Here the diapophysis is well projected horizontally, lies well above the centrum, somewhat centrally placed, and is hollowed underneath. In the last presacral, the rib facet has become short and rounded.

A somewhat specialized articulation between the successive vertebrae is seen particularly in the neck region. Anteriorly the neural arch pedicel contributes a pair of semi-ovoid facets facing forward and downward on either side of the angulated dorsal margin of the centrum. These are centrantra†, receiving correspondingly bevelled surfaces of centrosphenes† on the posterior face of the preceding centrum. These articular surfaces are appreciably reduced more posteriorly in the series (figure 15*h*).

The zygapophyseal facets are oval shaped and moderately tilted; the tilt is close to 45° throughout the series. The zygapophyses of all the presacrals project a little beyond the anterior and posterior edges of the centrum but to a variable degree.

The neural spine is compressed laterally and lies more or less toward the posterior half of

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† Case (1907) used these two terms in the opposite sense, i.e. centrosphene for the anterior articulation and centrantrum for the posterior articulation. In the case of hypantrum and zygantrum, the 'antrum' refers in derivation to the 'cavity', regardless of whether this is anterior or posterior. By analogy, the terms used by Case ought to be reversed, so that the centrantrum would be anterior and centrosphene would be posterior.

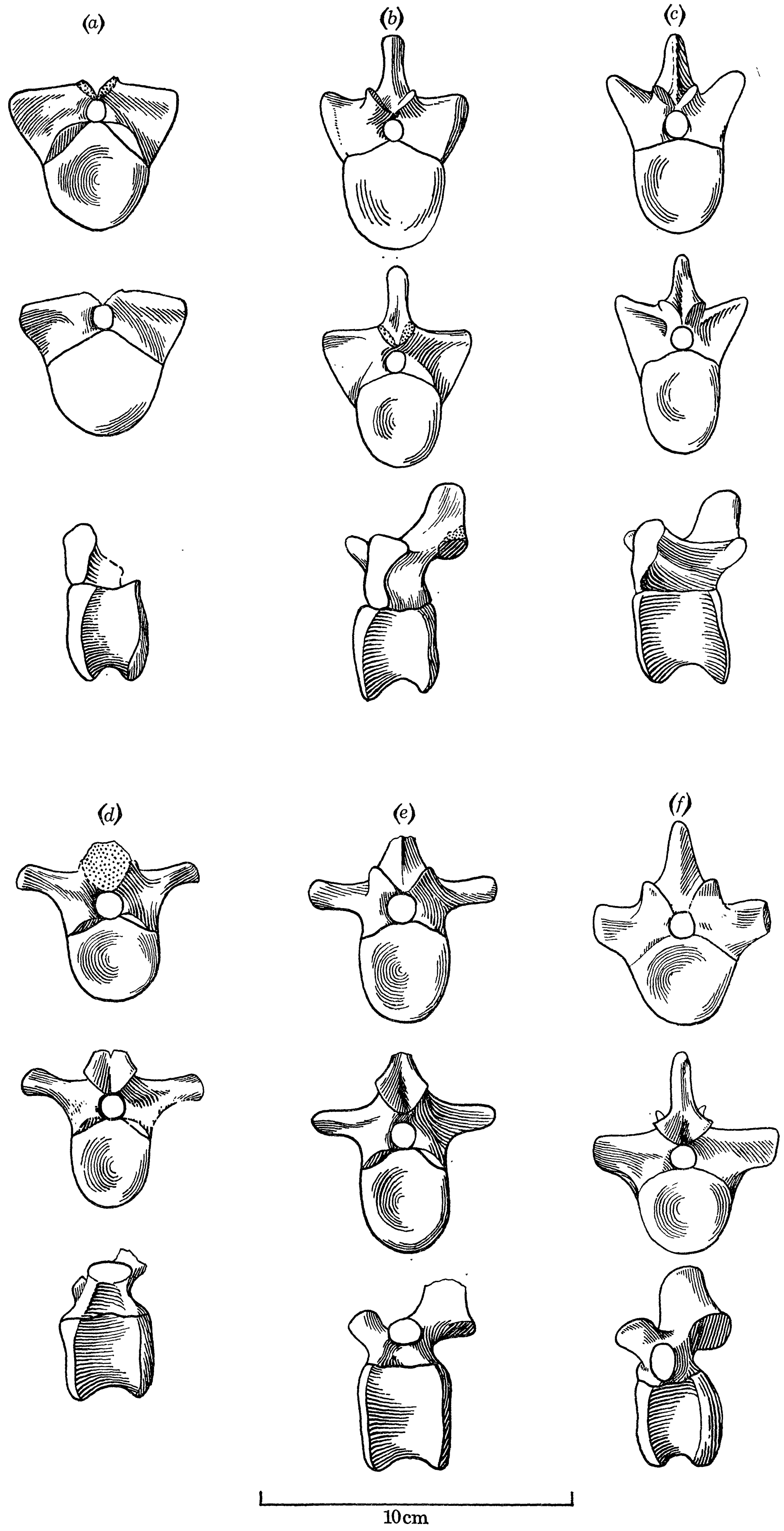

Figure 17. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Dorsal vertebrae. (*a*–*f*) Ninth, twelfth, sixteenth, twentieth, twenty-third and twenty-fifth vertebrae. The three views of each vertebra are, from top to bottom, anterior, posterior and lateral.

the centrum. The anterior margin of the spine is sharp, the posterior margin bifurcates and gradually diverges downward to connect with the postzygapophyses. A median ridge is seen between the bifurcated edges.

The attitude of the neural spine varies regionally. In the cervicals, the neural spines tend to be prolonged dorso-ventrally with a short base, and the narrow blade of the spine rises almost perpendicularly from the floor of the arch. In the dorsals, however, the spines gradually decline in length with a broad base, accompanied by a little tilt in the posterior direction. In the posterior dorsals, the spines are moderately inclined backwards, but the last presacral has a relatively upright spine.

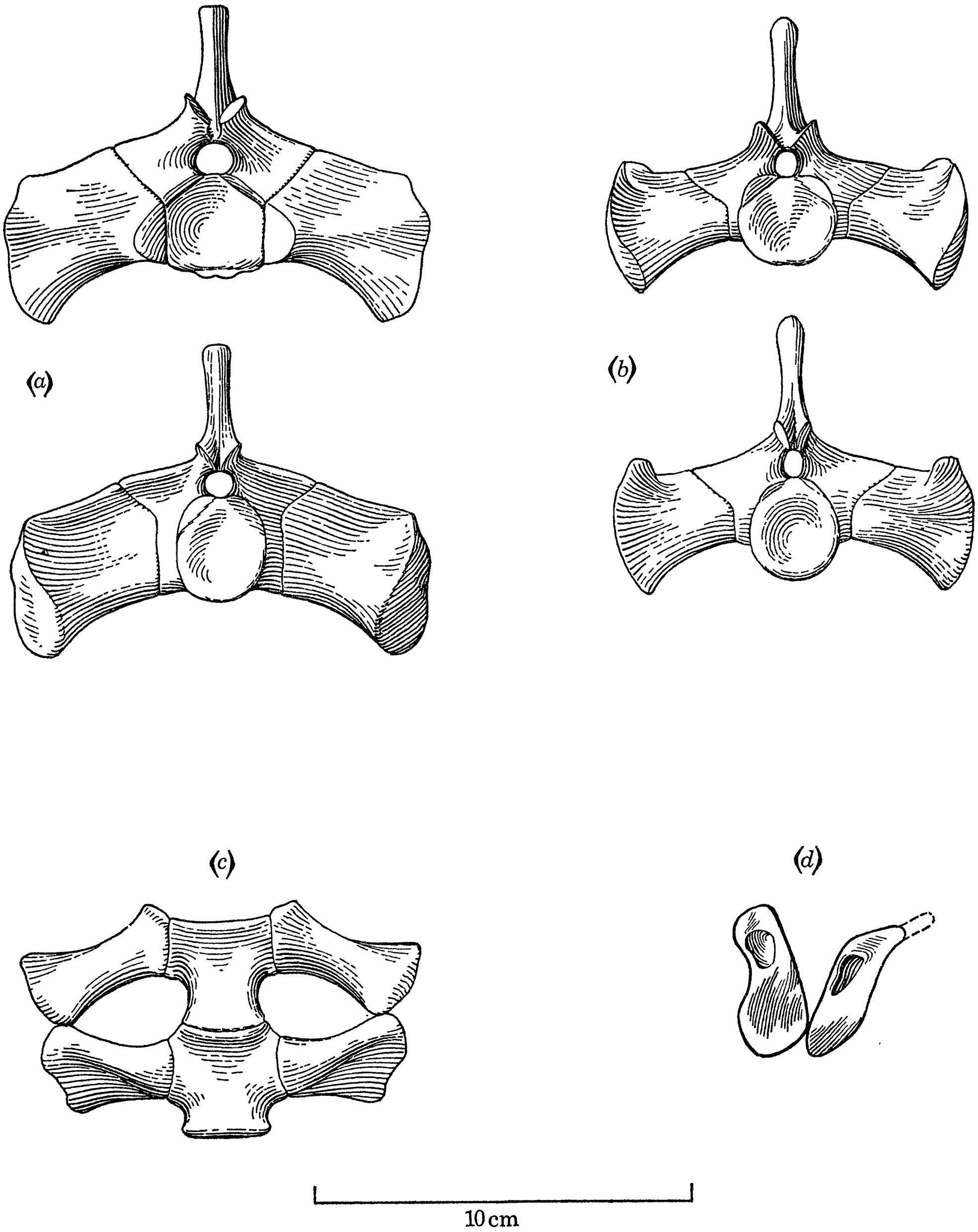

FIGURE 18. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Sacral vertebrae. (*a*, *b*) First and second sacrals; two views of each, from top to bottom, anterior and posterior; (*c*) ventral view of two sacral vertebrae in association; (*d*) lateral view of the distal ends of the sacral ribs in association.

Sacrum

The sacrum (figure 18) includes two separate vertebrae having the large and distinctive, wing-like, projecting pair of ribs. Both the centra are equally long antero-posteriorly, and slightly longer than the preceding ones, but differ from each other in their form. In the first sacral, the anterior face of the centrum is unusually pentagonal in outline with a flat base and a sharp mid-dorsal angulation. The centrantra are represented by a pair of thin bands of bone at the neural arch pedicel. In addition, the first sacral rib contributes a forwardly projected semicircular articular facet on either side of the centrum. These also contribute to the centrantra and lie facing each other, each developed on the capitulum. In the second sacral, the anterior face of the centrum is rounded on its ventral border and the neural arch bears the normal well developed centrantra. The bevelled centrosphene is only present in the posterior face of the first sacral, and is hardly seen in the second sacral.

The well-developed prezygapophyses of the first sacral are moderately tilted like those of the presacrals, and are oval shaped. The zygapophyses between the two sacrals are small and steeply inclined, the angle of inclination being 58° from the horizontal. The postzygapophyses of the second sacral are well developed and are set at a slightly higher level than the prezygapophyses. The neural spines have a shorter base, lie closer to each other than in the preceding vertebrae, and show a minor tilt in the posterior direction.

The first sacral rib is more robust, long, and takes the major share of articulation of the sacrum and the ilium. The distal articular end of the first sacral rib looks roughly like a figure 8, whereas in the second sacral, it is lens shaped. A shallow depression is present here in both the ribs (figure 18*d*).

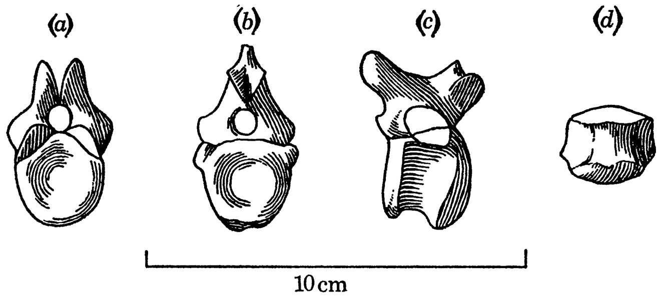

FIGURE 19. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Caudal vertebra. (*a* to *d*) Anterior, posterior, lateral and ventral views of the third caudal.

Caudals (*figure* 19)

The sacral vertebrae are followed by an unknown number of caudals estimated at about 25–30. Very little can be said safely about the nature of the neural spines and the zygapophyses as they are usually broken off in specimens of the caudal series. The serial changes affecting the centrum are the characteristic feature. Passing backwards the centrum becomes more and more laterally constricted and has become spool-shaped in the mid-caudal region. This is also coupled with the gradual diminishing in height of the centrum. The anterior face of the centrum is sharply angulated mid-dorsally, the posterior face is more or less rounded. The length of the centrum, however, does not change so rapidly. The posterior end of the abdominal cavity is recognized by the first appearance of the chevron facets on the ventral side of the centrum. In the associated specimen I.S.I.R. 1, the first chevron lies between the second and third caudals, but in the smallest individual (I.S.I.R. 3), the position of the first chevron is between the third and the fourth caudals. The variation in the position of the first chevron may perhaps be explained by sexual dimorphism. Usually the abdominal cavity in a female is larger than a male, so that the position in the caudal series at which the first chevron appears will be more posteriorly placed in the female form. The most anterior caudals, lying in the abdominal region, are ventrally rounded. Posterior to the abdomen, the ventral surface of the centrum exhibits a median furrow flanked on either side by a strong ridge terminating posteriorly in semicircular chevron facets. The facets are separate from each other and face postero-ventrally.

No haemapophysis is preserved in the associations. As the caudals are followed posteriorly the angle between the zygapophyseal facets decreases. In the anterior caudals, the rib facets are separate from each other. Moreover, the fact that the ribs are not co-ossified with the centra in the anterior caudals is rather unusual in tetrapods. The diameter of the neural canal steadily decreases posteriorly. The posterior caudals were probably more slender and delicate.

6. *Ribs*

Ribs are present throughout the presacral series and are continued farther backward as separate structures to the anterior caudals. Each rib has two distinct portions; an expanded articular head, and a long narrow shaft. A serial change in the articular head of the rib is seen (figure 20). In the cervicals, the head is forked into two branches; the dorsal tuberculum and the ventral capitulum. Passing backward the capitulum gradually approaches to the tuberculum, and ultimately the two articular portions become united and look like a figure 8. Beyond the 12th presacral, the head gradually diminishes in size and the capitulum becomes more and more prominent and extends forward. The two rib heads are still recognizable, separated posteriorly by a shallow longitudinal groove – the sulcus – which protected the segmental artery and vein. In the posterior dorsals, the tuberculum and capitulum lose their identities and the head is appreciably reduced in size. Each rib shaft is flattened antero-posteriorly in the proximal region, but becomes more rounded distally.

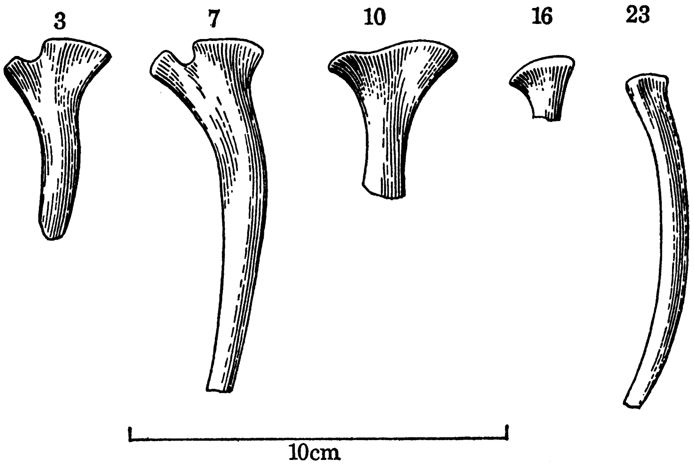

FIGURE 20. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Left presacral ribs which associate with the third, seventh, tenth, sixteenth and twenty-third vertebrae; anterior view.

7. *Chevron bones*

Although no chevron has been found in any of the associations, their existence is inferred from the ventral facets in the caudal centre (figure 19). The double facets on the centra indicate the dichocephalous nature of the chevra.

8. *Abdominal ribs*

Abdominal ribs are represented in specimen I.S.I.R. 1 by a bunch of toothpick-shaped rods. Each rib is circular to elliptical in cross-section, terminating in a thin edge. In a bunch as many as 20 rods have been counted. No natural arrangement of the abdominal ribs is seen in any Maleri specimen, but would be presumably in V-shaped rows as known in other rhynchosaurs (Woodward 1907, Pl. II, Fig. 4).

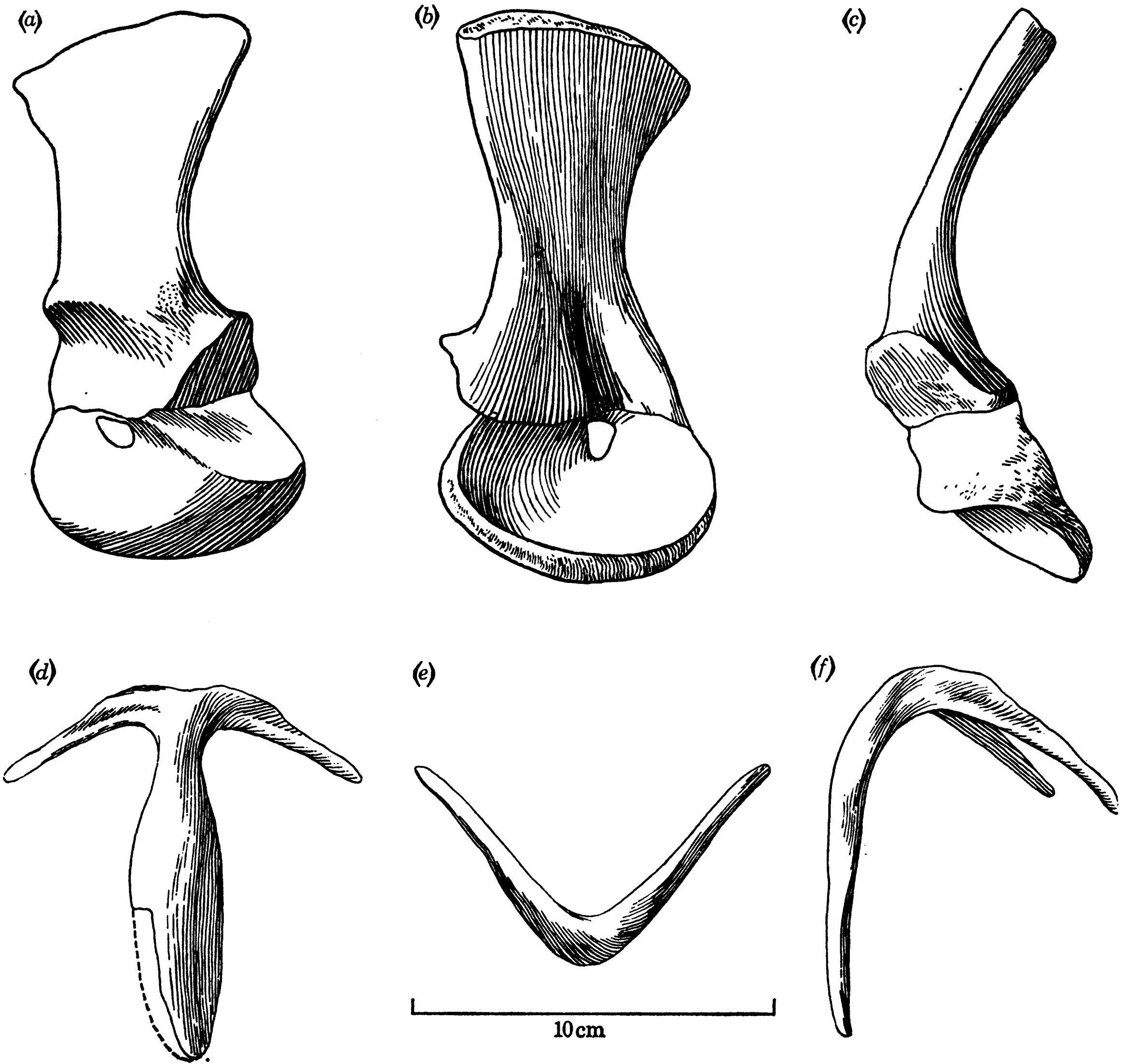

FIGURE 21. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Shoulder girdle. (*a*–*c*) Scapulocoracoid; lateral, medial and posterior views; (*d*–*f*) interclavicle; ventral, anterior and lateral views.

9. *The shoulder girdle*

The shoulder girdle includes three paired elements – scapulae, coracoids and clavicles, and a median ventral element, the interclavicle. Unfortunately no clavicle is found in our collections, and its character is inferred from other rhynchosaurs.

The *scapula* (figure 21) is broad and high. The height of the scapula is twice that of the coracoid. The dorsal end is a narrow strip of unfinished surface, slightly convex upward, above which the cartilaginous suprascapula probably extended. Passing downward, the bone gradually contracts its antero-posterior width down to the mid-height and then expands again to join the coracoid at the ventral edge by a strong horizontal suture. Below the mid-height, the anterior margin swells laterally into a pyramidal acromion process for the reception of the clavicle. The posterior margin is gradually thickened ventrally and is interrupted by the glenoid fossa. The glenoid lips face posteriorly and somewhat laterally. The scapula contributes a semi-elliptical face to the glenoid, whereas the corresponding coracoidal face is rhombic. The two glenoid surfaces diverge at an angle of 105°. Each of these surfaces is unfinished, and was probably lined with cartilage. Above the glenoid and near the posterior margin, a rugose scar indicates the site of the origin of the scapular head of the triceps muscle.

The *coracoid* is elliptical in outline as seen in ventro-lateral view. The outer surface is convex, the inner surface forms a deep hollow stretching in the antero-posterior direction. Below the scapular contact and anterior to the glenoid, the coracoid is fenestrated by the coracoidal foramen. The free edge of the coracoid is unfinished all the way round and was presumably capped by a cartilaginous rim. The posterior edge passes smoothly to the glenoid fossa, and is thicker than the anterior edge.

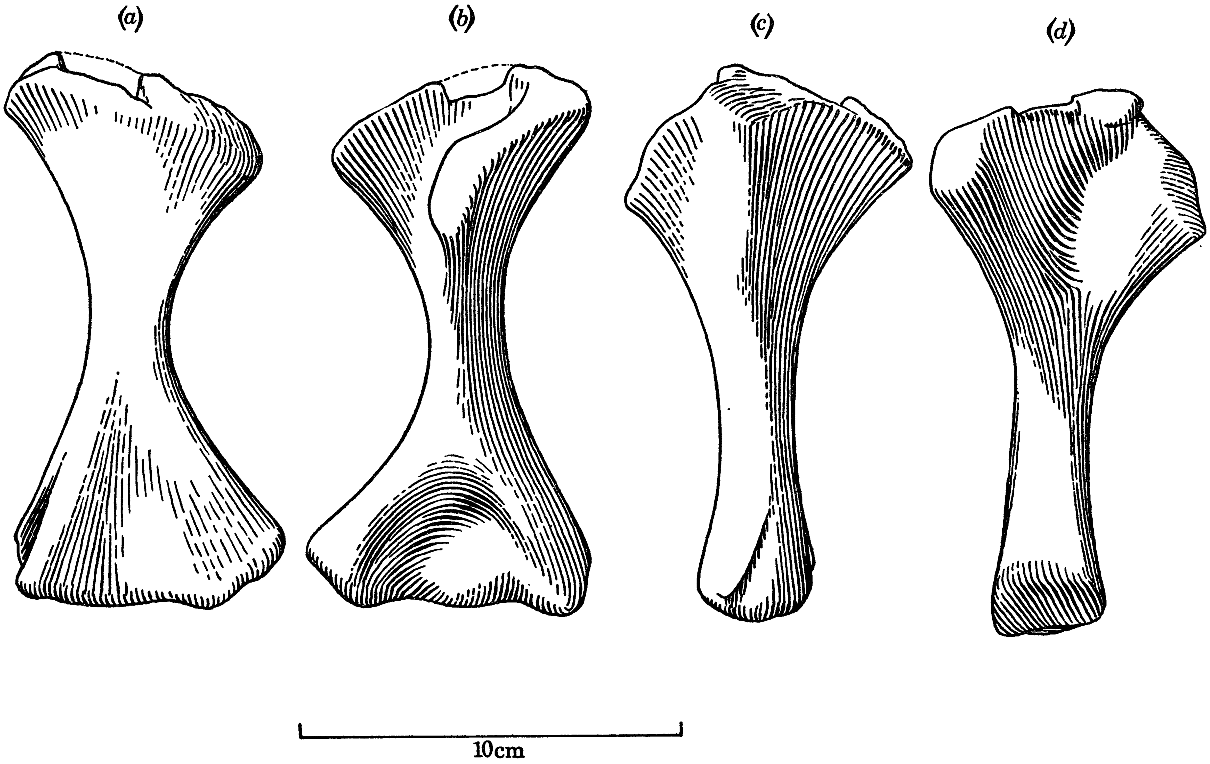

FIGURE 22. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Fore-limb. (*a–d*) Dorsal, ventral, anterior and posterior views of humerus.

The *interclavicle* (figure 21) is a triradiate structure. The median branch lies horizontally while the cross bars project upward and backward almost at a right angle from each other, to follow the contour of the neck. The crossbars are extremely narrow, triangular in cross-section and receive the clavicles anteriorly. The median branch looks like the blade of a dagger. It is extended posteriorly from the crossbars, is wide at the mid-length, and is flattened dorso-ventrally.

10. *The fore-limb*

The *humerus* (figure 22) is equally expanded at either end but slim in the shaft. The proximal and distal expansions are twisted in relation to one another on the connecting shaft. In dorsal aspect the proximal region divides into two distinct triangular surfaces, the broad antero-dorsal surface and the narrow antero-ventral surface, which are set almost at a right angle to each other. Proximally the antero-dorsal surface is terminated by the long curve of the glenoid articulation. The antero-ventral surface bears the lens-shaped deltopectoral crest.

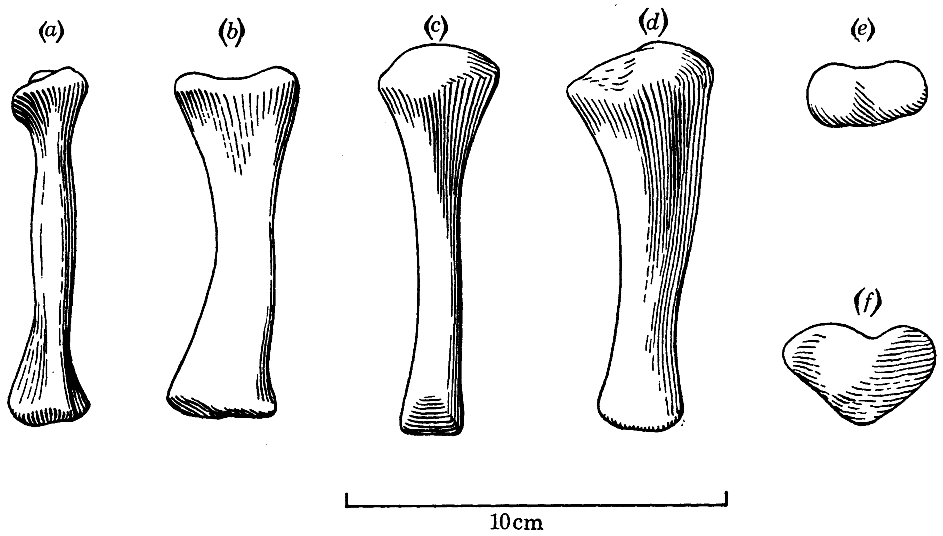

FIGURE 23. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Fore-limb. (*a*, *b*, *e*) Dorsal, medial and proximal views of the radius; (*c*, *d*, *f*) dorsal, medial and proximal views of the ulna.

Proximally, on the posterior surface, the large inter-trochanteric fossa is a major topographic feature. The fossa dies out in the shaft region. The shaft is short, smooth and subcircular in cross-section.

Passing distally from the shaft, the humerus is expanded again into a broad equilateral triangular plate. The dorsal surface is smooth; ventrally it is occupied by a semicircular depression. The epicondyles do not show any foramen. The anterior margin of the ectepicondyle bears a thin supinator crest, accompanied by a longitudinal groove which probably served in life for the passage of the radial nerve and blood vessels.

The distal articular end forms an elongate surface, narrow at the middle, and receives the radius and ulna separately.

The *radius* (figure 23) is slightly shorter than the ulna. The bone is symmetrically expanded dorso-ventrally at the proximal and distal ends. The oval proximal end is somewhat concave for articulation with the humerus. A slender extension of the articular surface curves down laterally on which the ulna rides. On the lateral surface a ridge runs obliquely from the proximo-ventral corner to the dorsal margin of the shaft. The medial surface of the shaft is smooth.

The shaft is long and straight and is elliptical in cross-section. Distally the lateral surface of the shaft bears a prominent ridge, continuing up to the distal end. The distal end is ovoid in outline and is faceted for the reception of the carpus.

The *ulna* (figure 23) has an enlarged proximal end, a narrow shaft, and a slightly expanded distal end. Seen in lateral view, the dorsal margin is more or less straight, the ventral margin is highly concave. The proximomedial corner laps against the extended articular surface of the radius. The proximal articular end is convex and cordate. From the apex of the cordate proximal end, a strong ridge projects from the medial surface of the shaft, but fades away further distally. Ventral to this ridge lies a shallow longitudinal groove. A similar longitudinal depression is seen on the lateral surface. The shaft is simple and slender, and is flattened mediolaterally. The distal end is oval and articulates with the carpus.

Metacarpals and phalanges

The carpus was not found preserved in any of the associations. The manus is poorly represented, except for the associated second toe in specimen I.S.I.R. 1. Other metacarpals and phalanges could not be arranged definitely in association. The length of the second metatarsal is 1.7 times that of the second metacarpal, and evidently the fore foot was shorter than the hind, as it is in other rhynchosaurs where both manus and pes are known.

11. *The pelvic girdle*

The *ilium* (figure 24) forms almost the whole of the imperforate acetabulum. It contracts to a neck above acetabulum and then expands again into the broad iliac blade. The thin dorsal edge of the blade is convex upward and contains rugose markings along its inner and outer peripheries. The iliac blade is equally projected anteriorly and posteriorly into narrow processes. Laterally, the major part of the blade is occupied by a shallow depression. Below this depression and immediately above the acetabulum lies a prominent rugose projection. Anteriorly the lower half of the ilium forms a broad surface which curves laterally to the acetabulum.

Internally, at the constricted neck region, the ilium shows two separate indentations for the reception of the sacral ribs (figure 24). Each is elliptical in outline, prolonged dorso-ventrally and is bordered by a raised rim, but the anterior indentation is larger than the posterior one. Below the sacral indentations the ilium expands antero-posteriorly and terminates ventrally in two articular surfaces lying at an angle of 138° to one another. The anterior surface for the pubis is shorter but more thickened than the posterior ischiadic surface.

The *ischium* is a broad, semicircular plate curving postero-ventrally from the acetabulum. The free posterior margin of the bone joins the two ends of the semicircle. The arc of the semicircle contains separate facets for ilium, pubis and the median symphysis at the dorsal, anterior and postero-ventral borders respectively. Dorsally the bone is appreciably thickened and shows a smooth acetabular surface which is separated from the rugose articular surface for the ilium by a sharp edge. Below the iliac articulation, the anterior edge of the ischium becomes tapered to meet the pubis. Further postero-ventrally the bone swells medially into an elongate facet for symphysial union. On the medial surface a strong ridge runs down from the iliac articular facet to the symphysial facet.

The *pubis* is characterized by the presence of the prominent processus lateralis at the antero-lateral margin, which projects almost ventro-laterally from the pubo-ischiadic plane and terminates in an unfinished surface. The processus lateralis imparts a concavity to the outer surface.

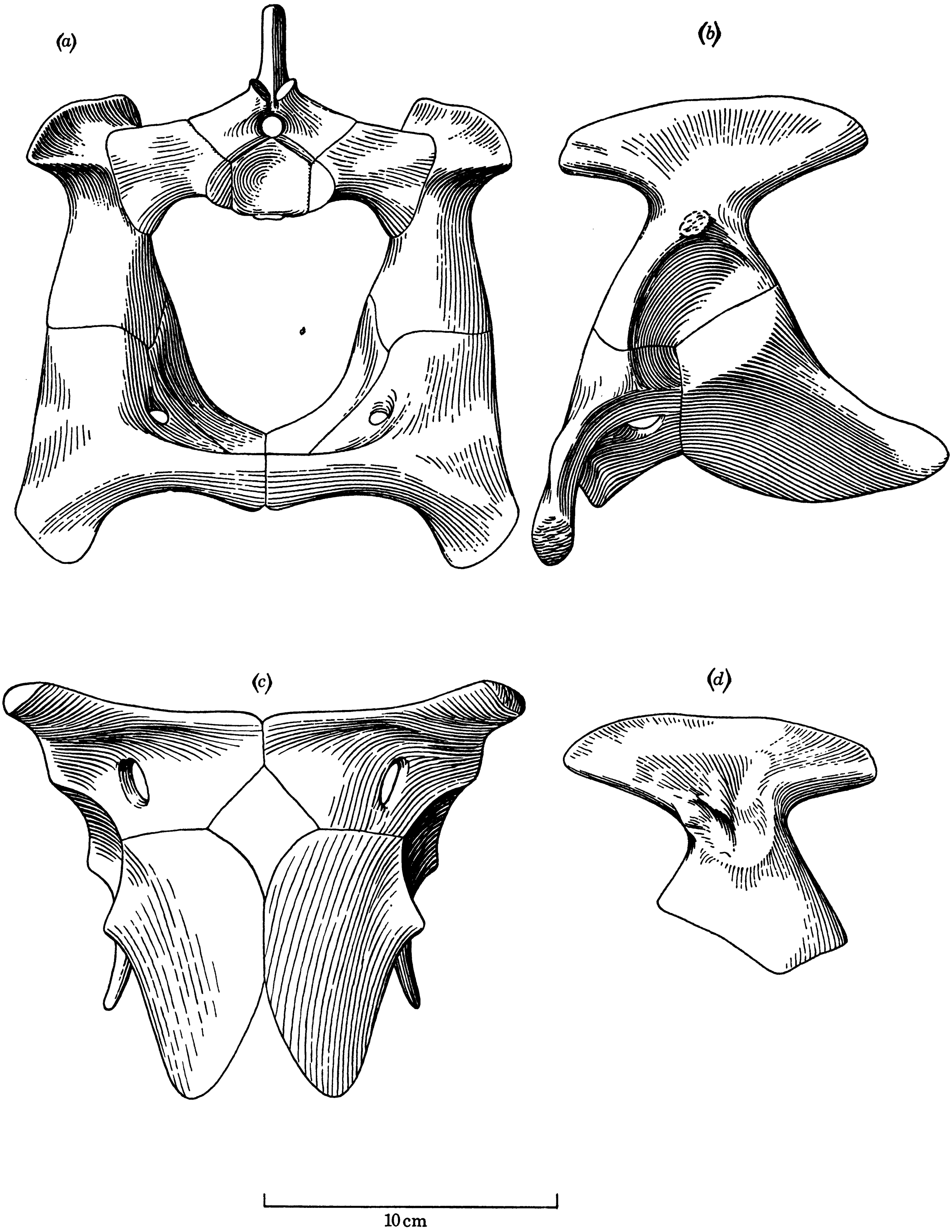

FIGURE 24. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Composite restoration of the pelvic girdle. (*a*) Pelvis and sacrum in anterior view; (*b*) pelvis in lateral view; (*c*) pelvis in ventral view; (*d*) medial view of the ilium showing the indentations for the sacral ribs.

The thickened dorsal edge of the pubis has a similar build to that of the ischium and divides into an acetabular surface and an articular surface for the ilium. The posterior margin makes a straight contact with the ischium. Anterior to the ischiadic contact, and beneath the ventral rim of the acetabulum, a large elliptical foramen served for the passage of the obturator nerve. When viewed anteriorly, the pubis forms a similar broad surface in continuation with that of the ilium, but divides ventrally into two branches. The ventro-lateral branch is the anterior aspect of the processus lateralis. The ventro-medial branch curves medially and terminates in a strong facet for the symphysis.

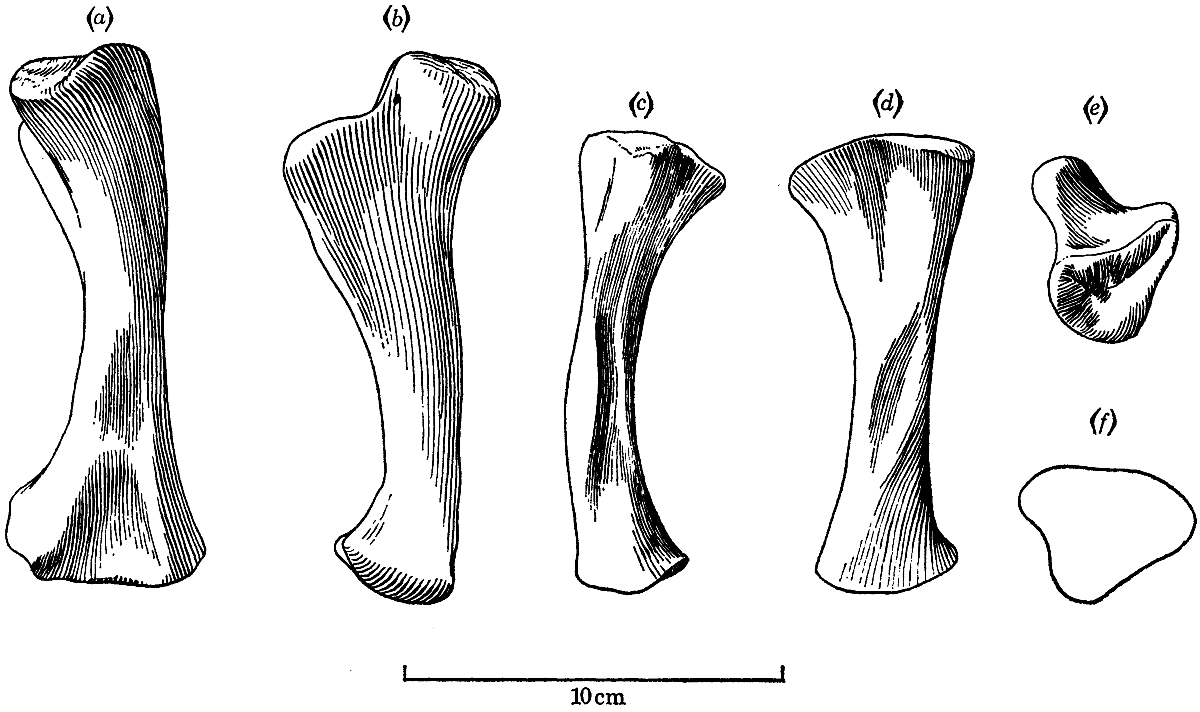

FIGURE 25. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Hind-limb. (*a, b, e*) Dorsal, anterior and proximal views of femur; (*c, d, f*) dorsal, medial and proximal views of tibia.

12. *The hind-limb*

There is some degree of difference between the left and right hind limbs in specimen I.S.I.R. 1. Both limbs are undistorted, but the left is noticeably more slender than the right. This feature of asymmetry in the skeleton is known in other fossil forms, e.g. *Stagonolepis* (Walker, personal communication), *Typothorax* (Sawin 1947).

Epiphyses are recognized only in the larger individual (specimen I.S.I.R. 2, femur length 22.8 cm), but seem to be lost in smaller associations (specimen I.S.I.R. 1, femur length 14.4 cm; specimen I.S.I.R. 3, femur length 8.5 cm).

The *femur* (figure 25) is marked by expanded proximal and distal ends and a constricted shaft. The head of the femur curves antero-dorsally from the shaft, while the distal end turns somewhat ventrally giving a general sigmoid curvature to the bone. The proximal articular area is a rugose oval.

Proximally the ventral surface accommodates the large inter-trochanteric fossa in between two prominent flanges which die out distally along the shaft. The anterior flange forms the internal trochanter which projects almost at right angles to the posterior flange, and is separated from the articular head by a distinct neck. The posterior flange is less pronounced than the anterior one and continues proximally to the articular end.

Distally the femur broadens again to differentiate into two distinct tuberosities for the epipodial articulations. Proximal to the tuberosities lies the shallow popliteal concavity on the ventral aspect. The major part of the distal articular end is occupied by the tibia; the fibula is received in the posterior surface of the posterior tuberosity.

The *tibia* (figure 25) is heavily built and arched medially in the shaft. The bone expands proximally into a broad triangular head for the reception of the femoral tuberosities. The lateral surface bulges proximally to form the apex of the triangular head. Below the articular head, the dorsal surface bears the prominent cnemial crest to which the triceps femoris attached. The medial surface is flat, but from the proximal end a shallow longitudinal depression runs distally for about one third of the length.

The shaft is long, ovoid in cross-section, and is narrow medio-laterally. Medially a prominent oblique ridge runs from the proximo-dorsal to the disto-medial extremities of the shaft. The ridge bears a prominent rugose scar below the mid-length of the bone. A second ridge starts at about the middle of the length of the shaft, immediately lateral to the previously described one, and continues to the distal end.

Distally the tibia is expanded to give an oval configuration of the articular surface. The surface is somewhat angulated into two planes for the tibiale and intermedium respectively.

The *fibula* (figure 26) is a slender spatulate bone, expanded distally. The proximal articular end is a featureless ovoid surface without any expansion in relation to the shaft. In the proximal half, the lateral surface is smooth, but the medial surface bears a prominent longitudinal ridge running for a short distance. Below this ridge, the shaft is twisted on its axis. Above the twist the shaft is arched dorsally, and below the twist it is bowed away from the tibia to form a large interosseal space between these two bones. Further distally, the shaft gradually expands medio-laterally but is flattened dorso-ventrally to form a broad spatulate blade. The distal end is a narrow elongated surface for articulation with the facet formed by the combined fibulare and intermedium.

The *tarsus* is well represented in our collections by two almost complete specimens I.S.I.R. 1 and I.S.I.R. 2. The striking feature of the rhynchosaur tarsus (figure 26*e*) is the presence of three proximal elements, namely tibiale, intermedium and fibulare (Huene 1938, Hughes 1968). No centrale is known. There are four distal tarsalia associated with metatarsals 1 to 4.

The *tibiale* is the most medial element in the proximal row, relatively large and subrounded in shape. The lateral surface fits against the similar facet of the intermedium. The medial surface is free. Proximally the bone receives part of the distal end of the tibia. The distal surface bears a shallow pit for the reception of the first of the distal tarsalia.

The *intermedium* occupies the position between the tibiale and the fibulare. It is the largest tarsal element, hexagonal in outline, with its long axis lying transversely. Proximally it bears two elliptical facets for the epipodials. These two facets are separated from each other by a notch. The fit of the intermedium against the tibiale and fibulare is exact and close, and the latter two bones each contribute part of the articular facets to receive the epipodials.

The dorsal surface is depressed. Distally it shows a rolling surface for the distal tarsal elements.

The *fibulare* is a bone resembling a sacral rib in shape. It is elongate transversely and is appreciably thickened mesially where it articulates with the intermedium. From this contact, the bone gradually contracts to a neck and then flares again at the lateral termination. The proximal surface is narrow and receives part of the distal end of the fibula. Distally near the intermedium, it shows a swollen convexity for articulation with distal tarsale 4.

The four distal tarsalia are arranged in a separate row. They are small, irregularly shaped bones and difficult to describe. The first distal tarsale is the smallest, is ovoid, and lies between the tibiale and the first metatarsal. The second distal tarsale is rectangular in shape and joins the tibiale, intermedium and the second metatarsal. The third distal tarsale is triangular and articulates with the intermedium and the third metatarsal. The fourth distal tarsale is the largest and bears separate facets for articulations with the fifth metatarsal, the third distal tarsale, and the distal surface of the intermedium and fibulare.

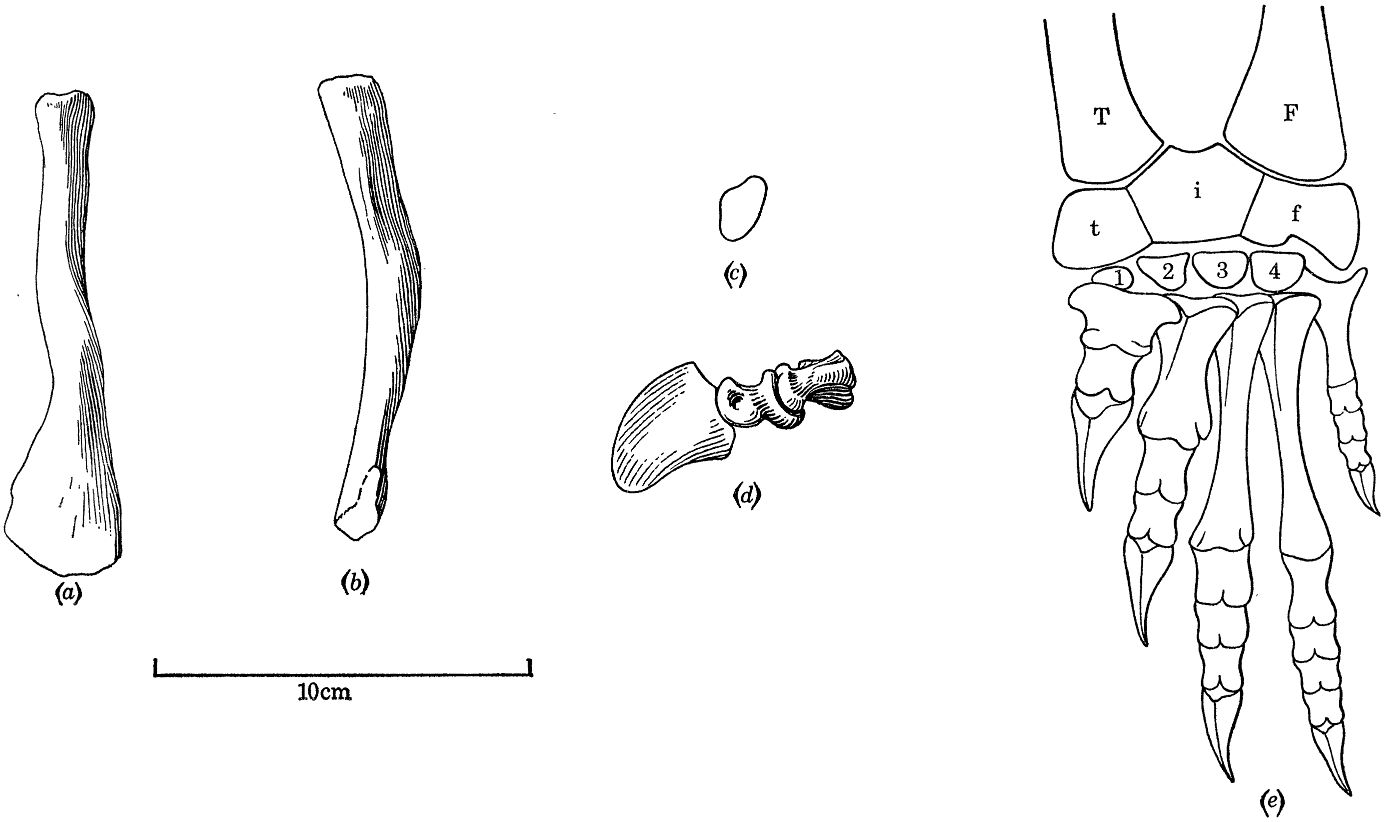

Figure 26. *Paradapedon huxleyi* (Lydekker) (magn. × 0.5). Hind-limb. (*a* to *c*) Dorsal, medial and proximal views of fibula; (*d*) left lateral view of the first toe; (*e*) composite restoration of the tarsus and pes.

Hughes (1968) has discussed the ankle movements of rhynchosaurs in some detail. According to him, the movement was essentially mesotarsal, acting between the proximal and distal tarsalia. The proximal elements were firmly attached to the epipodials to form a penultimate segment of the limb, and prohibiting any movement between them. The distal tarsalia were part of the pes. The extension of the foot was accompanied by gliding of the joint surfaces, and probably some rotation on the fourth distal tarsale.

The relative sizes of the *metatarsals* and *phalanges* can be seen from figure 26. The metatarsals increase in length but decrease in width from the first to the fourth, and the fifth is hooked. The first metatarsal is very short and broad and looks like a phalanx. Metatarsals II, III and IV are progressively more elongated with the development of long shafts. The fifth metatarsal is Y-shaped; its lateral edge thickens ventrally to form the hamate process.

The phalangeal formula is 2–3–4–5–4. The phalanges are all similar in form, although differing in size in the various digits. Each phalanx is expanded proximally and distally; the proximal surface is a shallow saddle-shaped concavity, the distal end forms a hemicylindrical rolling surface. Claws are present in all digits, decreasing in length in proportion laterally. Each claw is bilaterally compressed to form a sharp edge on the ventral margin.

VI. Restoration of the skeleton

In a restoration of the skeleton of *Paradapedon* (figure 27; figure 28, plate 7), based mainly on I.S.I.R. 1, the association of articulated vertebrae reveals the curvature of the backbone; the cervical vertebrae, their anterior and posterior faces oblique to the vertebral axis, suggest a slight up-curving of the neck; the caudal vertebrae, on analogy with other rhynchosaurs, are taken to be about 34; gastralia are present, but many ribs and all chevrons are hypothetically restored; the vertebrae, articulated at shared apophyses, display intervertebral gaps taken into account in an estimate of head-to-tail length (about 1.4 m in I.S.I.R. 1).

When the skull is alined horizontally, the orbits are directed upwards and forwards; for 'normal' vision in a horizontal field a downward head-tilt of some 45° is indicated by the shape of the occipital condyle, the smooth convexity of whose articulating surface is postero-ventral rather than posterior.

The attitude of the shoulder girdle is less readily determined, but when in a series of 'natural' poses of the fore-limb the humerus is articulated with the glenoid, the scapulocoracoid hangs from the dorsal ribs with a slight forward tilt. The coracoids were probably separated by a slight ventral gap, between which lay the median branch of the interclavicle. The form of the clavicle in other rhynchosaurs is used in the reconstruction.

The sacral attachment fixes the position of the pelvis. The upturned head of the femur, set at an angle to the shaft, indicates the limbs not to have been sprawling with the crus and pes directly posteriorly – as Woodward (1907, p. 194) postulated for *Rhynchosaurus* – but were carried close to the side of (but not directly underneath) the body with the pes pointing forward – as Huene (1942, figure 65) postulated for *Cephalonia* (= *Scaphonyx*). The claws of the pes are unusually large. The manus is partly restored from other rhynchosaurs.

VII. Mode of life

The physical environment in which *Paradapedon* lived is partially recorded in the Maleri sediments – clays, sandstones, and 'lime-pellet' rocks, of which clays are dominant. The rocks are interpreted as fluviatile channel, inter-channel, and back swamp deposits (Sengupta 1966; Kutty 1971), the poorly bedded clays were probably deposited during waning floods, the sands, often cross-bedded, possibly represent point bars and similar lenticles. The red haematite of the clays suggests an alkaline oxidizing depositional environment, but, in the absence of desiccation cracks, footprints and signs of evaporites, scarcely arid. The 'lime-pellet' rocks also hint at a 'subtropical climate with alternate hot and dry seasons and a sufficiently high rainfall' (Robinson 1964). There are few records of contemporary flora, mainly as fragments of *Dadoxylon*, *Araucarioxylon* and *Mesembrioxylon* (Pascoe 1959, p. 971).

In skeletal form *Paradapedon* was not adapted to an aquatic mode of life. There is no failure of ossification of carpus and tarsus, or reduction in length of propodials. The limbs are robust; the ratio of femur diameter to femur length (0.14:1) is greater than that of femora in *Varanus*

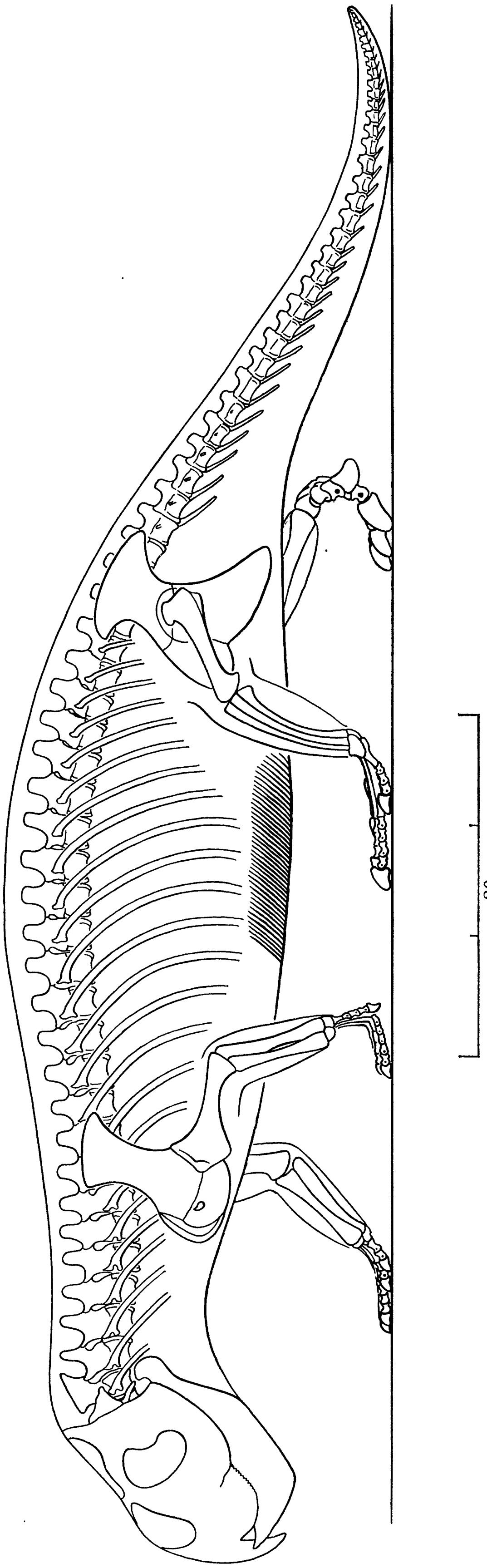

FIGURE 27. *Paradapedon huxleyi* (Lydekker). Restoration of the skeleton in left lateral view. One-sixth natural size.

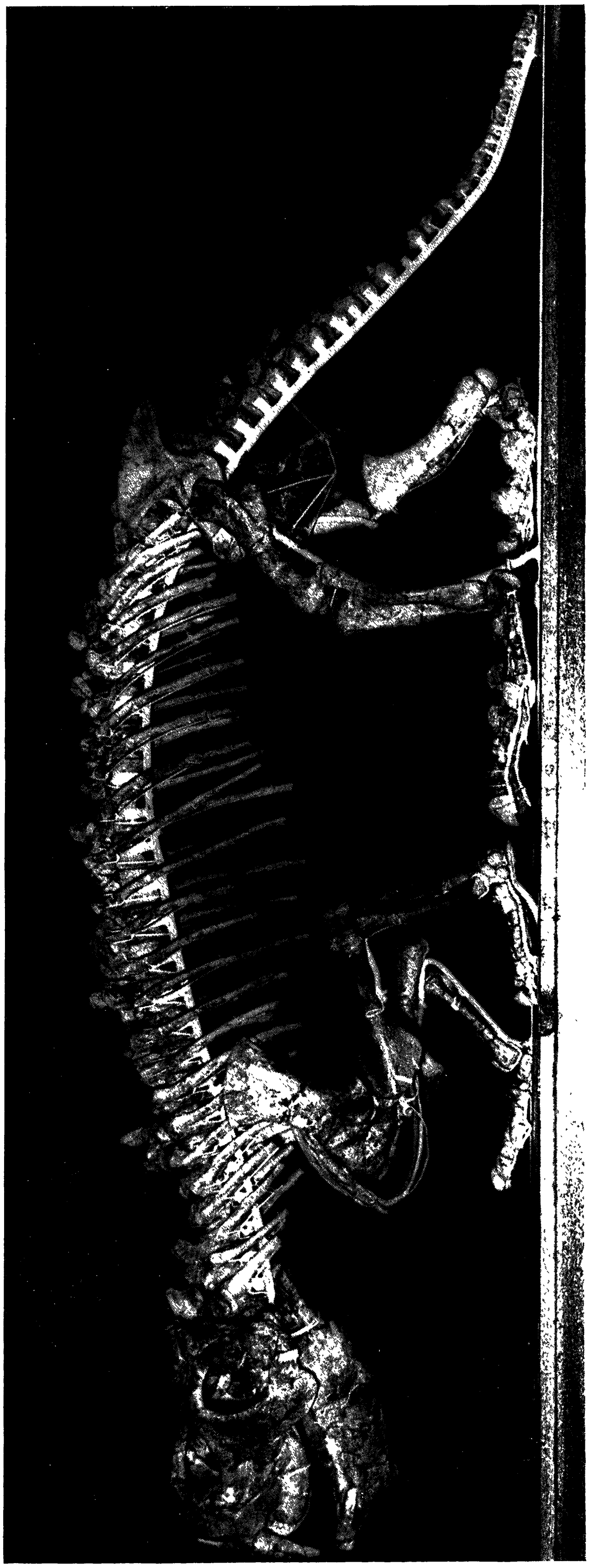

FIGURE 28. *Paradapedon huxleyi* (Lydekker). Specimen I.S.I.R. 1. Skeleton as mounted by P. K. Mazumdar. Lateral view of the left side (magn. $\times \frac{1}{6}$), housed in the Geology Museum of the Indian Statistical Institute, Calcutta.

komodoensis (0.10:1), the largest living lizard, and *Alligator mississipiensis* (0.10:1–0.12:1. The fossil remains are commonly found in the flood-plain clays with phytosaurs and metoposaurs, not in the beds containing the typically aquatic members of the Maleri fauna – being fish (*Ceratodus*) and unionids (*Tikhia*).

Speculation on the diet of *Paradapedon*, based on the pattern of dentition, has ranged from Lydekker (1885), who thought that animals with hard integument furnished the food, to Huene (1939*b*), who suggested rhizomes, especially equisetalian, and Romer (1960) who favoured hard-shelled ginkgoalian and cycad seeds. The osteological evidence tends to suggest a specialized feeding habit.

The powerful elongate down-curving premaxillae meet the upward-curving anterior ends of the dentaries like a pair of tongs, a prominent worn facet being recognizable at the contact surface. The whole arrangement allowed the animal to grip, tear or strip softer food. The smoothed and polished anterior part of the premaxillae indicates a use in digging. The posterior part of the jaw apparatus may have been suited for chopping and crushing, but a lack of a grinding surface on the maxillary tooth plates discourages a postulate of grazing or browsing. The sharp-toothed dorsal edge of the dentary bites against the longitudinal groove of the maxilla; but there are many maxillary teeth set well away from the bite which show small worn facets on their crowns, and which thus suggest mastication or crushing of hard food. The greatly expanded temporal region with large temporal fenestrae indicate powerful jaw musculature. Deep palatal channels extending posteriorly from the choanae (figure 4*c*) imply a soft palate (compare Walker 1961, p. 194) and a kind of food that needed some degree of mastication. A longitudinal channel along the inner side of each dentary may have lodged a prehensile tongue. Prominent retractor fossae suggest strong development of the retractor bulbi group of eye muscles, the eyes, frontal in position, perhaps having binocular vision (see Walls 1963, p. 290).

The cumulative osteological evidence, and the ecological hints in the associated sediments, suggest that while *Paradapedon* might well have enjoyed such vegetable foods as rhizomes and seeds if they were available, it is much more likely to have survived mainly on a diet of mussels, abundant in the Maleri sediments – the tongs of premaxillae and dentaries used to gather the shells, the hinder part of the jaws to crack the shells, the numerous small projecting maxillary teeth to hold the shells in position in the mouth, the long tongue to select the food and to eject broken shell. Analogy in habit is with the tuatara and the caiman lizard (*Dracaena*).

The heavy build, the large manus and pes, the blunt claws, the blunt premaxillae discourage the view that *Paradapedon* might have been a predatory hunter, although it might have been a carrion-feeder at times.

VIII. NOMENCLATURE

A critical examination of all the available material indicates that there is only one genus of rhynchosaur in the Maleri collection to date, and this genus is monotypic. In recent times, some confusion has arisen over the question of priority between the two generic names *Paradapedon* and *Parasuchus* for the Indian rhynchosaur. One of the reasons is due to the fact that none of the earlier workers designated precisely the holotype material representing the names given to either the rhynchosaur or the phytosaur found in India.

Paradapedon Huene, 1938, has as type-species *Hyperodapedon huxleyi* Lydekker, 1881, based on syntypic tooth plates, the generic name being later than *Parasuchus* Huxley, 1870, validated Lydekker, 1885. The type-species of *Parasuchus hislopi* Lydekker, 1885, unfortunately has as syntype material a rhynchosaurian basicranium mixed with phytosaurian bones, scutes and teeth. The basicranium was identified by Huene (1940, p. 6 and Pl. III, Fig. 1) as belonging to *Paradapedon huxleyi*, the legend of the figure continues by saying that the name *Parasuchus hislopi* has to be abandoned. In the text (p. 7) Huene ambiguously referred to the basicranium as 'Lydekker's type' as if Lydekker regarded it as the holotype of *Parasuchus hislopi*, and thus was initiated the confusion. But Lydekker did not consider this basicranium as the holotype of *Parasuchus hislopi*. Thus the ambiguous designation of Huene is not valid (Stoll *et al.* 1964, Article 67*c*). In fact the specimens described by Lydekker (1885) as *Parasuchus hislopi* are a series of syntypes each of equal rank with the others for nomenclatorial purposes (Article 73*c*), and any one of the syntypes can be designated as the lectotype (Article 74*a*).

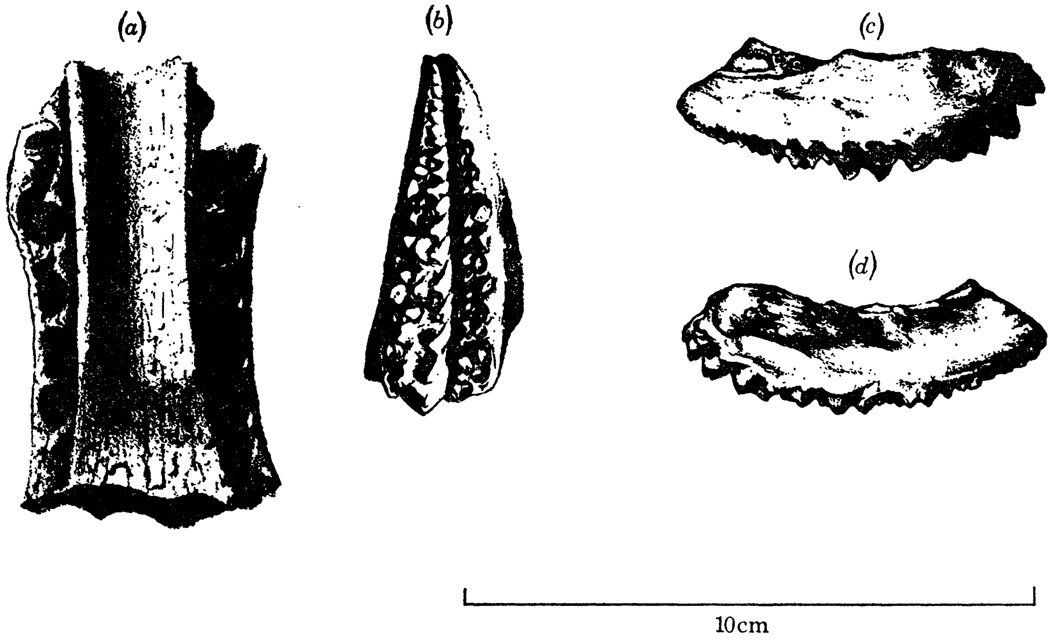

FIGURE 29. (*a*) Lectotype of *Parasuchus hislopi* Lydekker from the Maleri formation; ventral view of premaxillary rostrum; specimen no. GSI. H20/11, housed in Indian Museum, Calcutta. (From Lydekker (1885), Pl. III, Fig. 3.) (*b*, *c*, *d*) Lectotype of *Paradapedon huxleyi* (Lydekker); right maxilla in occlusal, medial and lateral views; specimen no. G.S.I. 281/1a, housed in Indian Museum, Calcutta. (From Lydekker (1885), Pl. I, Figs. 2, 2*a*, 2*b*.)

If this basicranium is chosen as the lectotype of *Parasuchus hislopi*, then *Paradapedon* is a junior synonym of *Parasuchus; Parasuchus* is a rhynchosaur and not a phytosaur; *hislopi* is a junior synonym of *huxleyi*, and the phytosaurian material hitherto placed in *Parasuchus* remains unnamed. To meet Lydekker's original intention and to avoid nomenclatural confusion, it is now proposed that a new lectotype for *hislopi* be chosen – the phytosaurian premaxillary rostrum illustrated in Lydekker (1885, Pl. I, Fig. 3) – and the suppression of *hislopi* and *Paradapedon* avoided (figure 29*a*).

Once the lectotype of *Parasuchus hislopi* is fixed, the name *Paradapedon* is open to apply to the Indian rhynchosaur without any further confusion. However, the above-mentioned basicranium cannot be designated as the lectotype of *Paradapedon huxleyi*, since it did not form part of the original type series of the species. For this purpose, a right maxillary tooth plate (Lydekker 1885, Pl. I, Fig. 2) is designated the lectotype of *Paradapedon huxleyi* (figure 29*b*, *c*, *d*).

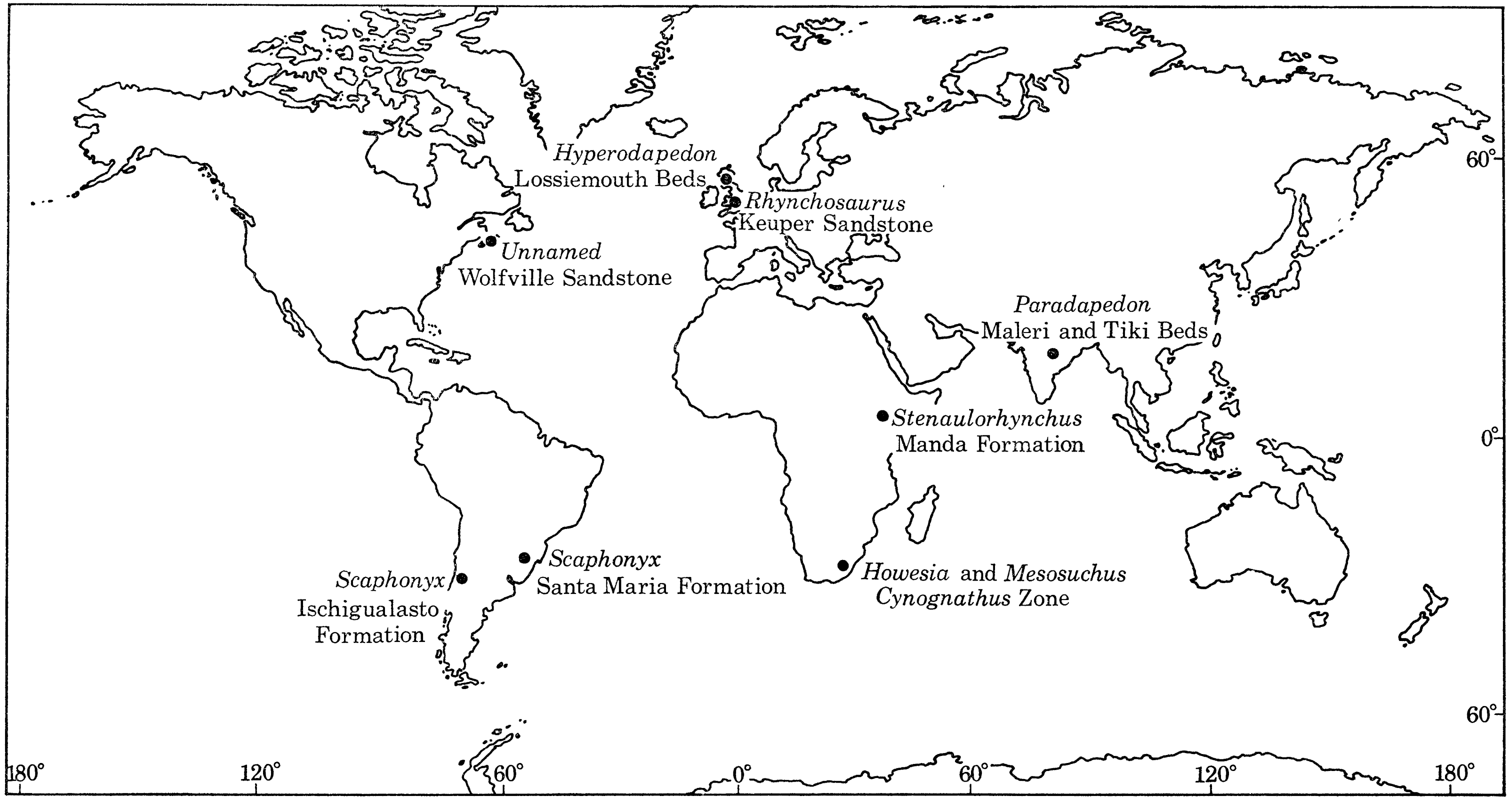

FIGURE 30. Distribution of the genera of Rhynchosauridae.

IX. Distribution, evolution and stratigraphic significance of the Rhynchosauridae

Distribution

Rhynchosaurs were an exclusively Triassic group of reptiles recorded from all continents except Australia and Antarctica (figure 30). At present the family Rhynchosauridae includes seven well-established genera: *Howesia* and *Mesosuchus* from the *Cynognathus* Zone of the Beaufort Series of the Karroo System of South Africa, *Stenaulorhynchus* from the Manda Formation of Tanzania, *Rhynchosaurus* from the 'Keuper' Sandstone and Waterstones of England, *Hyperodapedon* from the Lossiemouth Beds of Scotland, *Paradapedon* from the Maleri and Tiki Formations of India, and *Scaphonyx* from the Santa Maria Formation of Brazil and Ischigualasto Formation of Argentina. The only rhynchosaur from North America is reported, but not yet described, by Baird (1962) from the Wolfville Sandstone of Nova Scotia. *Stenometopon* from the Lossiemouth Beds of Scotland is believed to be a crushed *Hyperodapedon* specimen (A. D. Walker, personal communication).

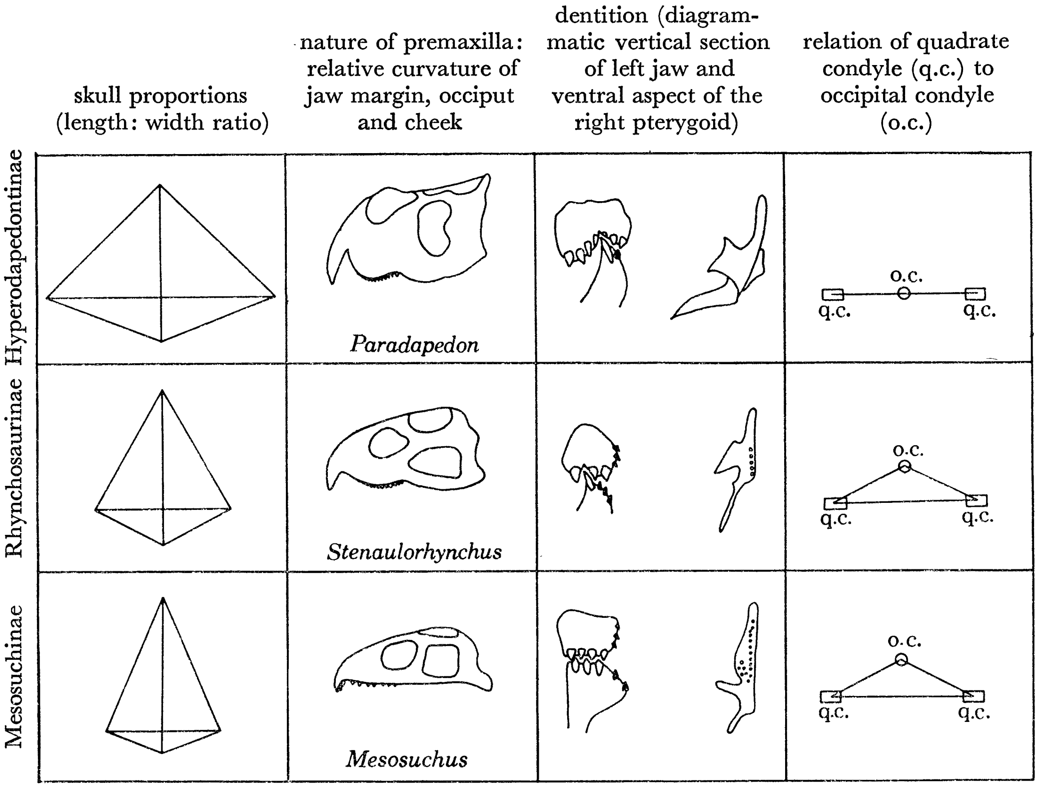

Figure 31. Evolution of rhynchosaurian skull characters. *Mesosuchus* (from Haughton 1924, Broom 1925); *Stenaulorhynchus* (Huene 1938). In the third column, the semi-diagrammatic vertical section of the jaw of *Howesia*, not labelled, is composed from Malan (1963), and the palate from Broom (1906). Re-examination of Huene's figured specimen (no. 317*a*, housed in the Museum of Tübingen University) disclosed a single mesial row of teeth on the pterygoid of *Stenaulorhynchus*; this has not previously been recorded in this genus.

Evolution

Although the detailed phyletic relationships among the different rhynchosaur genera are not well known, Walker (1969) has suggested that *Rhynchosaurus* and *Hyperodapedon* represent a line of development separate from the *Scaphonyx–Paradapedon* group of Gondwanaland, characterized by having the greater number of tooth-rows on the medial side of the groove.

Chatterjee (1969) has erected a horizontal classification of the rhynchosaurs, grouping them into three well-defined subfamilies on the basis of their skull characters (figure 31). The least specialized subfamily, Mesosuchinae (Nopcsa 1928 *nom. transl. ex* Mesosuchidae Haughton 1924) includes *Mesosuchus* and *Howesia*. The intermediate sub-family Rhynchosaurinae (Nopcsa, 1923 *nom. transl. ex* Rhynchosauridae Gervais, 1859? Cope 1870) includes *Rhynchosaurus* and *Stenaulorhynchus*. The most highly specialized forms, *Hyperodapedon*, *Paradapedon* and *Scaphonyx*, may be grouped into a new subfamily for which the name Hyperodapedontinae is here proposed (*nom. transl. ex* Hyperodapedontidae Lydekker, 1885). These three subfamilies represent grades of evolution within the family.

A brief account of the morphological changes affecting the rhynchosaurs through the different phases of the Trias is summarized here. There is an overall increase in size. The skull is gradually

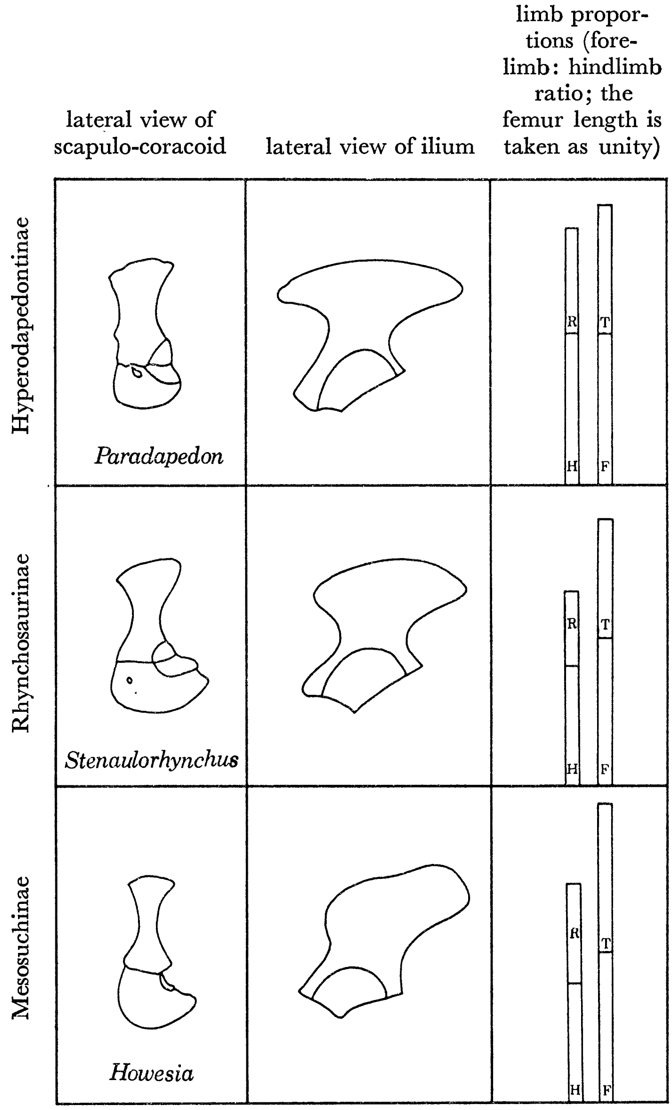

FIGURE 32. Evolution of some postcranial characters in rhynchosaurs. *Howesia* (from Broom 1906); *Stenaulorhynchus* (From Huene 1938).

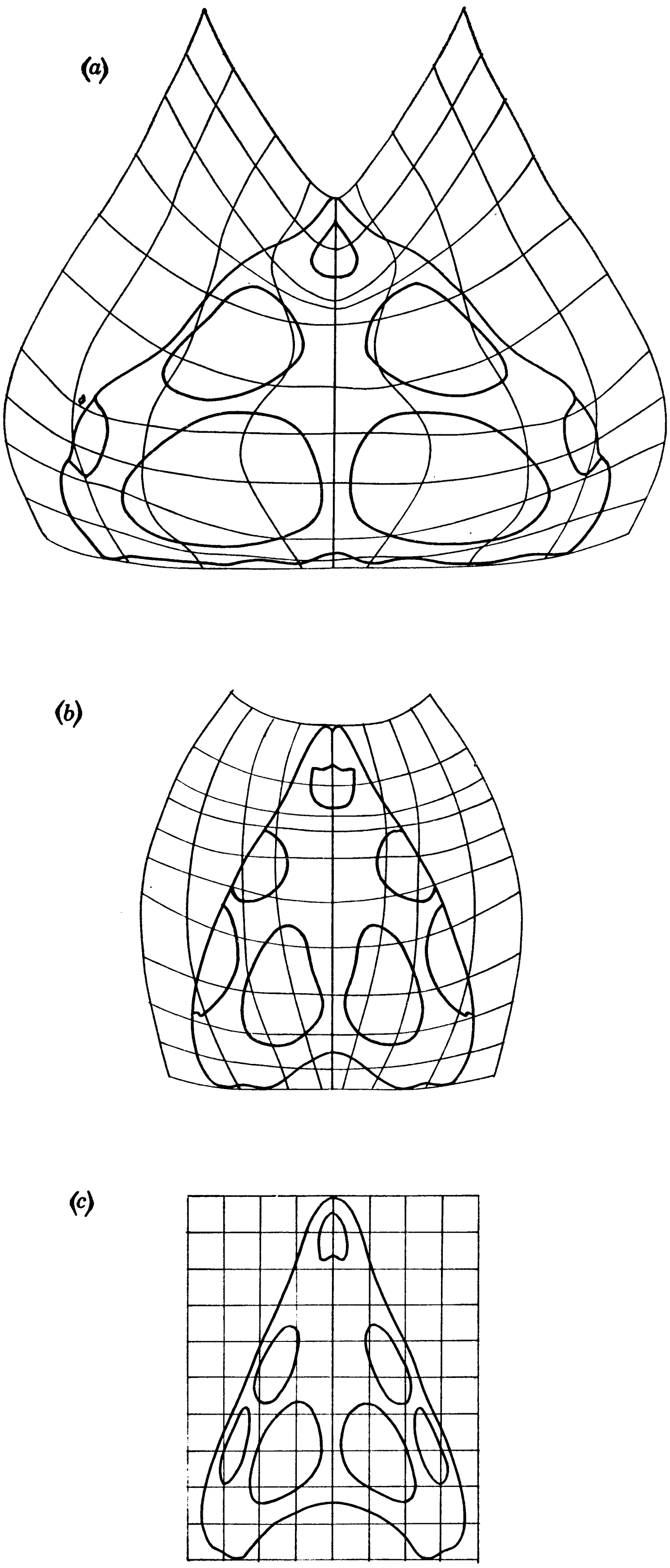

Figure 33. Evolution of rhynchosaur skulls, shown in Cartesian co-ordinate deformation. (*a*) *Mesosuchus* (from Broom 1925); (*b*) *Stenaulorhynchus*; (*c*) *Paradapedon*.

widened and this is coupled with an expansion of the cheek region. The premaxillae become edentulous and enlarged to hook down between the anterior ends of the dentaries. The jaw margin becomes more and more curved. There are changes in the shape and size of the various skull openings. The pineal foramen is lost. The crossbars of the parietal are directed laterally from the primitive postero-lateral direction. The supratemporal bone disappears. In both the maxilla and the dentary, the single marginal tooth row becomes complex, with multiplication of tooth rows. In the maxilla, the tooth plate is traversed by a longitudinal groove. In the dentary however, the multiple tooth rows show a secondary simplification, and are reduced to a single row. The lingual tooth rows on the maxilla and the dentary, absent in the early forms, become numerous, and then secondarily simplify to a single row, and ultimately they are lost. In the pterygoid the numerous rows of teeth become a single row and then disappear. The quadrate, at first slanting back posteroventrally from its articulation with the squamosal, becomes more and more vertical and its condyle migrates forward to lie on the same level with the occipital condyle (figure 31).

Well-marked evolutionary changes also affect the postcranial characters of rhynchosaurs. The disparity of length between the forelimb and the hind limb is reduced. The scapula becomes expanded, the coracoid shortens posteriorly until it shows no projection beyond the glenoid. The glenoid is enlarged. The anterior process of the ilium becomes more and more prominent (figure 32).

The progressive change in the shape of the skull in the three different subfamilies of rhynchosaurs can be shown by using D'Arcy Thompson's method (1942) of Cartesian transformations (figure 33). This method was designed to show how one organ or organism, viewed in two dimensions, can be transformed into a 'homoeomorphic' form by inscribing its outline in a system of Cartesian co-ordinates and then deforming it along simple and recognized lines, i.e. by altering the direction of axes, or the ratios of $x:y$ or by substituting for x and y some more complicated expressions. Thus a new figure is obtained which represents the old figure under a more or less homogeneous 'strain'. These figures, when composed, give one instantly the sense and trend of transformation.

Stratigraphic significance

The stratigraphy of the rhynchosaur-bearing formations is discussed in a separate paper (Chatterjee 1969). It is concluded that three subfamilies of rhynchosaurs are considered characteristic of Lower, Middle and Early Upper Triassic respectively (keeping the Santa Maria Formation as Upper Trias). Thus the rhynchosaurs, when split into three grades, seem to be extremely useful in continental Triassic correlation in both the northern and the southern hemispheres. The type sequence of the Trias is in Germany, where it is divisible into lower, middle and upper phases, Bunter, Muschelkalk and Keuper respectively (neglecting Rhaetic here). Bunter and Keuper are continental deposits, whereas the intervening Muschelkalk is marine. Thus the Middle Triassic terrestrial vertebrate faunas in the other parts of the globe cannot be directly correlated with the German Muschelkalk vertebrate faunas, as most of the latter are highly peculiar and consist mainly of aquatic forms. Moreover, the Triassic faunal elements which are common elsewhere, i.e. the therapsids and rhynchosaurs, are totally absent throughout the whole German sequence. This is why correlation of wholly continental Triassic sequences with the Germano-type sequence presents considerable difficulties. On the other hand, the continental terrestrial faunas cannot easily be related to the ammonite zones of the Alpine sequence except in the case of certain horizons in the Germano-type sequence. The

TABLE 4. TRIASSIC STRATIGRAPHIC CORRELATION

	European Stages	Germany Type Triassic	Great Britain	India	South Africa	East Africa	Brazil	Argentina	Nova Scotia
UPPER	NORIAN	Knollenmergel		Dharmaram	Stormberg Series Cave Sandstone and Red Beds		Sao Bento Series	Los Colorados Formation	Newark Group Scots Bay Formation. Basalt Blomidon Shale Basalt
		Stubensandstein	Lossiemouth Bed†	Maleri and Tiki Formations†					Wolfville Sandstone†
		Buntemergel							
	CARNIAN	Schilfsandstein					Santa Maria Formation†	Ischigualasto Formation†	
		Gipskeuper	Keuper Marl						
MIDDLE	LADINIAN	Lettenkohle						Los Rastros	
			Keuper Sandstone†	?Bhimaram Sandstone	Molteno Beds			Ischicuca	
	ANISIAN	Muschelkalk		Yerrapalli		Manda Beds†			
						Ntawere			
LOWER	SCYTHIAN (EOTRIASSIC)	Bunter	Upper Mottled Sandstone		Beaufort Series Cynognathus Zone†				
			Bunter Pebble Beds						

† Rhynchosaur-bearing horizon.

continental Middle Trias might be defined on the occurrence of the 'intermediate' type of rhynchosaur, the Lower and Upper Trias being recognized by the presence of 'primitive' and 'advanced' genera respectively (table 4).

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EXPLANATION OF ABBREVIATONS USED IN FIGURES

Skull

a	angular	per	perilymphatic duct
ar	articular	pf	postfrontal
asc	anterior semicircular canal	pl	palatine
bo	basioccipital	pm	premaxilla
bpt	basipterygoid process	po	postorbital
bs	basisphenoid	pr	pro-otic
c	coronoid	pra	prearticular
d	dentary	prf	prefrontal
ec	ectopterygoid	psc	posterior semicircular canal
ef	endocranial fenestra	pt	pterygoid
end	endolymphatic duct	q	quadrate
eo	exoccipital	qj	quadratojugal
fo	fenestra ovalis	ref	retractor fossa
hsc	horizontal semicircular canal	sa	surangular
ic	foramen for internal carotid	soc	supraoccipital
j	jugal	sp	splenial
jf	jugular foramen	sq	squamosal
l	lacrimal	ss	sinus superior of the utriculus
m	maxilla	st	supratemporal
n	nasal	tb	tabular
op	opisthotic	v	vomer
p	parietal		

Foramina for cranial nerves in Roman numerals.

L1, L2, successive longitudinal tooth rows lateral to the longitudinal groove of the maxilla.

M1, M2, successive longitudinal tooth rows medial to the longitudinal groove of the maxilla.

Postcranial skeleton

ca	centrantrum	pub	pubis
cor	coracoid	rad	radius
cs	centrosphene	scap	scapula
f	fibulare	t	tibiale
fem	femur	tib, T	tibia
fib, F	fibula	uln	ulna
hum	humerus		
i	intermedium	1–4	distal tarsalia 1–4
icl	interclavicle	I–V	metatarsals I–V
il	ilium	l	left
isch	ischium	r	right

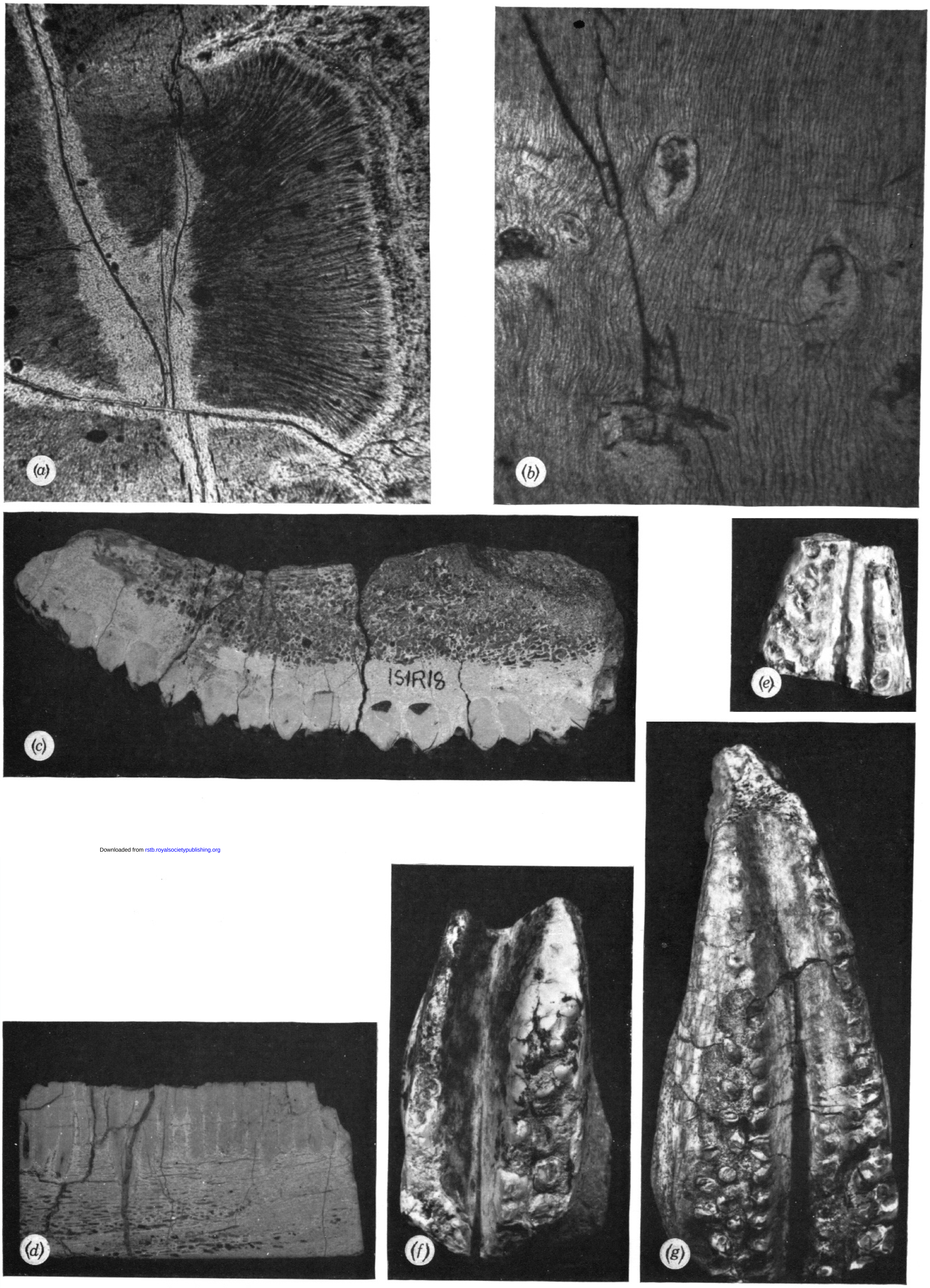

FIGURE 10. *Paradapedon huxleyi* (Lydekker). Dentition. (*a*) Photomicrograph of maxillary dentition showing enlarged view of the portion of the fluting mentioned in figure 9 (magn. × 20). (*b*) Photomicrograph of maxillary dentition showing the enlarged view of the portion of the canalicular system mentioned in figure 9*b* (magn. × 20). (*c*) Vertical section of the maxillary tooth plate showing ankylothecodont type of tooth implantation (natural size). (*d*) Vertical section of the dentary showing ankylothecodont type of tooth implantation (natural size). (*e*, *f*, *g*) Occlusal views of three isolated maxillary tooth plates showing the wear of the longitudinal groove (natural size).

FIGURE 11. *Paradapedon huxleyi* (Lydekker). Three views of the skull (magn. × 0.5). (*a*) Right lateral; (*b*) left lateral; (*c*) occipital. Specimen I.S.I.R.1.

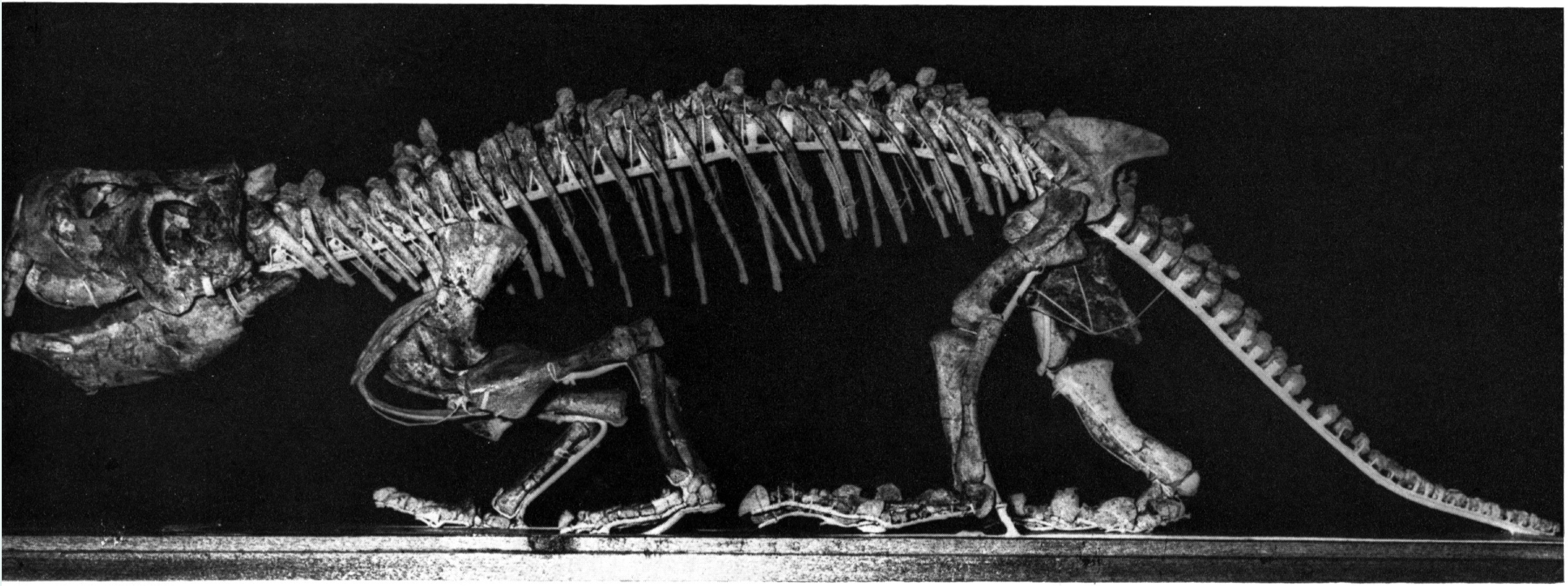

FIGURE 28. *Paradapedon huxleyi* (Lydekker). Specimen I.S.I.R. 1. Skeleton as mounted by P. K. Mazumdar. Lateral view of the left side (magn. $\times \frac{1}{6}$), housed in the Geology Museum of the Indian Statistical Institute, Calcutta.