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**1981**
Bernard Price Institute for Palaeontological Research
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*Palaeont. afr.*, **24** (1981)

# *HOVASAURUS BOULEI*, AN AQUATIC EOSUCHIAN FROM THE UPPER PERMIAN OF MADAGASCAR

by

**P.J. Currie**

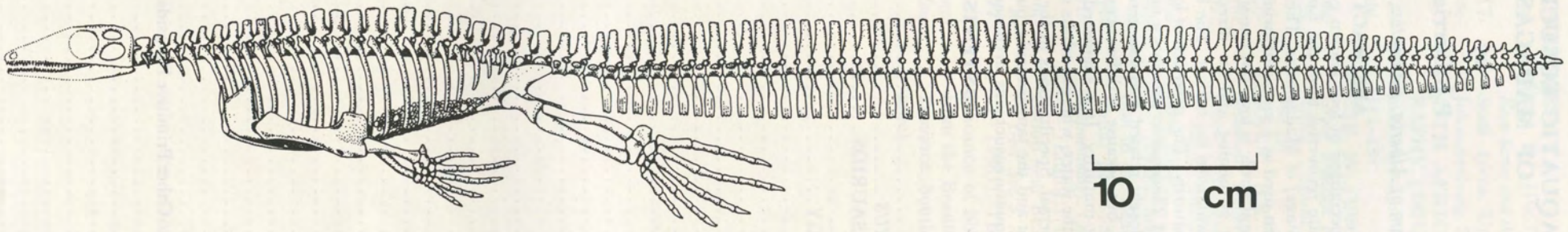
*Provincial Museum of Alberta, Edmonton, Alberta, T5N OM6, Canada*

## ABSTRACT

*Hovasaurus* is the most specialized of four known genera of tangasaurid eosuchians, and is the most common vertebrate recovered from the Lower Sakamena Formation (Upper Permian, Dzulfian Standard Stage) of Madagascar. The tail is more than double the snout-vent length, and would have been used as a powerful swimming appendage. Ribs are pachyostotic in large animals. The pectoral girdle is low, but massively developed ventrally. The front limb would have been used for swimming and for direction control when swimming. Copious amounts of pebbles were swallowed for ballast. The hind limbs would have been efficient for terrestrial locomotion at maturity. The presence of long growth series for *Hovasaurus* and the more terrestrial tangasaurid *Thadeosaurus* presents a unique opportunity to study differences in growth strategies in two closely related Permian genera. At birth, the limbs were relatively much shorter in *Hovasaurus*, but because of differences in growth rates, the limbs of *Thadeosaurus* are relatively shorter at maturity. It is suggested that immature specimens of *Hovasaurus* spent most of their time in the water, whereas adults spent more time on land for mating, laying eggs and/or range dispersal. Specilizations in the vertebrae and carpus indicate close relationship between *Youngina* and the tangasaurids, but eliminate tangasaurids from consideration as ancestors of other aquatic eosuchians, archosaurs or sauropterygians.

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Reconstruction of the skeleton of *Hovasaurus boulei*, an aquatic eosuchian from the Late Permian of Madagascar.

## ABBREVIATIONS

*Institutions*

AMNH — American Museum of Natural History
MNHN — Museum National d'Histoire Naturelle, Paris
SAM — South African Museum

*Muscles*

aq — anconaeus quartus
b — biceps
br — brachialis inferior
cb — coracobrachialis brevis
cbl — coracobrachialis longus
de — deltoids
et — epitrochleoanconaeus
ex — extensors
fcr — flexor carpi radialis
fl — flexors
ld — latissimus dorsi
pc — palmaris communis profundus
pe — pectoralis
pq — pronator quadratus
s — supinator manus
sc — supracoracoideus
scs — subcoracoscapularis
sh — scapulohumeralis
sl — supinator longus
tr — triceps
trl — triceps laterialis (short head)
trm — triceps medialis (short head)

*Osteological*

a — astragalus
an — angular
ar — articular
ATL-c — atlantal centrum
ATL-na — atlantal neural arch
AX — axial intercentrum
bo — basioccipital
bps — combined basisphenoid and parasphenoid
C — clavicle
c — capitellum
cal — calcaneum
CL — cleithrum
co — coronoid
COR — coracoid
cr — cervical rib
d — dentary
e — ectepicondyle
ef — entepicondylar foramen
eo — exoccipital
ep — epipterygoid
F — femur
f — frontal
FIB — fibula
H — humerus
h — hyoid
ha — haemal arch
i — intermedium
IC — interclavicle
ic — intercentrum
IL — ilium
IS — ischium
j — jugal
l — lacrimal
lc — lateral centrale
m — maxilla
mc — medial centrale
n — nasal
op — opisthotic
p — parietal
pal — palatine
pf — postfrontal
pi — pisiform
po — postorbital
pr — prearticular
prf — prefrontal
pro — prootic
pt — pterygoid
ptf — transverse flange of the pterygoid
PU — pubis
q — quadrate
qj — qudratojugal
R — radius
r — radiale
S — scapula
sa — surangular
sp — splenial
sq — squamosal
sr — sacral rib
ST — sternum
st — supratemporal
sta — stapes
T — tibia
U — ulna
u — ulnare
1–5 — distal carpals, distal tarsals
I–V — metacarpals, metatarsals

## INTRODUCTION

In 1914, Robert Broom announced the discovery of a new type of diapsid reptile from the Upper Permian Karoo beds of South Africa. *Youngina* had the characteristic lateral and dorsal temporal fenestra in the skull, but overall had a more primitive level of organization than any diapsids known until that time. Broom created a new reptilian suborder, the Eosuchia, for *Youngina*.

Since Broom's original description of *Youngina*, a large number of genera from around the world have been referred to the Eosuchia. The earliest record, according to Reisz (1981), is *Petrolacosaurus* from the Upper Pennsylvanian strata of Kansas. The greatest diversity appears to have been in Late Permian times, and there was a gradual decline during the Triassic when derived groups rose in prominence. Two eosuchians, *Champsosaurus* (Erickson 1972) and *Simoedosaurus* (Russell-Sigogneau and Russell 1978), survived until the Eocene.

By the Late Permian, at least three major lines of eosuchians had evolved. One line, characterized by *Prolacerta* (Gow 1975) and *Protorosaurus* (Watson 1957), was long thought to have been the ancestral stock of lizards. This is no longer accepted by most palaeontologists, but the line appears to have led to the highly specialized *Tanystropheus* of the Middle Triassic of Europe (Wild 1973). Research by Carroll (1975a, b, 1977) has shown that paliguanids are more suitable lizard ancestors than prolacertiform eosuchians. Carroll considers paliguanids to be primitive lizards, but in a horizontal classifica-

tion they would be classified as eosuchians. The third major line of eosuchians had radiated in the Permian into a diverse and successful assemblage of terrestrial forms like *Youngina* (Gow 1975) and aquatic forms such as *Tangasaurus* (Haughton 1924). This line appears to have given rise to archosaurs (Carroll 1976a) and sauropterygians (Carroll 1981).

Many genera of eosuchians independently became adapted for an aquatic existence. The Tangasauridae were close relatives of *Youngina* that lived in Africa and Madagascar during Permo-Triassic times. The family includes both terrestrial and aquatic forms, presenting a unique opportunity to study diversification within a well-defined unit of eosuchians.

*Tangasaurus* was a small, lizard-like reptile that was described by S.H. Haughton in 1924. The genus was based on two specimens from Upper Permian strata in the vicinity of Tanga, Tanzania (fig. 1a). The specimens are poorly preserved, but Haughton (1924) felt that several characters indicated that this genus was a swimming reptile.

Numerous well-preserved specimens from the Lower Sakamena Formation of Madagascar were identified as *Tangasaurus* by Piveteau (1926). These beds are considered as Upper Permian (Dzhulfian Stage) on the basis of pollen (Hart 1969, Anderson and Anderson 1970), plants (Anderson and Anderson 1970), invertebrates (Cox 1936, Brenon 1972), fish (Dr. B. Gardiner, pers. comm., 1976), and reptiles (Piveteau 1955a, Anderson and Cruickshank 1978). During the Permian, Madagascar was much closer to Tanzania (fig. 1a) than it is now, and the Mozambique Channel had just started to open (Bambach *et al.* 1980). This region has been referred to as the Tangasaurid Province of the ancient continent Gondwanaland (Anderson and Cruickshank 1978). Re-examination of the specimens from Madagascar previously identified as *Tangasaurus* has shown that they represent a different genus, *Thadeosaurus* (Carroll 1981), known only from the Upper Permian of Madagascar.

Piveteau (1926) tentatively referred several specimens collected in Madagascar to the European genus *Datheosaurus*. However, *Datheosaurus* is a junior synonym of *Haptodus*, the name given to a sphenacodont pelycosaur (Currie 1979). The specimens from Madagascar belong to an eosuchian, and have been renamed *Thadeosaurus* (Carroll 1981).

*Kenyasaurus* from the Lower Triassic of Kenya was assigned by Harris and Carroll (1977) to the Tangasuridae on the basis of general body form, the presence of a sternum and particularly the anatomy of the foot.

In 1926, J. Piveteau established the genus *Hovasaurus* on the basis of a large collection of specimens from the Upper Permian of Madagascar. The paper was well illustrated with photographic plates and line drawings, but because of the nature of the specimens and lack of comparative material the description was based on only seven of the several hundred specimens in the Muséum National d'Histoire Naturelle (Paris). Although *Hovasaurus* was recognized as an aquatic reptile, it was assumed to be related to *Mesosaurus*. After Haughton's paper of 1930 demonstrated the anatomical similarities between *Tangasaurus* and *Hovasaurus*, these genera were usually included as the only known representatives of the Tangasauridae (Camp 1945, Piveteau 1955a, Romer 1956, 1966, Orlov 1964, Kuhn 1969). Subsequent papers by other researchers have mentioned *Hovasaurus*, but no detailed description has been undertaken, and this genus has remained poorly understood.

All known specimens of *Hovasaurus* were found in finely laminated nodules of siltstone. The abdominal cavity was the centre of nodule formation. The action of nodule formation usually did not persist long enough for the head and tail to be included, and these portions of the body are almost invariably lost. In most cases, only part of each nodule was recovered, and the soft split bone had already eroded out. Latex and silicone rubber casts were made from the high fidelity, natural moulds as an aid in studying the specimens (Baird 1951).

The orientations of the nodules are unknown. The centre of gravity would have been low in *Hovasaurus*, so most of the specimens probably settled upright in the mud. The disarticulation pattern of the skeleton supports this supposition in most specimens. For example, in MNHN 1908-32-24 the ventral bones have maintained their correct relationship to each other, but the dorsals appear to have collapsed. The scapular blades protrude dorsally above the vertebrae and ribs. The mid-dorsal vertebrae with their high neural spines have fallen on their sides, but the sacrals and anterior caudals have remained upright because of the fused ribs that extend laterally from the centra.

It appears that in all cases the connective tissues disintegrated and the bones collapsed into a single plane before the carcase was covered to any appreciable depth by the fine sediments. There is no evidence of macrophagous scavenging of any of the specimens, and the relatively minor amount of disarticulation evident can be accounted for by settling and gentle currents in the water.

*Hovasaurus boulei* is represented by more than 300 specimens representing most of the life span, which permits the study of morphological variation and the changes undergone during growth in a single species. The length of an average dorsal centrum of the largest known specimen of *Hovasaurus* is 3,5 times the length of the same dimension in the smallest known specimen (table 1). It is evident from the ossification of the largest specimens that these were mature animals when they died. The expected adult-to-hatchling length ratio for *Hovasaurus* (adult length 550 mm) is 4,6 (95 per cent confidence interval is 4,3–4,8) (Currie 1981b). The adult-to-juvenile length ratio of the vertebrae indicate that the smallest known specimens of *Hovasaurus* were not very old when they died, but were not hatchlings. Because reptiles generally double their

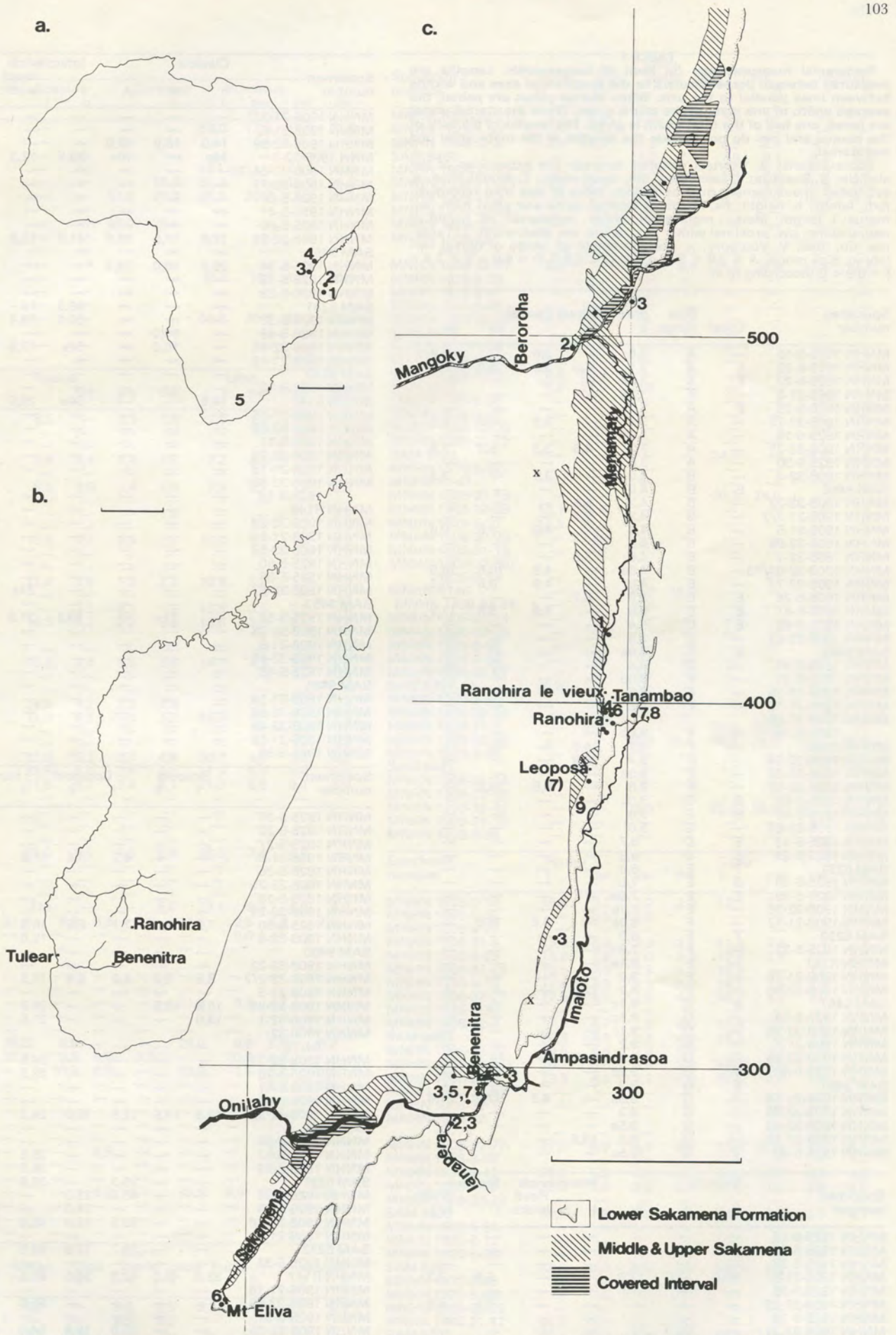



Figure 1. Eosuchian localities of Africa and Madagascar. a, Madagascar has been moved on the map to its probable position at the end of the Permian. 1, Mount Eliva. 2, Ranohira. 3, Tanga, Tanzania. 4, Mariakani, Kenya. 5, *Youngina* Localities. Scale = 1 000 km; b, the island of Madagascar; c, collecting localities for amphibians and reptiles of the Lower Sakamena Formation. 1, *Rhinesuchus;* 2, isolated bones of ?labyrinthodont amphibians; 3, isolated bones of reptiles; 4, *Barasaurus besairiei* Piveteau; 5, *?Acerosodontosaurus;* 6, *Hovasaurus boulei* Piveteau; 7, *Claudiosaurus germaini* Carroll; 8, *?Daedalosaurus;* 9, articulated, unidentified reptile remains in nodules. *Hovasaurus* remains were recovered also from unknown localities in the lower course of the Sakamena and Ianapera rivers. *Thadeosaurus, Coelurosauravus* and *Daedalosaurus* collected from a site in the Sakamena River Valley. Isolated therapsid remains are probably from the Benenitra area. Scale is 50 kilometres. After Piveteau 1926, Tortochaux 1950, and Besairie 1953.

**TABLE 1**

**Postcranial measurements (in mm) of tangasaurids. Lengths are measured between perpendiculars to the longitudinal axes and widths between lines parallel to the axis. When sternal plates are paired, the average width of one plate of the pair is given. When the sternal plates are fused, one half of the total width is given. The lengths of digits IV of the manus and pes do not include the lengths of the metacarpal and metatarsal.**

Abbreviations: A, shortest distance between the extremities of the clavicle; B, Besakoa; c, calculated; dw, distal width; E, Mount Eliva; e, estimated (measurement may be slightly more or less than recorded); fem, femur; h, height; hs, length of haemal spine and arch; hum, humerus; l, length; Metac., metacarpal; Metat., metatarsal; ns, height of neural spine; pw, proximal width; rad, radius; sw, shaft width; T, Tanzania; tib, tibia; V, Vohibory; *x*, average length of centra of dorsal vertebrae. Size range; A ≤ 3,9 < B ≤ 4,9 < C ≤ 5,9 < D ≤ 6,9 < E ≤ 7,9 < F ≤ 8,9 < G (according to *x*).

| Specimen number | Local | Size range | Vertebrae x | Dorsal ns | Caudal l | Caudal ns | Caudal hs |
|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | A | 3,0 | — | 3,0 | — | 6,3 |
| MNHN 1925-5-20 | E | A | 3,1 | 4,0 | 3,2 | 4,0 | 6,5 |
| MNHN 1925-5-27 | E | A | 3,1c | — | — | — | — |
| MNHN 1908-21-8 | — | A | 3,2e | — | — | — | — |
| MNHN 1925-5-25 | E | A | 3,2 | — | — | — | — |
| MNHN 1908-32-29 | — | A | 3,3 | — | 3,1 | 4,0 | 6,5 |
| MNHN 1925-5-18 | — | A | 3,5 | — | — | — | — |
| MNHN 1908-32-21 | — | A | 3,7 | 4,6 | 3,3 | 5,0 | 7,5 |
| MNHN 1925-5-30 | — | A | 3,8 | — | — | — | — |
| MNHN 1908-32-4 | — | B | 4,0 | — | 3,9 | — | 8,3 |
| SAM 9460 | E | B | 4,0 | — | — | — | — |
| MNHN 1908-32-22 | — | B | 4,2 | 5,6 | — | — | — |
| MNHN 1908-21-2/7 | — | B | 4,2 | 5,7 | — | — | — |
| MNHN 1908-21-5 | — | B | 4,4 | — | 4,0 | 6,0 | 9,0 |
| MNHN 1908-32-99 | — | B | 4,8 | — | — | — | — |
| MNHN 1908-32-1 | — | B | 4,8 | 7,8 | — | — | — |
| MNHN 1908-32-64/73 | — | B | 4,9e | — | 4,9 | 10,0 | 10,5 |
| MNHN 1908-32-77 | — | B | 4,9 | — | 4,9 | 8,5 | 10,7 |
| MNHN 1925-5-28 | E | C | 5,0 | 6,7 | — | — | — |
| MNHN 1925-5-41 | E | C | 5,0 | — | 4,9 | 9,8 | 11,2 |
| MNHN 1925-5-60 | E | C | 5,4 | — | — | — | — |
| MNHN 1908-32-23 | — | C | 5,5 | — | — | — | — |
| SAM 9459 | E | C | 5,9c | — | — | — | — |
| MNHN 1925-5-34 | — | D | 6,4 | — | — | — | — |
| MNHN 1925-5-31 | — | F | 8,5c | — | — | — | — |
| MNHN 1908-32-25 | — | F | 8,5 | — | — | — | — |
| MNHN 1908-21-18 | — | F | 8,6 | — | — | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | F | 8,6c | — | — | — | — |
| MNHN R146 | — | F | 8,7 | 14,0 | — | — | — |
| MNHN 1908-32-24 | — | F | 8,7 | 14,8 | — | — | — |
| MNHN 1908-21-24 | — | F | 8,8c | — | — | — | — |
| MNHN 1908-32-58 | — | F | 8,8 | — | 8,8 | 18,0 | — |
| MNHN 1925-5-50 | B | G | 9,0c | — | — | — | — |
| MNHN 1925-5-56 | B | G | 9,0 | — | — | — | — |
| MNHN 1908-32-67 | — | G | 9,0 | — | — | — | — |
| MNHN 1925-5-12 | E | D | 6,7 | — | — | — | — |
| MNHN 1925-5-29 | E | D | 6,9 | — | — | — | — |
| SAM 6231 | T | E | 6,6 | — | — | — | — |
| MNHN 1925-5-38 | B | E | 7,5 | — | — | — | — |
| MNHN 1925-5-49 | E | E | 7,6e | — | — | — | — |
| MNHN 1908-32-26 | — | E | 7,7e | — | — | — | — |
| MNHN 1908-21-12 | — | F | 8,0e | — | 8,0 | 16,0 | — |
| SAM 6232 | T | F | 8,0 | — | — | — | — |
| MNHN 1925-5-32 | — | F | 7,9+ | — | — | — | — |
| MNHN R147 | — | F | 8,1e | — | — | — | — |
| MNHN 1908-21-16 | — | F | 8,2 | — | — | — | — |
| MNHN 1908-32-59 | — | F | 8,2 | 12,3 | — | — | — |
| SAM 9457 | E | G | 9,1c | — | — | — | — |
| MNHN 1925-5-54 | — | G | 9,1c | — | — | — | — |
| MNHN 1908-32-38 | — | G | 9,1c | — | — | — | — |
| MNHN 1908-21-6 | — | G | 9,2 | — | — | — | — |
| MNHN 1908-32-45 | — | G | 9,2 | 14,7 | — | — | — |
| MNHN 1925-5-46 | V | G | 9,2c | — | — | — | — |
| SAM 9461 | E | G | 9,3 | — | — | — | — |
| MNHN 1908-21-14 | — | G | 9,3e | — | 8,2 | 17,0 | 21,0 |
| MNHN 1908-32-60 | — | G | 9,3 | — | — | — | — |
| MNHN 1908-32-49 | — | G | 9,5e | — | — | — | — |
| MNHN 1908-21-19 | — | G | 9,6 | 14,8 | — | — | — |
| MNHN 1925-5-36 | V | G | 10,5c | — | — | — | — |

| Specimen number | Clavicle h | Clavicle w | Clavicle A | Interclavicle l | Interclavicle Head width | Sternum l | Sternum Width ($x\frac{1}{2}$) |
|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | — | — | — | — | — |
| MNHN 1925-5-20 | — | — | — | — | — | — | — |
| MNHN 1925-5-27 | — | — | — | — | — | — | — |
| MNHN 1908-21-8 | 10,0 | 7,0 | 12,0 | — | — | 5,8 | 3,3 |
| MNHN 1925-5-25 | — | — | — | — | — | — | — |
| MNHN 1908-32-29 | — | — | — | — | — | 5,5 | 4,0 |
| MNHN 1925-5-18 | — | — | — | — | — | — | — |
| MNHN 1908-32-21 | — | — | — | — | — | — | — |
| MNHN 1925-5-30 | — | — | — | — | — | 7,5 | 5,1 |
| MNHN 1908-32-4 | — | — | — | — | — | 10,3 | 7,4 |
| SAM 9460 | — | — | — | — | — | — | — |
| MNHN 1908-32-22 | — | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | — | — | — | — | — | 8,0 | 6,0 |
| MNHN 1908-21-5 | — | — | — | — | — | — | — |
| MNHN 1908-32-99 | 14,0 | 13,0 | 18,0 | — | — | — | — |
| MNH 1908-32-1 | 14e | — | 16e | 39,5 | 12,3 | — | — |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | — | — | — | — | — | 12,5 | 8,8 |
| MNHN 1925-5-28 | — | — | — | — | — | — | — |
| MNHN 1925-5-41 | — | — | — | — | — | — | — |
| MNHN 1925-5-60 | — | — | — | — | — | — | — |
| MNHN 1908-32-23 | 17,0 | 17,5 | 20,0 | 41,0 | 15,0 | 16,3 | 11,2 |
| SAM 9459 | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | 20,5 | 16,0 | 23,5 | — | — | — | — |
| MNHN 1925-5-12 | — | — | — | — | — | 25,0 | 19,5 |
| MNHN 1925-5-29 | — | — | — | — | — | 21,0 | 14,0 |
| SAM 6231 | — | — | — | 49,0 | 14– | 21,8 | 12,6 |
| MNHN 1925-5-38 | — | — | — | 50,0 | 19,4 | — | 21,0 |
| MNHN 1925-5-49 | — | 18,0 | — | — | — | — | — |
| MNHN 1908-32-26 | — | 16,0 | — | 52e | 17,0 | 29,0 | 16,5 |
| MNHN 1908-21-12 | — | — | — | — | — | — | — |
| SAM 6232 | — | — | — | — | — | 30,3 | 14,6 |
| MNHN 1925-5-32 | — | — | — | — | — | — | — |
| MNHN R147 | 18,5 | — | — | 54e | 20,0 | 34,1 | 20,0 |
| MNHN 1908-21-16 | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | — | — | — | — | — | 31,0 | 20,0 |
| MNHN 1925-5-31 | — | — | — | — | — | — | — |
| MNHN 1908-32-25 | — | — | — | — | — | 28,5 | 18,0 |
| MNHN 1908-21-18 | — | — | — | — | — | 37,5 | 23,0 |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — | — | — | — |
| MNHN R146 | — | — | — | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — | — | — | 18,0 |
| MNHN 1908-21-24 | — | — | — | — | — | — | 21,0 |
| MNHN 1908-32-58 | — | — | — | — | — | — | — |
| MNHN 1925-5-50 | — | — | — | — | — | — | — |
| MNHN 1925-5-56 | — | — | — | — | — | — | — |
| MNHN 1908-32-67 | — | — | — | — | 21e | 33,5 | 21,0 |
| SAM 9457 | — | — | — | — | — | — | — |
| MNHN 1925-5-54 | — | 21+ | — | 59,5 | 21,5 | — | 20,0 |
| MNHN 1908-32-38 | — | — | — | — | — | 41,0 | 21,0 |
| MNHN 1908-21-6 | — | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | — | — |
| MNHN 1925-5-46 | — | — | — | — | — | — | — |
| SAM 9461 | — | — | — | — | — | — | 27,0 |
| MNHN 1908-21-14 | — | — | — | — | — | — | — |
| MNHN 1908-32-60 | — | — | — | — | — | 32,5– | — |
| MNHN 1908-32-49 | — | — | — | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — | — |

| Specimen number | Scapula l | Scapula h | Coracoid l | Coracoid h | Humerus l | Humerus pw | Humerus sw | Humerus dw |
|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-20 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-27 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-8 | — | — | 4,7 | 3,6 | 11,0 | 4,2 | 3,2 | 5,9 |
| MNHN 1925-5-25 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-29 | — | — | — | — | — | — | 3,2 | 6,0 |
| MNHN 1925-5-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-21 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-30 | 7,2 | 7,0 | 7,1 | 6,6 | 16,0 | 4,5 | 4,5 | 6,5 |
| MNHN 1908-32-4 | — | — | — | — | 15,6 | 4,9 | 3,5 | 6,8 |
| SAM 9460 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-22 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-2/7 | 8,5 | 9,0 | 8,0 | 6,9 | 17,5 | 5,0 | 4,6 | 7,3 |
| MNHN 1908-21-5 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-99 | 10,8 | 10,5 | — | — | 20,0 | — | 4,2 | 8,6 |
| MNHN 1908-32-1 | 13,0 | — | — | — | 21,5 | 7,0 | 6,0 | 9,2 |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | — | — | — | — | 24,0 | 7,4 | 6,5 | 11,0 |
| MNHN 1925-5-28 | — | — | — | — | 22,5 | 7,5 | 5,5 | 8,5 |
| MNHN 1925-5-41 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-60 | — | — | — | — | — | — | — | 10,5 |
| MNHN 1908-32-23 | 12,5 | 14,5 | 12,5 | 10,0 | 25,3 | 8,0 | 6,9 | 11,5 |
| SAM 9459 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | — | — | — | — | — | — | — | 18,6 |
| MNHN 1925-5-12 | — | — | — | — | 35,5 | 10,5 | 9,2 | 17,0 |
| MNHN 1925-5-29 | — | — | — | — | 36,0 | 8,7 | 7,5 | 16,5 |
| SAM 6231 | — | — | 25,3 | — | 36,0 | — | 8,3 | 15,8 |
| MNHN 1925-5-38 | — | — | 45,0 | 23,0 | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | 24,0 | — | 12,2 | 8,0 | — |
| MNHN 1908-32-26 | — | — | 33,5 | 18,0 | 45,0 | 13,5 | 10,0 | 18,5 |
| MNHN 1908-21-12 | — | — | — | — | — | — | — | — |
| SAM 6232 | — | — | 31,7 | 17,8 | 48,5 | — | 12,0 | 20,3 |
| MNHN 1925-5-32 | — | — | — | — | — | — | — | — |
| MNHN R147 | 32,0 | 45,0 | 42,0 | 24,5 | 60,0 | 14,0 | — | 23,0 |
| MNHN 1908-21-16 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | — | — | — | — | 55,0 | — | 12,0 | — |
| MNHN 1925-5-31 | — | — | — | — | — | — | — | 24,0 |
| MNHN 1908-32-25 | — | — | 35,0 | 19,8 | 54,0 | 13,7 | 11,5 | 20,5 |
| MNHN 1908-21-18 | — | — | — | 27.0 | 62,0 | 19,5 | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — | — | — | — | 22,0 |
| MNHN R146 | — | — | — | — | — | — | — | — |

(Table 1 cont.)

| Specimen number | Scapula l | Scapula h | Coracoid l | Coracoid h | Humerus l | Humerus pw | Humerus sw | Humerus dw |
|---|---|---|---|---|---|---|---|---|
| MNHN 1908-32-24 | — | — | — | — | 54,0 | 13,5 | 11,0 | 21,8 |
| MNHN 1908-21-24 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-50 | — | — | — | — | 55+ | — | 14,0 | 28,0 |
| MNHN 1925-5-56 | — | — | — | 26,0 | 61,0 | — | 13,2 | 26,2 |
| MNHN 1908-32-67 | — | — | 47,5 | 26,0 | 66,0 | 20,7 | 9,5 | 26,2 |
| SAM 9457 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-54 | — | — | 45,0 | 25+ | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-46 | — | — | — | — | 55? | 18? | 14,5 | 30,0 |
| SAM 9461 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-60 | — | — | — | — | 64,0 | 20,0 | 15,5 | 29,5 |
| MNHN 1908-32-49 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — | 14,8 | — |

| Specimen number | Radius l | Radius pw | Radius sw | Radius dw | Ulna l | Ulna pw | Ulna sw | Ulna dw |
|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 8,5 | — | 1,1 | 1,4 | 7,6 | 2,4 | 1,2 | 1,8 |
| MNHN 1925-5-20 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-27 | — | — | — | — | — | — | — | 1,8 |
| MNHN 1908-21-8 | 7,9 | 2,4 | 1,4 | 1,9 | 7,2 | 2,5 | 1,4 | 2,0 |
| MNHN 1925-5-25 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-29 | 8,5 | 2,0 | 1,4 | 2,0 | 7,5 | 2,2 | 1,4 | 2,0 |
| MNHN 1925-5-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-21 | — | — | — | 1,9 | — | — | — | 2,0 |
| MNHN 1925-5-30 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-4 | 10,9 | 2,7 | 1,8 | 2,5 | 10,0 | 3,0 | 1,8 | 2,9 |
| SAM 9460 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-22 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | 11,6 | 3,0 | 1,9 | 2,3 | 10,5 | 3,0 | 1,9 | 2,4 |
| MNHN 1908-21-5 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-99 | — | 3,3 | 2,1 | — | 13,5 | 3,5 | 2,0 | — |
| MNHN 1908-32-1 | 14,5 | 4,2 | 2,7 | 3,0 | 13,5 | 3,8 | 2,6 | 3,7 |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | 15,5 | 4,4 | 2,5 | 3,6 | 14,1 | 4,3 | 2.5 | 4,0 |
| MNHN 1925-5-28 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-41 | — | — | — | — | — | — | — | - |
| MNHN 1925-5-60 | 18,5 | 4,2 | 2,2 | 2,9 | — | — | — | — |
| MNHN 1908-32-23 | 17,0 | 4,1 | 3,0 | 3,2 | 16,0 | 4,9 | 2,7 | 3,9 |
| SAM 9459 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-12 | 22,0 | 5,3 | 3,7 | 4,6 | 20,0 | 6,8 | 3,2 | 6,5 |
| MNHN 1925-5-29 | 23,5 | 6,0 | 3,8 | 4,0 | 21,3 | 6,0 | 3,4 | 5,0 |
| SAM 6231 | 21,6 | 5,7 | 3,4 | 5,1 | 21,0 | 5,8 | 3,1 | 4,9 |
| MNHN 1925-5-38 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-26 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-12 | — | — | — | — | — | — | — | — |
| SAM 6232 | 29,0 | 8,0 | 4,6 | 5,9 | 28,0 | 7,4 | 4,6 | — |
| MNHN 1925-5-32 | — | — | — | — | — | — | — | — |
| MNHN R147 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | 31e | — | — | 5,0 | 29,1 | 9,3 | 4,0 | 8,0 |
| MNHN 1925-5-31 | 31,0 | 6,8 | 5,5 | 6,5 | 31,0 | 9,5 | 4,2 | 7,3 |
| MNHN 1908-32-25 | — | — | — | — | — | 9,0 | — | — |
| MNHN 1908-21-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-68/1925-8-14 | — | — | — | — | — | — | — | — |
| MNHN R146 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — | 31,0 | 8,5 | 4,7 | — |
| MNHN 1908-21-24 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-50 | 28,5 | 8,9 | — | — | 29,0 | 9,8 | 5,6 | 8,2 |
| MNHN 1925-5-56 | 32,0 | 9,5 | 6,0 | 7,0 | — | 10,0 | 6,2 | — |
| MNHN 1908-32-67 | — | 10,2 | 6,0 | — | 33,0 | 11,5 | 5,2 | 10,1 |
| SAM 9457 | — | — | — | — | — | — | 4,2 | 8,9 |
| MNHN 1925-5-54 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-46 | — | — | 6,5 | — | — | — | 4,0 | — |
| SAM 9461 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-60 | — | — | 6,2 | — | 35,5 | 9,0 | 6,0 | 10,0 |
| MNHN 1908-32-49 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — | — | — |

| Specimen number | Metac. IV | Digit IV | Ilium blade l | Ilium base l | Pubis l | Pubis h | Ischium l | Ischium h |
|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 2,8 | — | 9,6 | 5,5 | 5,2 | 6,5 | 6,9 | 6,0 |
| MNHN 1925-5-20 | — | — | 9,9 | 5,0 | — | — | — | — |
| MNHN 1925-5-27 | 3,2 | 8,8 | — | — | — | — | — | — |
| MNHN 1908-21-8 | 2,5 | 7,0 | — | 5,4 | 5,0 | 7,0 | 7,3 | 6,2 |
| MNHN 1925-5-25 | — | — | — | — | 5,5 | 6,0 | 6,7 | 6,0 |
| MNHN 1908-32-29 | 2,9 | 8e | — | — | 6,5 | 6,8 | 7,2 | 6,2 |
| MNHN 1925-5-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-21 | 3,2 | 9,9 | 12,0 | 6,3 | — | — | — | — |
| MNHN 1925-5-30 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-4 | 3,9 | 12,0 | 13,3 | — | 6,9 | 8,7 | 8,9 | 7,7 |
| SAM 9460 | — | — | 14,0 | 7,3 | 7,8 | 9,2 | 9,5 | 8,4 |
| MNHN 1908-32-22 | — | — | 12,3 | 6,3 | 7,9 | 9,0 | 10,0 | 7,9 |
| MNHN 1908-21-2/7 | 4,0 | 12,3 | 13,2 | 7,0 | 7,9 | 9,0 | 10,5 | 8,0 |
| MNHN 1908-21-5 | — | — | 14,0 | 7,0 | 8,7 | 10,0 | 10,3 | 8,3 |
| MNHN 1908-32-99 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-1 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | 5,0 | — | 16,5 | 8,9 | 9,6 | 10,6 | 12,4 | 10,2 |
| MNHN 1925-5-28 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-41 | — | — | 16,5 | — | — | — | — | — |
| MNHN 1925-5-60 | — | 19,6 | — | — | — | — | — | — |
| MNHN 1908-32-23 | 6,1 | 17,2 | — | — | — | — | — | — |
| SAM 9459 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-12 | 8,2 | — | — | — | — | — | — | — |
| MNHN 1925-5-29 | 8,5 | 22,3 | — | — | — | — | — | — |
| SAM 6231 | 8,0 | 21,0 | 23,0 | — | — | — | — | — |
| MNHN 1925-5-38 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-26 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-12 | — | — | — | — | — | — | — | — |
| SAM 6232 | — | — | — | — | 14,7 | — | 19,6 | — |
| MNHN 1925-5-32 | — | — | — | — | — | — | 21,0 | 19,0 |
| MNHN R147 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — | 20,7 | 26,0 | — | — |
| MNHN 1908-32-59 | 10,1 | 28,9 | — | — | — | — | — | — |
| MNHN 1925-5-31 | 10,5 | 30,3 | — | — | — | — | — | — |
| MNHN 1908-32-25 | — | 29,2e | — | — | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-68/1925-8-14 | — | — | — | — | — | — | — | — |
| MNHN R146 | — | — | 30,5 | 16,2 | — | — | — | — |
| MNHN 1908-32-24 | — | — | 30,5 | — | — | — | — | — |
| MNHN 1908-21-24 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-50 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-56 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-67 | — | — | — | — | — | — | — | — |
| SAM 9457 | 10,5 | — | — | — | — | — | — | — |
| MNHN 1925-5-54 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | 29e | — | — | 20,0 | 23,0 | — | — |
| MNHN 1908-32-45 | — | — | 31,0 | 18,5 | 20,5 | 25,5 | 27,0 | 22,0 |
| MNHN 1925-5-46 | — | — | — | — | — | — | — | — |
| SAM 9461 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-60 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-49 | — | — | 32,0 | — | 22,5 | 29,0 | 28,0 | 24,0 |
| MNHN 1908-21-19 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — | — | — |

| Specimen number | Femur l | Femur pw | Femur sw | Femur dw | Tibia l | Tibia pw | Tibia sw | Tibia dw |
|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 15,0 | 3,2 | 2,2 | 2,8 | 13,1 | 2,2 | 1,7 | 2,1 |
| MNHN 1925-5-20 | — | 3,0 | 2,0 | — | — | — | 1,2 | 2,0 |
| MNHN 1925-5-27 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-8 | 13,5 | 4,0 | 2,3 | 3,5 | 11,3 | 2,6 | 1,7 | 2,5 |
| MNHN 1925-5-25 | 14,5 | 2,8 | 2,0 | 3,3 | 12,6 | 2,4 | 1,5 | 2,0 |
| MNHN 1908-32-29 | 15,5 | 4,0 | 2,5 | 3,2 | 13,5 | — | 1,8 | 2,3 |
| MNHN 1925-5-18 | 17,0 | 3,9 | 2,3 | 3,0 | 14,1 | 2,6 | 1,7 | 3,0 |
| MNHN 1908-32-21 | 17,5 | 4,1 | 2,5 | 4,0 | 15,1 | 3,2 | 2,0 | 3,2 |
| MNHN 1925-5-30 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-4 | 17,7 | 4,7 | 2,8 | 4,0 | 15,9 | 3,4 | 1,8 | 2,7 |
| SAM 9460 | 20,8 | 4,6 | 2,8 | 4,0 | 19,0 | — | 2,4 | 3,5 |
| MNHN 1908-32-22 | 19,5 | 4,6 | 2,3 | 3,7 | — | 3,2 | 1,7 | — |
| MNHN 1908-21-2/7 | 20,7 | 5,0 | 3,0 | 3,8 | 17,3 | 3,9 | 2,0 | 3,3 |
| MNHN 1908-21-5 | 23,3 | 4,5 | 3,2 | 4,5 | 20,6 | 4,0 | 2,6 | 4,0 |
| MNHN 1908-32-99 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-1 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | 27,0 | 6,0 | 4,0 | 5,0 | 23,9 | 5,0e | 3,0 | 4,2 |
| MNHN 1925-5-28 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-41 | 26,5 | 5,5 | 4,2 | 4,5 | 23,0 | 4,7 | 3,2 | 4,8 |
| MNHN 1925-5-60 | 33,0 | 7,5 | 3,5 | 5,2 | 27,8 | 7,0 | 2,8 | 4,0 |
| MNHN 1908-32-23 | — | — | — | — | — | — | — | — |
| SAM 9459 | 30,5 | 7,8 | 4,5 | — | 26,0 | 6,0 | 3,0 | 4,7 |
| MNHN 1925-5-34 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-12 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-29 | — | — | — | — | — | — | — | — |
| SAM 6231 | 39,0 | 8,0 | 5,9 | 7,3 | 34,0 | 6,0 | 4,5 | 5,4 |
| MNHN 1925-5-38 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-26 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-12 | 50,0 | 11,5 | 6,0 | (13,0) | — | — | — | — |
| SAM 6232 | 47,2 | 11,0 | 6,2 | 8,5 | 40,0 | 7,5e | 5,2 | 6,9 |
| MNHN 1925-5-32 | — | 12,0 | 6,2 | — | — | — | 4,9 | 7,0 |
| MNHN R147 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | — | — | — | — | — | — | — | — |

(Table 1 cont.)

| Specimen number | Femur l | pw | sw | dw | Tibia l | pw | sw | dw |
|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-31 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-25 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-68/ 1925-9-14 | — | — | — | — | — | — | — | — |
| MNHN R146 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-24 | — | 9,7 | 6,8 | 8,0 | 46,0 | — | — | 7,8 |
| MNHN 1908-21-24 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-50 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-56 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-67 | — | — | — | — | — | — | — | — |
| SAM 9457 | — | — | 7,3 | 10,0 | — | 10,5 | — | — |
| MNHN 1925-5-54 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-46 | — | — | — | — | — | — | — | — |
| SAM 9461 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | 51,0 | 10,0 | 5,4 | 10,0 |
| MNHN 1908-32-60 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-49 | 60e | 15,5 | 8,5 | — | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — | — | — |

| Specimen number | Fibula l | pw | sw | dw | Metat. IV | Digit IV (Pes) |
|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 12,0 | — | 1,2 | 1,6 | 6,4 | — |
| MNHN 1925-5-20 | 12,5 | — | 1,2 | 1,6 | 6,2 | 11,2 |
| MNHN 1925-5-27 | — | — | — | — | — | — |
| MNHN 1908-21-8 | 10,5 | — | 1,2 | 1,7 | 5,1 | 10,4 |
| MNHN 1925-5-25 | — | — | 1,1 | 1,7 | 6,4 | — |
| MNHN 1908-32-29 | 13,0 | 1,3 | 1,2 | 1,7 | 6,1 | 10,8 |
| MNHN 1925-5-18 | 13,2 | — | 1,3 | — | 7,2 | — |
| MNHN 1908-32-21 | 13,1 | 1,7 | 1,4 | 2,1 | 7,3 | 13,3 |
| MNHN 1925-5-30 | — | — | — | — | — | — |
| MNHN 1908-32-4 | 14,6 | — | 1,4 | 2,3 | — | — |
| SAM 9460 | — | — | — | — | — | — |
| MNHN 1908-32-22 | — | 1,9 | 1,6 | — | — | — |
| MNHN 1908-21-2/7 | 15,7 | — | 1,6 | 2,7 | 8,6 | 17,2 |
| MNHN 1908-21-5 | 18,5 | 2,3 | 1,9 | 2,9 | 9,6 | 20,2 |
| MNHN 1908-32-99 | — | — | — | — | — | — |
| MNHN 1908-32-1 | — | — | — | — | — | — |
| MNHN 1908-32-64/73 | — | — | — | — | — | — |
| MNHN 1908-32-77 | 21,5 | — | 1,8 | 3,4 | 11,3 | 21,7 |
| MNHN 1925-5-28 | — | — | — | — | — | — |
| MNHN 1925-5-41 | 21,5 | 2,9 | 2,2 | 3,6 | 11,5 | 22,4 |
| MNHN 1925-5-60 | — | — | 2,1 | — | — | — |
| MNHN 1908-32-23 | — | — | — | — | — | — |
| SAM 9459 | — | — | 2,1 | 3,6 | — | — |
| MNHN 1925-5-34 | — | — | — | — | — | — |
| MNHN 1925-5-12 | — | — | — | — | — | — |
| MNHN 1925-5-29 | — | — | — | — | — | — |
| SAM 6231 | 31,0 | — | 3,2 | 4,3 | 17,4 | 32,2 |
| MNHN 1925-5-38 | — | — | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | — | — | — |
| MNHN 1908-32-26 | — | — | — | — | — | — |
| MNHN 1908-21-12 | — | — | — | — | — | — |
| SAM 6232 | 37,0 | — | 3,7 | 5,5e | 20,5 | 37,1 |
| MNHN 1925-5-32 | — | — | 3,5 | 6,5 | 21,2 | 42,1e |
| MNHN R147 | — | — | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — | — | — |
| MNHN 1908-32-59 | — | — | — | — | — | — |
| MNHN 1925-5-31 | — | — | — | — | — | — |
| MNHN 1908-32-25 | — | — | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — | 24,0 | — |
| MNHN R146 | — | — | — | — | — | — |
| MNHN 1908-32-24 | 44,0 | 4,0 | 4,0 | 5,7 | 24,7 | — |
| MNHN 1908-21-24 | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — |
| MNHN 1925-5-50 | — | — | — | — | — | — |
| MNHN 1925-5-56 | — | — | — | — | — | — |

| Specimen number | Fibula l | pw | sw | dw | Metat. IV | Digit IV (Pes) |
|---|---|---|---|---|---|---|
| MNHN 1908-32-67 | — | — | — | — | — | — |
| SAM 9457 | 42,0 | — | 3,8 | 8,5 | — | — |
| MNHN 1925-5-54 | — | — | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | — |
| MNHN 1925-5-46 | — | — | — | — | — | — |
| SAM 9461 | — | — | — | — | — | — |
| MNHN 1908-21-14 | 46,6 | 5,7 | 4,3 | 8,2 | — | — |
| MNHN 1908-32-60 | — | — | — | — | — | — |
| MNHN 1908-32-49 | — | — | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — | — | — |

| Specimen number | Proportions hum/fem | rad/hum | tib/fem | rad/tib |
|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | 0,87 | 0,65 |
| MNHN 1925-5-20 | — | — | — | — |
| MNHN 1925-5-27 | — | — | — | — |
| MNHN 1908-21-8 | 0,81 | 0,72 | 0,84 | 0,70 |
| MNHN 1925-5-25 | — | — | 0,87 | — |
| MNHN 1908-32-29 | — | — | 0,87 | 0,63 |
| MNHN 1925-5-18 | — | — | 0,83 | — |
| MNHN 1908-32-21 | — | — | 0,86 | — |
| MNHN 1925-5-30 | — | — | — | — |
| MNHN 1908-32-4 | 0,88 | 0,70 | 0,90 | 0,69 |
| SAM 9460 | — | — | 0,91 | — |
| MNHN 1908-32-22 | — | — | — | — |
| MNHN 1908-21-2/7 | 0,85 | 0,66 | 0,84 | 0,67 |
| MNHN 1908-21-5 | — | — | 0,88 | — |
| MNHN 1908-32-99 | — | — | — | — |
| MNHN 1908-21-1 | — | 0,67 | — | — |
| MNHN 1908-32-64/73 | — | — | — | — |
| MNHN 1908-32-77 | 0,89 | 0,65 | 0,89 | 0,65 |
| MNHN 1925-5-28 | — | — | — | — |
| MNHN 1925-5-41 | — | — | 0,87 | — |
| MNHN 1925-5-60 | — | — | 0,84 | 0,67 |
| MNHN 1908-32-23 | — | 0,67 | — | — |
| SAM 9459 | — | — | 0,85 | — |
| MNHN 1925-5-34 | — | — | — | — |
| MNHN 1925-5-12 | — | 0,62 | — | — |
| MNHN 1925-5-29 | — | 0,65 | — | — |
| SAM 6231 | 0,92 | 0,60 | 0,87 | 0,64 |
| MNHN 1925-5-38 | — | — | — | — |
| MNHN 1925-5-49 | — | — | — | — |
| MNHN 1908-32-26 | — | — | — | — |
| MNHN 1908-21-12 | — | — | — | — |
| SAM 6232 | 1,00 | 0,62 | 0,85 | 0,73 |
| MNHN 1925-5-32 | — | — | — | — |
| MNHN R147 | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — |
| MNHN 1908-32-59 | — | 0,56 | — | — |
| MNHN 1925-5-31 | — | — | — | — |
| MNHN 1908-32-25 | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — |
| MNHN R146 | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — |
| MNHN 1908-21-24 | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — |
| MNHN 1925-5-50 | — | 0,52 | — | — |
| MNHN 1925-5-56 | — | 0,52 | — | — |
| MNHN 1908-32-67 | — | — | — | — |
| SAM 9457 | — | — | — | — |
| MNHN 1925-5-54 | — | — | — | — |
| MNHN 1908-32-38 | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — |
| MNHN 1925-5-46 | — | — | — | — |
| SAM 9461 | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — |
| MNHN 1908-32-60 | — | — | — | — |
| MNHN 1908-32-49 | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — |
| MNHN 1925-5-36 | — | — | — | — |

length within the first year of life, the smallest specimens would have been less than one year old.

For convenience of reference, the series of *Hovasaurus* specimens has been subdivided into life stages A to G on the basis of vertebral length (table 1). In most cases these do not correspond to life stages A to E used by Piveteau (1926) and Haughton (1930), which were based on an irregular size progression representing only the early stages of the life history.

*Thadeosaurus*, a closely related genus, is known from a smaller number of specimens. However, essentially the same range of life stages is represented. This provides a unique opportunity to study differences in allometric growth, relative dimensions, and variability in closely related Permian genera that exploited different ecosystems.

## DISTRIBUTION OF *HOVASAURUS*

During the Late Permian, the known sites for

tangasaurid eosuchians in Madagascar, Tanzania and Kenya were geographically close (fig. 1a). *Tangasaurus* and *Kenyasaurus* are known from only one site each, whereas fossil reptiles are known from many Upper Permian sites in Madagascar (fig. 1c). The precise location of Colcanap's discoveries is unknown; there are discrepancies between locality names in the catalogues and the literature, and reptiles from some sites have been misidentified. It is important to clear up some of these problems if we are to interpret the depositional environment that contributed to the preservation of the tangasaurids of Madagascar, and to understand the palaeoecology of the Lower Sakamena environments.

The first collection made by Colcanap includes the tangasaurid *Thadeosaurus* associated with *Glossopteris*, *Atherstonia*, *Coelurosauravus* and *Daedalosaurus*. This material probably came from a single site in the Sakamena River Valley, but not Mt. Eliva as Piveteau (1926) assumed. The absence of *Hovasaurus* is noteworthy because both *Atherstonia* and *Glossopteris* are found with *Hovasaurus* at Mt. Eliva, suggesting that both sites are probably synchronous. A single rib of *Daedalosaurus* was found in a nodule with a skeleton of *Claudiosaurus* near Ranohira, but *Thadeosaurus* and *Coelurosauravus* have not been found in any other localities.

Piveteau collected more than 200 fossils in 1925 from the Permian beds between Mt. Eliva and Ranohira. The Paris catalogues state that 40 specimens were collected near the village of Besakoa on the lower course of the Sakamena River, 45 specimens were from the lower course of the Ianapera near the village of Vohibory, 60 were from Mt. Eliva, and 30 from the Imaloto River near Ampasindrasoa and Ranohira. However, Piveteau (1926) only mentions Mt. Eliva and shows neither Besakoa nor Vohibory on his maps. Villages of these names are not marked on any recent maps of the lower courses of the Sakamena or Ianapera rivers. It seems possible that all of Piveteau's specimens were recovered from the Mt. Eliva region and that the catalogues are in error. There are two reasons for this assumption. The lower course of the Sakamena passes through Lower Triassic beds where one would not expect to find *Hovasaurus*. Although the Lower Sakamena Formation is exposed along the lower courses of the Ianapera River, only disarticulated bones were found there by Tortochaux (1950).

A large number of disarticulated bones were collected from numerous sites in the Lower Sakamena Formation by Tortochaux (1950). Most were identified as *Tangasaurus* and *Hovasaurus* on the basis of erroneous criteria, and the identifications have been published by Tortochaux (1949), Besairie (1971) and others. Because the identifications of the specimens are questionable and their present location unknown, most localities cited by Tortochaux are meaningless.

The most common eosuchian in the Lower Sakamena Formation is *Hovasaurus*. Colcanap collected many specimens of this genus somewhere in the Sakamena Valley in 1908, Piveteau recovered more from the foot of Mt. Eliva and about a kilometre to the west of the rest-stop named Sakamena in 1925, and Besairie collected at least eight from Mt. Eliva between 1926 and 1929.

Near Ranohira (fig. 1), west of the junction of the Beroroha–Ihosy routes, there is a bed of siltstone nodules containing reptile and plant remains. The bed was first noticed by Gence in 1938 (Tortochaux 1950). Quartz pebbles are found in the abdominal region of the partial skeletons. The sternum is ossified, the humerus is curved with a greatly enlarged distal end, and the tail is specialized for swimming; these features are all typical of *Hovasaurus*.

A specimen of *Hovasaurus* (AMNH 5333) collected at Kalivari on Madagascar is in the collections of the American Museum of Natural History. Kalivari is not on any of the maps of Madagascar that I have access to, and the specimen has no other information.

## PALAEOECOLOGY OF TANGASAURIDS

The known fauna and flora of the Lower Sakamena Formation are summarized in Appendix I. The specimens were collected from strata representing many different depositional environments. The formation is extensive, both horizontally and vertically. The number of specimens collected from each site and the associated data are usually inadequate. Even so, faunal differences can be seen at different sites.

Many plant genera considered typical of the *Glossopteris* flora of the southern hemisphere have not been found in Madagascar, and the flora lacks variety. The low diversity and the presence of growth rings in silicified wood suggests seasonal variability. Seasonal stress is expected because the study area was located at a high latitude, 60°S during Permian times (Bambach *et al.* 1980).

The remains of reptiles are the most commonly preserved vertebrate fossils in the Lower Sakamena Formation. The reptile fauna, dominated by eosuchians, strongly contrasts with the contemporary faunas of South Africa where therapsids are the dominant vertebrates. For a long time it seemed that therapsids were not present in Madagascar, but a single vertebra was recovered recently from the red beds of the underlying Sakoa Formation (Besairie 1971). A number of isolated therapsid bones were found in collections from the Lower Sakamena Formation of the Benenitra region (Carroll, pers. comm., 1975). These have been tentatively identified as a dicynodont vertebra and tusk, and the anterior end of the dentary of a carnivorous therapsid. It appears highly probable that the rarity of therapsids in the Lower Sakamena can be attributed to a different habitat from that represented by the Karoo System of South Africa.

The osteology of *Thadeosaurus* and its association with *Coelurosauravus* and the gliding reptile *Daedalosaurus* suggests that this animal could have been

terrestrial. Fish remains found at the site show that the depositional environment was aqueous, but the articulated nature of the terrestrial specimens suggests that it was not far from land. The absence of the aquatic tangasaurid *Hovasaurus* is interesting because it appears to have been a contemporary of *Thadeosaurus* (both genera are associated with *Glossopteris* and *Atherstonia)*.

*Hovasaurus* is common in Lower Sakamena strata at Mt. Eliva, and is probably also present at a site near Ranohira. At this time, it can be associated with only two other animals from the Sakamena River Valley — one specimen of the palaeoniscoid fish *Atherstonia* and a single specimen of the eosuchian *Acerosodontosaurus* (Currie 1980).

The remains of *Claudiosaurus* (Carroll 1981) are common at Benenitra and Leoposa, and one specimen was found near Ranohira. Because *Acerosodontosaurus* is associated with both *Claudiosaurus* and *Hovasaurus,* it seems likely that the latter two genera were contemporaries. This view is supported by the fact that *Claudiosaurus* fossils have been found at stratigraphic levels above and below the *Hovasaurus* level at Ranohira. The apparent absence of *Hovasaurus* from sites where *Claudiosaurus* is abundant implies that these two swimming reptiles inhabited two distinct aquatic environments in the same general region during early Sakamena times.

Clearly any conclusions about Lower Sakamena despositional environments and palaeoecology are speculative at this time. The data suggest at least four distinct palaeoenvironments distinguished by the following faunal associations:

1. Marine invertebrates. No identifiable reptiles.
2. Dominated by terrestrial reptiles *(Thadeosaurus, Daedalosaurus, Coelurosauravus)*. The palaeoniscoid *Atherstonia* makes up 25 per cent of the specimens.
3. Strongly dominated by *Hovasaurus* (97–99 per cent). *Acerosodontosaurus* and *Atherstonia* present.
4. Dominated by *Claudiosaurus*. Associated terrestrial elements include *Acerosodontosaurus, Daedalosaurus* and therapsids.

Fieldwork concentrating on the detailed stratigraphy, taphonomy and palynology of fossiliferous sites is necessary to confirm the significance of these associations.

## MEASUREMENTS

Specimens of *Acerosodontosaurus, Thadeosaurus* and *Hovasaurus* are preserved in siltstone nodules with calcareous, siliceous cement (Tortochaux 1950). When collected, most of the bone had eroded out of the split nodules, leaving only the natural moulds of the bones in the counterpart blocks. High fidelity latex or silicone rubber casts were made from the moulds as an aid in studying the specimens. All measurements were taken from the casts for consistent results, even though the nodules were available for some of the specimens. A hundred comparative measurements were made between the original specimens and casts to determine how much shrinkage had occurred in the reproductions. It was found that the average shrinkage in latex casts was 1,2 per cent, while in casts of silicone rubber shrinkage was 1,0 per cent. This amount of shrinkage is negligible for the majority of measurements because of the small size of the bones, hence no attempt was made to add a correction factor to measurements made from casts.

All measurements were made by means of a calliper to the nearest tenth of a millimetre. Because of the large number of specimens involved and the large number of measurements per specimen, most measurements were made only once. Bivariate graphs were made, comparing the length or width of the element being studied ($y$) with the average length of a dorsal centrum ($x$) (fig. 2). Any points on the graphs that were inconsistent with the general trends were noted. Once the list was long enough to eliminate all memory of why a particular point was inconsistent, the measurement of the inconsistent points were taken again. This time each dimension was measured four times and the average measurement was taken as the final figure. In most cases there was not a significant difference from the original measurement, but some mistakes were found.

Lengths were measured between perpendiculars to the longitudinal axes of the bones, and widths between lines parallel to the longitudinal axes. Limb bone measurements of length, proximal width and distal width were made between the points of greatest separation, whereas shaft width was taken from the narrowest region of the shaft.

In general, the skeletons had collapsed into a single plane, but show signs of crushing and distortion only in the largest bones. Crushing has little effect on the length measurements of limb elements, but width measurements are more variable (Currie 1981b).

Comparison of measurements is one way to answer questions of identification or relationship of extinct and living taxa. This proved critical in this study because *Hovasaurus* and *Thadeosaurus* are so similar anatomically that many specimens could only be identified by comparative measurements. It was only after the identifications were made that it became apparent that the genera are locality-specific. There are many ways to analyse the measurements made on specimens, and each method has some advantages.

Multivariate analysis summarizes large numbers of observations into a small number of axes (Gould 1967). There are numerous programs available that permit rapid computer analysis. Multivariate analysis has been used with pelycosaurs (Gould 1967, Gould and Littlejoin 1973) and modern reptiles (Dodson 1975a, b), and proved useful for establishing general trends. However, it did not provide information specific enough for detailed comparisons between genera, and therefore was not used in this investigation.

More specific comparisons are possible if they are bivariate, provided a suitable standard for comparison can be established. Romer and Price

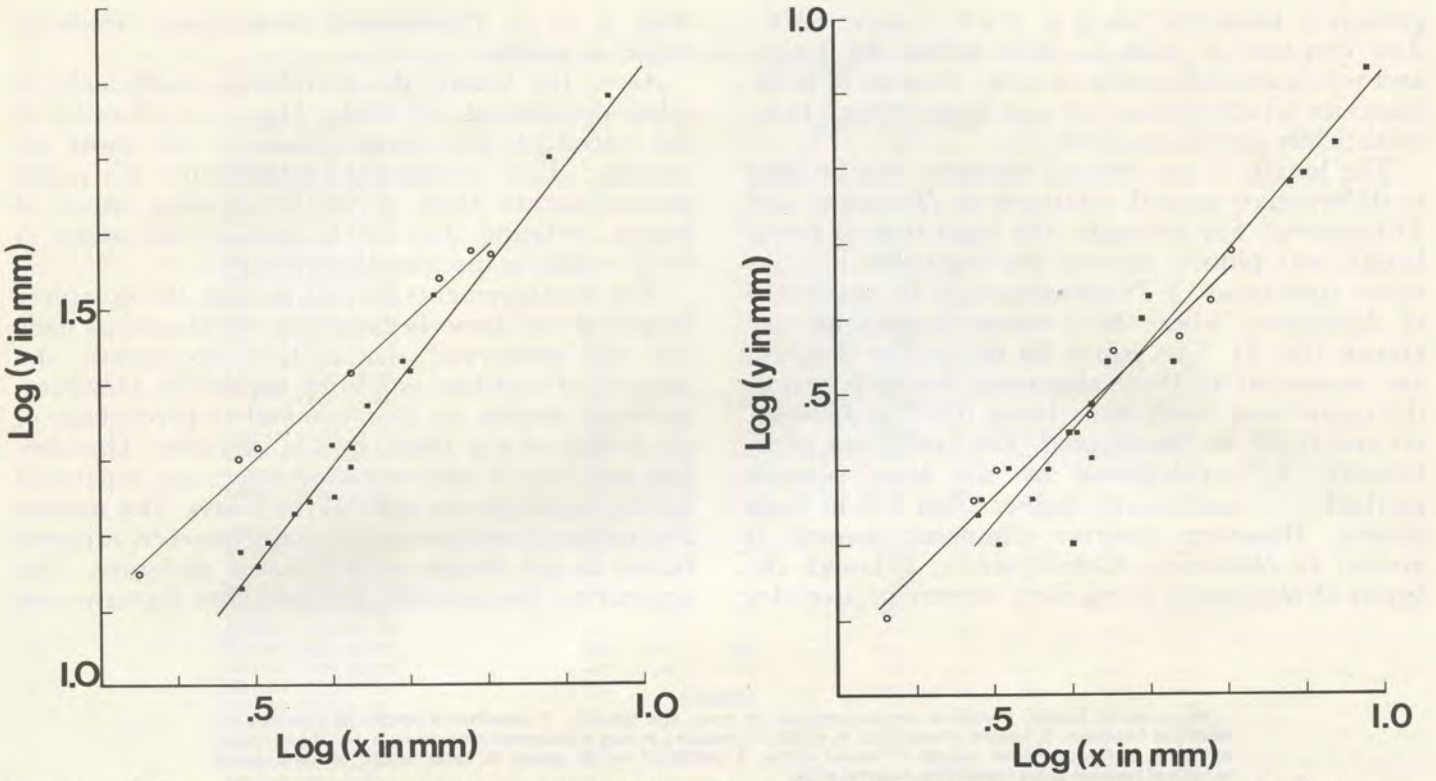



Figure 2. Relationship between length (a) or width (b) of femur (y) and length of associated thoracic centrum ($x$) in *Thadeosaurus* (circles) and *Hovasaurus* (squares). All measurements converted to logarithms. Data from Currie 1981b.

(1940) developed a standard of measurement that allowed them to compare objectively the relative dimensions of bones of animals of different sizes. The standard was based on half the transverse width of a vertebral centrum ($r$) from the middle or posterior dorsal region. The orthometric linear unit, $r^{2/3}$ (Romer 1948), is proportional to the weight of the animal when it was alive, and appears to be the ideal yardstick for measuring bones. If the length of a bone is divided by the orthometric linear unit (OLU), the resulting figure is called the unit measurement. This measurement should be constant for any bone in closely related adult animals, regardless of differences in their absolute size.

However, Currie (1978) has pointed out that the OLU is based on only isometric, interspecific size changes in its derivation, and should therefore be restricted to these same dimensions in its application. The orthometric linear unit should not be used in studying sub-mature specimens because the coefficient of allometry is not the same in ontogenetic and interspecific series when $r$ is used as the basis for comparison. Therefore, this system of unit measurement cannot be used directly with *Hovasaurus* and *Thadeosaurus* because most specimens are immature.

Unit measurement based on the OLU is useful for intergeneric comparisons of mature animals. The largest known specimens of *Hovasaurus* and *Thadeosaurus* are mature but incomplete specimens. However, if the allometric equation for growth is known for any element, an estimated mean value for the length or width of this element can be calculated from the known value of $r$ of the largest specimen (table 4). The unit length can then be calculated by dividing the estimated length by the OLU, and this can be compared with the unit lengths of the same element in other reptiles.

Because of its relationship to the OLU, the ideal standard of measurement for ontogenetic series in *Hovasaurus* and *Thadeosaurus* would have been $r$. The unit measurements could have been solved by simply substituting the values of b′ and k′ of the ontogenetic power equation and $r$ of a mature animal into the equation
b (unit measurement) = $b' r^{k'-2/3}$ (Currie 1978).
Unfortunately, $r$ can be measured directly in very few specimens.

The length of a dorsal centrum can be measured easily in most specimens, and has a simple, direct relationship to $r$. Where it could be measured, it was found that in *Hovasaurus* the width ($2r$) of the dorsal centrum was on the average 84 per cent the length of the centrum regardless of the animal's age at the time of death. Furthermore, the relative lengths of dorsal centra are far more consistent in relation to $r$ in eosuchians than length of cervical vertebrae, length of limb bones, width of any element or total body length. For these reasons, the dimension selected to be the standard of measurement in this investigation is the average length of a dorsal centrum, $x$.

In the equation $y = b'x^{k'}$, $y$ is the length or width of the element being studied, $x$ is the average length of a dorsal centrum, and b′ and k′ are constants. The length of the centrum is not dependent on weight in ontogenetic development, so

growth is isometric when k′ = 1,0 (Currie 1978). The constant b′ and k′ were solved for length and width measurements of every element of *Hovasaurus* for which the sample was large enough to be statistically significant (table 4).

The length of the skeletal elements can be used to differentiate growth strategies in *Hovasaurus* and *Thadeosaurus*. For example, the logarithm of femur length was plotted against the logarithm of *x* for seven specimens of *Thadeosaurus* and 16 specimens of *Hovasaurus* where both these dimensions are known (fig. 2). The points on the scatter diagram are consistent in their alignment for each genus, the correlation coefficients being 0,991 in *Hovasaurus* and 0,995 in *Thadeosaurus*. The coefficient of allometry, $k_{yx}'$ (calculated by the least squares method), is significantly higher than 1,0 in both genera. However, positive allometric growth is greater in *Hovasaurus*. Consequently, although the femur of *Hovasaurus* is relatively shorter in juveniles than it is in *Thadeosaurus*, it becomes relatively longer in adults.

As in the femur, the correlation coefficients of other dimensions are high. This is a reflection of the excellent size range available for most elements. The correlation coefficients of width measurements tend to be lower than those of length, relating directly to greater distortion in bone widths as discussed previously.

The measurements do not include the complete length of the bone because the cartilaginous ends are not preserved. In mature specimens, the amount of cartilage would be negligible. However, cartilage makes up a much higher percentage of the length of any limb bone in juveniles. The ossified portions of adjacent limb bones are separated by the cartilaginous ends of the bones. The unossified region is represented by gaps between adjacent bones in the fossils of articulated skeletons. The separation between the humerus and forearm was

**TABLE 2**

***Hovasaurus boulei*. Vertebral measurements (in mm) and growth. 1, maximum length of centrum; 2, width of centrum; 3, height of centrum; 4, width of vertebra across transverse processes; 5, height of neural spine; 6, anteroposterior length of neural spine; 7, width of neural spine; 8, total height of vertebra; 9, length of haemal spine (excluding haemal arch).**

Note: allometric growth of neural spine of caudals and haemal spine calculated by comparison with the maximum length of the associated caudal centra and not with x.

| Specimen number | | Anterior dorsal | | 15th – 18th | | | | | | 19th–22nd |
|---|---|---|---|---|---|---|---|---|---|---|
| | x | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 5 |
| MNHN R146 | 8,7 | — | — | — | — | — | — | — | — | 14,0 |
| MNHN 1908-21-2/7 | 4,2 | — | — | 4,2 | — | — | — | 5,2 | — | 5,7 |
| MNHN 1908-21-5 | 4,4 | — | — | 5,0 | — | — | — | — | — | — |
| MNHN 1908-21-6 | 9,2 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-8 | 3,2e | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-11 | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-12 | 8,0e | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | 9,3e | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-16 | 8,2 | — | — | 7,9 | — | — | — | 12,3 | — | — |
| MNHN 1908-21-18 | 8,6 | — | — | 8,6 | — | — | — | — | — | — |
| MNHN 1908-21-19 | 9,6e | — | 4,0 | — | — | — | — | — | — | 14,8 |
| MNHN 1908-32-1 | 4,8 | — | — | 4,8 | — | — | — | — | — | 7,8 |
| MNHN 1908-32-4 | 4,0 | — | — | 4,3 | — | — | — | 4,7 | — | — |
| MNHN 1908-32-21 | 3,7 | — | — | 3,6 | — | — | — | 4,4 | — | 4,6 |
| MNHN 1908-32-22 | 4,2 | — | — | 4,1 | — | — | — | — | — | 5,6 |
| MNHN 1908-32-23 | 5,5 | — | — | 5,4 | — | — | — | — | — | — |
| MNHN 1908-32-24 | 8,7 | 4,9 | 3,8 | 8,9 | — | — | 11,7 | 14,0 | 6,1 | 14,8 |
| MNHN 1908-32-25 | 8,5 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-29 | 3,3 | — | — | 3,3 | — | — | — | 4,0 | — | — |
| MNHN 1908-32-45 | 9,2 | — | — | 9,2 | — | — | — | 13,4 | — | 14,7 |
| MNHN 1908-32-49 | 9,5e | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | 8,8 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | 8,2 | 6,1 | 4,5 | 8,2 | — | — | 10,6 | 13,2 | 6,9 | 12,3 |
| MNHN 1908-32-60 | 9,3 | 7,0 | 4,0 | 9,3 | — | — | 12,6 | 13,0 | 7,9 | — |
| MNHN 1908-32-64/73 | 4,9e | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-67 | 9,0 | — | — | 9,0 | — | — | — | 13,9 | — | — |
| MNHN 1908-32-75 | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | 4,9 | — | — | 4,9 | — | — | — | — | — | — |
| MNHN 1908-32-99 | 4,8 | — | — | 4,8 | 4,1 | 2,8 | 6,6 | 5,8 | — | — |
| MNHN 1925-5-10 | 3,0 | — | — | 2,9 | — | — | — | — | — | — |
| MNHN 1925-5-12 | 6,7 | — | — | 6,7 | — | — | — | — | — | — |
| MNHN 1925-5-18 | 3,5 | — | — | 3,9 | — | — | — | — | — | — |
| MNHN 1925-5-20 | 3,1 | — | — | — | — | — | — | — | — | 4,0 |
| MNHN 1925-5-25 | 3,2 | — | — | 3,2 | — | 2,0 | 5,0 | 3,4 | — | — |
| MNHN 1925-5-27 | 3,1c | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-28 | 5,0 | — | — | 4,8 | — | — | — | 6,9 | — | 6,7 |
| MNHN 1925-5-29 | 6,9 | — | — | 6,8 | — | 4,6 | — | — | — | — |
| MNHN 1925-5-30 | 3,8 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | 6,4 | — | — | 6,4 | — | — | — | — | — | — |
| MNHN 1925-5-41 | 5,0 | — | — | 5,0 | — | — | — | — | — | — |
| MNHN 1925-5-60 | 5,4 | — | — | 5,4 | — | — | — | — | — | — |
| SAM 9456 | — | — | — | — | — | — | — | — | — | — |
| SAM 9461 | 9,3 | 6,7 | — | 9,3 | 7,8 | 6,0 | — | 16,5 | 7,8 | — |
| SAM 9462 | — | — | — | — | — | — | — | — | — | — |
| SAM 9463 | — | 6,1 | 3,5 | 7,0 | 5,6 | 4,6 | 10,7 | 14,3 | 6,2 | — |
| N | — | — | — | — | — | — | — | 15 | — | 11 |
| R | — | — | — | — | — | — | — | 0,98 | — | 0,99 |
| $k_{yx}$ | — | — | — | — | — | — | — | 1,34 | — | 1,20 |
| $b'$ | — | — | — | — | — | — | — | 0,89 | — | 1,03 |

(Table 2 cont.)

| Specimen number | 20th – 25th 1 | 2 | 3 | 4 | 5 | 6 | 7 | S1 5 | S2 5 |
|---|---|---|---|---|---|---|---|---|---|
| MNHN R146 | 8,7 | 7,2 | 5,1 | 14,4 | 14,3 | 7,6 | 2,3 | — | — |
| MNHN 1908-21-2/7 | 4,4 | — | — | — | 5,3 | — | — | 5,4 | — |
| MNHN 1908-21-5 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | 9,9 | — | — | — | — | — | — | — | — |
| MNHN 1908-21-8 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-11 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-12 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-16 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-19 | 9,7 | — | — | 14,4 | 13,9 | 7,3 | 2,9 | 12,5 | — |
| MNHN 1908-21-1 | 5,0 | — | — | — | 5,8 | — | — | — | — |
| MNHN 1908-32-4 | — | — | — | — | — | — | — | 4,0 | 4,0 |
| MNHN 1908-32-21 | 3,8 | — | — | — | 4,2 | — | — | 3,7 | 4,0 |
| MNHN 1908-32-22 | 4,3 | — | 3,1 | — | 4,8 | — | — | 5,1 | — |
| MNHN 1908-32-23 | 5,6 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-24 | 9,0 | — | — | — | 15,4 | 7,5 | 2,9 | 12,0 | — |
| MNHN 1908-32-25 | 8,3 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-29 | 3,6 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-45 | — | — | — | — | — | 8,3 | — | — | — |
| MNHN 1908-32-49 | 9,2 | — | — | — | — | — | — | — | — |
| MNHN 1908-32-58 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | — | — | — | — | 11,0 | — | 2,8 | — | — |
| MNHN 1908-32-60 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-64/73 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-67 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-75 | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-77 | 5,0 | — | 3,3 | — | — | — | — | — | — |
| MNHN 1908-32-99 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-10 | 3,0 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-12 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-18 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-20 | 3,0 | — | — | — | 3,3 | — | — | 3,1 | 3,3 |
| MNHN 1925-5-25 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-27 | 3,1 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-28 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-29 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-30 | 3,8 | — | — | — | — | — | — | — | — |
| MNHN 1925-5-34 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-41 | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-60 | 5,4 | — | — | — | — | — | — | — | — |
| SAM 9456 | — | — | — | — | — | — | — | — | — |
| SAM 9461 | — | — | — | — | — | — | — | — | — |
| SAM 9462 | — | — | — | — | — | — | — | — | — |
| SAM 9463 | — | — | — | — | — | — | — | — | — |
| N | — | — | — | — | 9 | — | — | — | — |
| R | — | — | — | — | 0,99 | — | — | — | — |
| $k_{yx}$ | — | — | — | — | 1,33 | — | — | — | — |
| b' | — | — | — | — | 0,74 | — | — | — | — |

| Specimen number | 10th – 15th 1 | 5 | 8 | caudal 9 |
|---|---|---|---|---|
| MNHN R146 | — | — | — | — |
| MNHN 1908-21-2/7 | — | — | — | — |
| MNHN 1908-21-5 | 4,0 | 6,0 | 13,0 | 9,0 |
| MNHN 1908-21-6 | — | — | — | — |
| MNHN 1908-21-8 | — | — | — | — |
| MNHN 1908-21-11 | — | — | — | — |
| MNHN 1908-21-12 | 8,0 | 16,0 | 24,0 | — |
| MNHN 1908-21-14 | 8,2 | 17,0 | 27,0 | 21,0 |
| MNHN 1908-21-16 | — | — | — | — |
| MNHN 1908-21-18 | — | — | — | — |
| MNHN 1908-21-19 | — | — | — | — |
| MNHN 1908-32-1 | — | — | — | — |
| MNHN 1908-32-4 | — | — | — | — |
| MNHN 1908-32-21 | 3,3 | 5,0 | 11,0 | 7,5 |
| MNHN 1908-32-22 | — | — | — | — |
| MNHN 1908-32-23 | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — |
| MNHN 1908-32-25 | — | — | — | — |
| MNHN 1908-32-29 | 3,1 | 4,0 | 9,0 | 6,5 |
| MNHN 1908-32-45 | — | — | — | — |
| MNHN 1908-32-49 | — | — | — | — |
| MNHN 1908-32-58 | 8,8 | 18,0 | 26,0 | — |
| MNHN 1908-32-59 | — | — | — | — |
| MNHN 1908-32-60 | — | — | — | — |
| MNHN 1908-32-64/73 | 4,9 | 10,0 | — | 10,5 |

| Specimen number | 10th – 15th 1 | 5 | 8 | caudal 9 |
|---|---|---|---|---|
| MNHN 1908-32-67 | — | — | — | — |
| MNHN 1908-32-75 | — | — | — | — |
| MNHN 1908-32-77 | 4,9 | 8,5 | 15,5 | 10,7 |
| MNHN 1908-32-99 | — | — | — | — |
| MNHN 1925-5-10 | 3,0 | — | — | 6,3 |
| MNHN 1925-5-12 | — | — | — | — |
| MNHN 1925-5-18 | — | — | — | — |
| MNHN 1925-5-20 | 3,2 | 4,0 | 8,0 | 6,5 |
| MNHN 1925-5-25 | — | — | — | — |
| MNHN 1925-5-27 | — | — | — | — |
| MNHN 1925-5-28 | — | — | — | — |
| MNHN 1925-5-29 | — | — | — | — |
| MNHN 1925-5-30 | — | — | — | — |
| MNHN 1925-5-34 | — | — | — | — |
| MNHN 1925-5-41 | 4,9 | 9,8 | — | 11,2 |
| MNHN 1925-5-60 | — | — | — | — |
| SAM 9456 | — | — | — | — |
| SAM 9461 | — | — | — | — |
| SAM 9462 | — | — | — | — |
| SAM 9463 | — | — | — | — |
| N | — | 10 | — | 9 |
| R | — | 0,98 | — | 0,99 |
| $k_{yx}$ | — | 1,43 | — | 1,18 |
| b' | — | 0,86 | — | 1,73 |

measured in the smallest specimens of both genera. If it is assumed that half the distance represents the cartilaginous distal end of the humerus, and that the cartilage of the proximal end would have been about the same length, then an estimate can be made of the percentage of total length of the humerus formed by cartilage. On the average, 16,2 per cent of the total length of the humerus was cartilaginous in *Hovasaurus* juveniles of life stages A and B (table 2). The average (15,5 per cent) cartilaginous composition for the same bone in *Thadeosaurus* is not significantly different.

Allometric growth rates are frequently referred to in this paper. The growth rates calculated are for the ossified lengths of the bones, and not the total lengths. In most cases the amount of cartilage cannot be estimated. There would have been none in the dermal bones, and the percentage in endochondral bones would vary. The difference in growth rate of the total bone and growth rate of the ossified portion can be estimated for the humerus. The coefficients of allometry for ossified lengths of the humeri of *Hovasaurus* and *Thadeosaurus* are 1,61 and 1,30 respectively. If we assume that the total length of the humerus is 16 per cent cartilage in the smallest specimens and 1 per cent at maturity, the coefficients of allometry for total bone lengths are calculated to be 1,50 in *Hovasaurus* and 1,16 in *Thadeosaurus*.

Because the percentages of cartilage in the bones of the two genera are apparently the same at equivalent life stages, differences in the growth rates of the ossified portions of the bones are biologically significant.

In summary, the large number of well-preserved tangasaurid specimens permits quantitative studies to supplement morphological information. *Thadeosaurus* and *Hovasaurus* are closely related, contemporary genera that had different habitat preferences. Comparative measurements make it possible to identify many partial skeletons that lack diagnostic morphological features. In the past, new fossil genera were often established on the basis of relative limb proportions that differ from those of known genera. Study of the growth series of tangasaurids is another indication of how much relative proportions can change in the life of a reptile. Relative limb proportions in adult animals can be used to indicate habitat preferences. Comparative study of growth rates indicates significant differences between the genera that reflect different life styles (prey preference, dispersal, etc.). These will be discussed in detail in subsequent sections.

## SYSTEMATIC PALAEONTOLOGY

Class REPTILIA LINNAEUS 1758
Subclass LEPIDOSAURIA Dumeril and Bibron 1839
Order EOSUCHIA Broom 1914
Suborder YOUNGINIFORMES Romer 1945
Family TANGASAURIDAE Camp 1945
Subfamily TANGASAURINAE Piveteau 1926

*HOVASAURUS* Piveteau 1926

*Diagnosis.* — The tangasaurid most highly specialized for an aquatic existence. The ratio of interorbital to intertemporal width is 0,4, compared with 1,1 in *Youngina;* jaw suspension slopes anteroventrally as in *Thadeosaurus;* triradiate jugal is relatively smaller than in *Thadeosaurus* or any other eosuchian known; supratemporal as long as but broader than in other eosuchians; distinctive rod-like, anteroventrally sloping ramus on squamosal; quadrate ramus of the pterygoid less than half the length of palatal ramus whereas it is more than half in *Youngina;* quadrate almost as wide as it is high as in *Thadeosaurus* but in contrast to *Youngina* where the width is half the height; external surface of opisthotic convex between main body and paroccipital process, rather than concave as in most eosuchians. Accessory intervertebral articulations on midline of neural spines more complex than in *Youngina* or other tangasaurids; mid-dorsal neural spines up to double the length of centra, and relatively higher than in any other eosuchian known; anterior and mid-dorsal neural spines thickened dorsally by mammillary processes; caudal neural spines distinctive in outline and up to 2,2 times the length of the centrum compared with 1,4 times in *Tangasaurus;* haemal spine expanded into large plate of bone that mimics neural spine in shape and size. Mid-dorsal ribs curved throughout their length; unlike other younginiform eosuchians, ribs pachyostotic in mature animals; up to 12 pairs of caudal ribs compared with 12 in *Tangasaurus,* 19 in *Thadeosaurus* and 28 in *Kenyasaurus;* anterior caudal ribs expanded distally. Ossified portion of scapular blade much shorter than in *Youngina* and extends less than 50 per cent up body wall; balance of scapulocoracoid almost horizontal; prominent process on scapula for long head of triceps lateralis. Cleithrum more strongly curved than in other eosuchians. Metacarpals II, III and IV subequal in length. Abdominal cavity usually includes more substantial ingested mass of pebbles than *Thadeosaurus.*

*HOVASAURUS BOULEI* Piveteau 1926

*Lectotype* — MNHN 1908-21-2, MNHN 1908-21-7, counterpart slabs in the Muséum National d'Histoire Naturelle, Paris.

*Referred specimens* — see Table 1.

*Horizon and Locality* — Lower Sakamena Formation, Upper Permian. Sakamena River Valley, southern Madagascar. Exact locality not recorded for lectotype, but probably from Mt. Eliva.

*Diagnosis* — same as for genus.

## DESCRIPTION

More than 300 specimens in the Muséum National d'Histoire Naturelle, the South African Museum, and the American Museum of Natural History, may be identified as *Hovasaurus boulei.* This study is based on 70 of the best specimens (tables 1, 2, 3). The specimen selected as the lectotype (fig. 3) is more complete than the other specimens of the series on which the original description of *Hovasaurus* was based (Piveteau 1926).

In life, *Hovasaurus* would have been lizard-like in general appearance. The snout-vent length of a mature animal would have been 30 to 35 cm assuming it did not have an elongate rostrum. The tail was exceptionally long, and a conservative estimate of tail length in a large animal would be 60 cm.

The majority of specimens are preserved in a similar "death pose". The front limb is folded back against the body with the dorsal surfaces of the humerus and manus facing upward. The outer digit of the manus is closer to the body than the inner

**TABLE 3**

**Manus and pes measurements (in mm) of *Tangasaurus* and *Hovasaurus*. a, sum of lengths of phalanges; b, sum of length of metapodial and phalanges; mp, metapodial. Proportions were calculated from b.**

| Specimen number | Manus Pes | I mp | 1 | 2 | a | b | II mp | 1 | 2 | 3 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | M | 1,8 | 2,0 | — | — | — | 2,8 | 1,8 | — | — | — | — |
| MNHN 1925-5-27 | M | 2,1 | 2,1 | 1,6 | 3,7 | 5,8 | 2,9 | 1,8 | 2,0 | 1,6 | 5,4 | 8,3 |
| MNHN 1908-21-8 | M | 1,5 | 1,4 | 1,1 | 2,5 | 4,0 | 2,1 | 1,3 | 1,5 | 1,4 | 4,2 | 6,3 |
| MNHN 1908-32-29 | M | 1,8 | 1,9 | 1,3 | 3,2 | 5,0 | 2,5 | 1,7 | 1,9 | 1,2 | 4,8 | 7,3 |
| MNHN 1908-32-21 | M | 2,2 | 2,3 | 1,6 | 3,9 | 6,1 | 3,0 | 2,0 | 2,3 | 1,6 | 5,9 | 8,9 |
| MNHN 1908-32-4 | M | 2,6 | 3,0 | 2,0e | 5,0e | 7,6e | 3,3 | 2,5 | 2,8 | 2,1e | 7,4e | 10,7e |
| MNHN 1908-32-22 | M | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | M | 2,5 | 2,7 | 2,0 | 4,7 | 7,2 | 3,7 | 2,5 | 2,8 | 2,2 | 7,5 | 11,2 |
| MNHN 1908-32-77 | M | 3,4 | — | — | — | — | 4,6 | 3,2 | 3,5 | 2,3 | 9,0 | 13,6 |
| MNHN 1925-5-60 | M | — | — | 3,0 | — | — | — | 4,0 | 4,1 | 3,1 | — | — |
| MNHN 1908-32-23 | M | 4,3 | 4,3 | 2,6 | 6,9 | 11,2 | 5,7 | 3,7 | 4,1 | 2,5e | 10,3e | 16,0e |

| Specimen number | III mp | 1 | 2 | 3 | 4 | a | b | IV mp | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 2,8 | 1,7 | 1,6 | — | — | — | — | 2,8 | 1,8 | — | — |
| MNHN 1925-5-27 | 3,1 | 2,0 | 1,8 | 2,0 | 1,5 | 7,3 | 10,4 | 3,2 | 2,0 | 1,8 | 1,7 |
| MNHN 1908-21-8 | 2,3 | 1,5 | 1,3 | 1,3 | 1,1 | 5,2 | 7,5 | 2,5 | 1,6 | 1,3 | 1,4 |
| MNHN 1908-32-29 | 2,6 | 1,7 | 1,5 | 1,7 | 1,4 | 6,3 | 8,9 | 2,9 | 1,8 | 1,6 | 1,5 |
| MNHN 1908-32-21 | 3,3 | 2,2 | 2,0 | 2,1 | 1,3 | 7,6 | 10,9 | 3,2 | 2,3 | 2,0 | 1,9 |
| MNHN 1908-32-4 | 4,0 | 2,8 | 2,3 | 2,8 | 2,1 | 10,0 | 14,0 | 3,9 | 2,4 | 2,2 | 2,3 |
| MNHN 1908-32-22 | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | 4,0 | 2,5 | 2,3 | 2,6 | 1,9 | 9,3 | 13,3 | 4,0 | 2,6 | 2,8 | 2,5 |
| MNHN 1908-32-77 | 5,0 | — | — | — | 2,2 | — | — | 5,0 | — | — | — |
| MNHN 1925-5-60 | 7,7 | 4,5 | 3,9 | — | — | — | — | — | 5,0 | 4,0 | 3,9 |
| MNHN 1908-32-23 | 6,1 | 3,6 | 3,5 | 4,0 | 2,6 | 13,7 | 19,8 | 6,1 | 4,1 | 3,4 | 3,4 |

| Specimen number | IV 4 | 5 | a | b | V mp | 1 | 2 | 3 | 4 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | 1,1 | — | — | 1,8 | — | — | — | — | — | — |
| MNHN 1925-5-27 | 1,8 | 1,5 | 8,8 | 12,0 | 2,1 | 2,0 | 2,1 | 1,5 | — | 5,6 | 7,7 |
| MNHN 1908-21-8 | 1,4 | 1,3 | 7,0 | 9,5 | 1,8 | 1,5 | — | — | — | — | — |
| MNHN 1908-32-29 | 1,7 | 1,4e | 8,0 | 10,9e | 1,9 | 1,7 | 1,8 | 1,1 | — | 4,6 | 6,5 |
| MNHN 1908-32-21 | 2,2 | 1,5 | 9,9 | 13,1 | 2,2 | 2,2 | 2,4 | 1,5 | — | 6,1 | 8,3 |
| MNHN 1908-32-4 | 2,6 | 2,5 | 12,0 | 15,9 | 2,9 | 2,3 | 2,9 | 1,8 | — | 7,0 | 9,9 |
| MNHN 1908-32-22 | 2,5 | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | 2,4 | 2,0 | 12,3 | 16,3 | 3,0 | 2,7 | 2,6 | 1,7 | — | 7,0 | 10,0 |
| MNHN 1908-32-77 | 3,1 | 2,1 | — | — | 3,8 | — | — | — | — | — | — |
| MNHN 1925-5-60 | 4,0 | 2,7 | 19,6 | — | — | — | 4,4 | 2,8 | — | — | — |
| MNHN 1908-32-23 | 3,8 | 2,5 | 17,2 | 23,3 | 4,6 | 3,7 | 3,9 | 2,5 | — | 10,1 | 14,7 |

| Specimen number | I/IV | II/IV | III/IV | V/IV | V/III | IV/x |
|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | — | — | — | — |
| MNHN 1925-5-27 | 0,48 | 0,69 | 0,87 | 0,64 | 0,74 | 3,87 |
| MNHN 1908-21-8 | 0,42 | 0,66 | 0,79 | — | — | 2,97 |
| MNHN 1908-32-29 | 0,46 | 0,67 | 0,82 | 0,60 | 0,73 | 3,30 |
| MNHN 1908-32-21 | 0,47 | 0,68 | 0,83 | 0,63 | 0,76 | 3,54 |
| MNHN 1908-32-4 | 0,48 | 0,67 | 0,88 | 0,62 | 0,71 | 3,98 |
| MNHN 1908-32-22 | — | — | — | — | — | — |
| MNHN 1908-21-2/7 | 0,44 | 0,69 | 0,82 | 0,61 | 0,75 | 3,88 |
| MNHN 1908-32-77 | — | — | — | — | — | — |
| MNHN 1925-5-60 | — | — | — | — | — | — |
| MNHN 1908-32-23 | 0,48 | 0,69 | 0,85 | 0,63 | 0,74 | 4,24 |

| Specimen number | Manus Pes | I mp | 1 | 2 | a | b | II mp | 1 | 2 | 3 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-12 | M | 5,3 | 5,5 | 4,0 | 9,5 | 14,8 | 7,2 | 4,7 | 5,1 | 4,0 | 13,8 | 21,0 |
| MNHN 1925-5-29 | M | 5,9 | 5,9 | 3,5 | 9,4 | 15,3 | 7,5 | 5,3 | 5,6e | 3,6 | 14,5e | 22,0e |
| SAM 6231 | M | 5,0 | 5,0 | 4,0 | 9,0 | 14,0 | 7,0 | 5,5 | 4,5 | 4,0 | 14,0 | 21,0 |
| MNHN 1908-21-16 | M | — | — | — | — | — | 9,5 | 7,0 | 7,0 | 5,1 | 19,1 | 28,6 |
| MNHN 1908-32-59 | M | 6,0 | 6,7 | 4,5 | 11,2 | 17,2 | 9,0 | 6,2 | 6,5 | 4,5e | 17,2e | 26,2e |
| MNHN 1925-5-31 | M | 6,8 | 7,1 | 5,5 | 12,6 | 19,4 | 9,5 | 5,5 | 6,7 | 6,0 | 18,2 | 27,7 |
| MNHN 1908-32-25 | M | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-24 | M | — | — | — | — | — | — | — | — | — | — | — |
| SAM 9457 | M | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-6 | M | — | — | 4,8 | — | — | — | 6,3 | 6,7 | 4,8e | — | — |

| Specimen number | III mp | 1 | 2 | 3 | 4 | a | b | IV mp | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-12 | 8,0 | 5,0 | 4,3 | 4,6 | 3,6 | 17,5 | 25,5 | 8,2 | 5,0 | 4,5 | — |
| MNHN 1925-5-29 | 8,3 | 5,2 | 4,8 | 4,7 | 3,5 | 18,2 | 26,5 | 8,5 | 5,1 | 4,5 | 4,4 |
| SAM 6231 | 7,5 | 5,0 | 5,5 | 5,0 | 4,0 | 19,5 | 27,0 | 8,0 | 5,0 | 4,0 | 4,5 |
| MNHN 1908-21-16 | — | — | — | — | 5,0 | — | — | — | — | — | — |
| MNHN 1908-32-59 | 10,0 | 6,2 | 5,4 | 5,7 | 4,5e | 21,8e | 31,8e | 10,1 | 6,0 | 6,3 | 5,6 |
| MNHN 1925-5-31 | 10,3 | 6,4 | 6,5 | 6,0 | 5,7 | 24,6 | 34,9 | 10,5 | 6,5 | 5,8 | 5,7 |
| MNHN 1908-32-25 | — | 6,2 | — | — | — | — | — | 10,3 | 6,6 | 5,7 | 5,6 |
| MNHN 1908-32-24 | — | — | — | — | — | — | — | — | 6,7 | — | — |
| SAM 9457 | 9,8 | 6,1 | 6,4 | — | — | — | — | 10,5 | 6,5 | 6,0 | — |
| MNHN 1908-21-6 | — | 6,6 | 6,3 | 6,6 | 5,5 | 25,0 | — | — | 6,6e | 5,7 | 5,7 |

(Table 3 cont.)

| Specimen number | IV 4 | 5 | a | b | V mp | 1 | 2 | 3 | 4 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-12 | — | — | — | — | 5,9 | 5,0 | 5,0 | — | — | — | — |
| MNHN 1925-5-29 | 4,7 | 3,6 | 22,3 | 30,8 | 6,2 | 5,5 | 5,6 | 3,5 | — | 14,6 | 20,8 |
| SAM 6231 | 4,0 | 3,5 | 21,0 | 29,0 | 5,0 | 5,0 | 5,5 | 4,0 | — | 14,5 | 19,5 |
| MNHN 1908-21-16 | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-32-59 | 6,0e | 5,0e | 28,9e | 39,0e | 8,0 | 6,2 | 6,3 | 5,0 | — | 17,5 | 25,5 |
| MNHN 1925-5-31 | 6,5 | 5,8e | 30,3e | 40,8e | 8,0 | 6,3 | 6,5 | 5,3 | — | 18,1 | 26,1 |
| MNHN 1908-32-25 | 6,2 | 5,1e | 29,2e | 39,5e | — | 6,1 | 7,0 | 5,1 | — | 18,2 | — |
| MNHN 1908-32-24 | — | — | — | — | 9,0 | 7,2 | 7,0 | 4,6 | — | 18,8 | 27,8 |
| SAM 9457 | — | 5,0 | — | — | 7,5 | 6,5 | — | 5,5 | — | — | — |
| MNHN 1908-21-6 | 6,2 | 4,8e | 29,0 | — | — | — | — | — | — | — | — |

| Specimen number | I/IV | II/IV | III/IV | V/IV | V/III | IV/x |
|---|---|---|---|---|---|---|
| MNHN 1925-5-12 | — | — | — | — | — | — |
| MNHN 1925-5-29 | 0,50 | 0,71 | 0,86 | 0,68 | 0,78 | 4,46 |
| SAM 6231 | 0,48 | 0,72 | 0,93 | 0,67 | 0,72 | 4,39 |
| MNHN 1908-21-16 | — | — | — | — | — | — |
| MNHN 1908-32-59 | 0,44 | 0,67 | 0,82 | 0,65 | 0,80 | 4,76 |
| MNHN 1925-5-31 | 0,48 | 0,68 | 0,86 | 0,64 | 0,75 | 4,80 |
| MNHN 1908-32-25 | — | — | — | — | — | 4,65 |
| MNHN 1908-32-24 | — | — | — | — | — | — |
| SAM 9457 | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — |

| Specimen number | Manus Pes | I mp | 1 | 2 | a | b | II mp | 1 | 2 | 3 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | P | 3,0 | — | — | — | — | 5,0 | — | — | — | — | — |
| MNHN 1925-5-20 | P | 3,0 | — | 2,6 | — | — | 4,6 | 2,5 | — | — | — | — |
| MNHN 1908-21-8 | P | 2,4 | 2,0 | 1,6 | 3,6 | 6,0 | 4,2 | 2,2 | 2,0 | 1,5 | 5,7 | 9,9 |
| MNHN 1925-5-25 | P | 2,8 | 2,4 | — | — | — | 5,0 | 2,5 | — | — | — | — |
| MNHN 1908-32-29 | P | 2,9 | 2,5 | 1,6 | 4,1 | 7,0 | 5,0 | 2,3 | 2,5 | 1,5 | 6,3 | 11,3 |
| MNHN 1925-5-18 | P | 3,3 | — | — | — | — | 5,5 | — | — | — | — | — |
| MNHN 1908-32-21 | P | 3,4 | 3,2 | 2,0 | 5,2 | 8,6 | 5,6 | 3,0 | 3,0 | 2,3 | 8,3 | 13,9 |
| MNHN 1908-21-2/7 | P | 4,0 | 3,8 | 2,4 | 6,2 | 10,2 | 6,9 | 3,3 | 3,3 | 2,5 | 9,1 | 16,0 |
| MNHN 1908-21-5 | P | 4,5 | 4,5 | 3,0 | 7,5 | 12,0 | 7,9 | 4,2 | 4,4 | 3,0 | 11,6 | 19,5 |
| MNHN 1908-32-77 | P | 5,8 | 4,9 | 3,1 | 8,0 | 13,8 | 9,0 | 4,3 | 4,5 | 3,0 | 11,8 | 20,8 |

| Specimen number | III mp | 1 | 2 | 3 | 4 | a | b | IV mp | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | 6,3 | — | — | — | — | — | — | 6,4 | — | — | — |
| MNHN 1925-5-20 | 5,8 | 2,7 | 2,0 | — | — | — | — | 6,2 | 3,3 | 2,3 | 2,1 |
| MNHN 1908-21-8 | 5,1 | 2,2 | 2,0 | 2,0 | 1,6 | 7,8 | 12,9 | 5,1 | 2,7 | 2,1 | 2,0 |
| MNHN 1925-5-25 | 6,0 | — | — | — | — | — | — | 6,4 | 3,2 | — | — |
| MNHN 1908-32-29 | 6,0 | 2,6 | 2,1 | 2,2 | 1,5 | 8,4 | 14,4 | 6,1 | 3,0 | 2,3 | 1,9 |
| MNHN 1925-5-18 | — | — | — | — | — | — | — | 7,2 | 3,8 | — | — |
| MNHN 1908-32-21 | 6,8 | 3,2 | 2,7 | 2,8 | 1,9 | 10,6 | 17,4 | 7,3 | 3,9 | 2,7 | 2,4 |
| MNHN 1908-21-2/7 | 8,0 | 4,0 | 3,2 | 3,4 | 2,4 | 13,0 | 21,0 | 8,6 | 4,9 | 4,0 | 3,0 |
| MNHN 1908-21-5 | 9,6 | 4,8 | 3,8 | 4,0 | 3,1 | 15,7 | 25,3 | 9,6 | 5,5 | 5,0 | 3,5 |
| MNHN 1908-32-77 | 11,0 | 5,2 | 4,0 | 4,1 | 3,0e | 16,3e | 27,3e | 11,3 | 6,2 | 4,5 | 4,0 |

| Specimen number | IV 4 | 5 | a | b | V mp | 1 | 2 | 3 | 4 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | — | — | 4,6 | — | — | — | — | — | — |
| MNHN 1925-5-20 | 2,0 | 1,5e | 11,2e | 17,4e | 4,5 | 3,9 | 2,6 | 2,3 | 1,2 | 10,0 | 14,5 |
| MNHN 1908-21-8 | 1,9 | 1,7 | 10,4 | 15,5 | 4,1 | 3,4 | — | — | 1,7 | — | — |
| MNHN 1925-5-25 | — | — | — | — | 5,0 | 3,9 | — | — | — | — | — |
| MNHN 1908-32-29 | 2,1 | 1,5e | 10,8 | 16,9 | 4,5 | 3,6 | 2,3 | 2,2 | 1,4 | 9,5 | 14,0 |
| MNHN 1925-5-18 | — | — | — | — | 5,5 | 4,4 | — | — | — | — | — |
| MNHN 1908-32-21 | 2,3 | 2,0 | 13,3 | 20,6 | 5,5 | 4,6 | 3,1 | 3,0 | 2,0e | 12,7e | 18,2e |
| MNHN 1908-21-2/7 | 3,0 | 2,3 | 17,2 | 25,8 | 6,9 | 5,5 | 3,5 | 3,2 | 2,2 | 14,4 | 21,3 |
| MNHN 1908-21-5 | 3,7 | 2,5 | 20,2 | 29,8 | 7,6 | 6,3 | 4,1 | 3,8 | 2,1 | 16,3 | 23,9 |
| MNHN 1908-32-77 | 4,0 | 3,0e | 21,7e | 33,0e | 8,4 | 7,0 | 4,8 | 4,2 | 2,4 | 18,4 | 26,8 |

| Specimen number | I/IV | II/IV | III/IV | V/IV | V/III | IV/x |
|---|---|---|---|---|---|---|
| MNHN 1925-5-10 | — | — | — | — | — | — |
| MNHN 1925-5-20 | — | — | — | 0,83 | — | 5,61 |
| MNHN 1908-21-8 | 0,39 | 0,64 | 0,83 | — | — | 4,84 |
| MNHN 1925-5-25 | — | — | — | — | — | — |
| MNHN 1908-32-29 | 0,41 | 0,67 | 0,85 | 0,83 | 0,97 | 5,12 |
| MNHN 1925-5-18 | — | — | — | — | — | — |
| MNHN 1908-32-21 | 0,42 | 0,67 | 0,84 | 0,88 | 1,05 | 5,57 |
| MNHN 1908-21-2/7 | 0,40 | 0,62 | 0,81 | 0,83 | 1,01 | 6,14 |
| MNHN 1908-21-5 | 0,40 | 0,65 | 0,85 | 0,80 | 0,94 | 6,77 |
| MNHN 1908-32-77 | 0,42 | 0,63 | 0,83 | 0,81 | 0,98 | 6,73 |

(Table 3 cont.)

| Specimen number | Manus Pes | I mp | 1 | 2 | a | b | II mp | 1 | 2 | 3 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-41 | P | 5,7 | 5,0 | 3,2 | 8,2 | 13,9 | 9,5 | 4,9 | 4,8 | 3,1 | 12,8 | 22,3 |
| SAM 6231 | P | 8,0 | 6,5 | 5,0 | 11,5 | 19,5 | 14,0 | 6,5 | 6,5 | 5,0 | 18,0 | 32,0 |
| SAM 6232 | P | 8,0 | 7,5 | 7,0 | 14,5 | 22,5 | 15,5 | 7,5 | 7,0 | 5,0 | 19,5 | 35,0 |
| MNHN 1925-5-32 | P | 10,6 | 9,9 | 7,0 | 16,9 | 27,5 | 17,5 | 8,6 | 8,6 | 7,5 | 24,7 | 42,2 |
| MNHN 1908-21-10 | P | 11,0 | 10,0 | 8,0e | 18,0e | 29,0e | 18,2 | 9,6 | 9,0 | 8,0e | 26,6e | 44,8e |
| MNHN 1908-32-68/ 1925-8-14 | P | 11,0e | — | — | — | — | — | — | — | — | — | — |
| MNHN 1925-5-61 | P | 12,1 | 9,2 | — | — | — | 19,9 | — | — | — | — | — |
| MNHN 1908-32-24 | P | 12,5 | 9,2 | — | — | — | 20,0 | 9,5 | 8,5 | — | — | — |
| MNHN 1908-21-6 | P | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | P | 12,0 | 9,5e | — | — | — | 19,5 | — | — | — | — | — |

| Specimen number | III mp | 1 | 2 | 3 | 4 | a | b | IV mp | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-41 | 11,0 | 5,5 | 4,5 | 4,7 | 3,0 | 17,7 | 28,7 | 11,5 | 6,5 | 4,7 | 4,0 |
| SAM 6231 | 17,0 | 7,5 | 6,5 | 6,0 | 5,5 | 25,5 | 42,5 | 17,4 | 10,0 | 6,5 | 5,5 |
| SAM 6232 | 18,5 | 9,0 | 7,0 | 7,0 | 5,0 | 28,0 | 46,5 | 20,5 | 11,5 | 7,4 | 7,5 |
| MNHN 1925-5-32 | 20,3 | 10,1 | 7,6 | 8,0 | 7,5e | 33,2e | 53,5e | 21,2 | 11,5 | 8,5 | 7,3 |
| MNHN 1908-21-10 | 21,3 | 10,6 | 8,0 | 8,0 | 7,5e | 34,1e | 55,4e | 22,6 | 12,9 | 8,8 | — |
| MNHN 1908-32-68/ 1925-8-14 | 22,1 | — | — | — | — | — | — | 24,0 | 12,8 | 8,5 | — |
| MNHN 1925-5-61 | 23,0 | — | — | — | — | — | — | 25,5 | — | — | — |
| MNHN 1908-32-24 | 23,1 | 10,5 | 7,5 | — | — | — | — | 24,7 | 12,5 | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — | — | — | — | — | — |
| MNHN 1908-21-14 | 23,0 | — | — | — | — | — | — | 24,8 | — | — | — |

| Specimen number | IV 4 | 5 | a | b | V mp | 1 | 2 | 3 | 4 | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN 1925-5-41 | 4,1 | 3,1e | 22,4e | 33,9e | 8,7 | 7,3 | 5,0 | 4,6 | 2,5 | 19,4 | 28,1 |
| SAM 6231 | 5,7 | 4,5 | 32,2 | 49,6 | 14,0 | 11,0 | 7,5 | 6,0 | 4,0 | 28,5 | 42,5 |
| SAM 6232 | 6,8 | 5,9 | 39,1 | 59,6 | 16,5 | 12,0 | 8,0 | 7,0 | 5,0 | 32,0 | 48,5 |
| MNHN 1925-5-32 | 7,3e | 7,5e | 42,1e | 63,3e | 17,5 | 13,3 | 8,6 | 7,9 | 5,2 | 35,0 | 52,5 |
| MNHN 1908-21-10 | — | — | — | — | 18,5 | 14,2 | 9,5 | — | — | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — | 18,6 | 15,0 | 9,4 | 8,6 | — | — | — |
| MNHN 1925-5-61 | — | — | — | — | 20,6 | — | — | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — | 20,0 | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | 21,0 | 15,4 | 10,0 | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | 20,0 | — | — | — | — | — | — |

| Specimen number | I/IV | II/IV | III/IV | V/IV | V/III | IV/x |
|---|---|---|---|---|---|---|
| MNHN 1925-5-41 | 0,41 | 0,66 | 0,85 | 0,83 | 0,98 | 6,78 |
| SAM 6231 | 0,39 | 0,65 | 0,86 | 0,86 | 1,00 | 7,52 |
| SAM 6232 | 0,38 | 0,59 | 0,78 | 0,81 | 1,04 | 7,45 |
| MNHN 1925-5-32 | 0,43 | 0,67 | 0,85 | 0,83 | 0,98 | 8,01– |
| MNHN 1908-21-10 | — | — | — | — | — | — |
| MNHN 1908-32-68/ 1925-8-14 | — | — | — | — | — | — |
| MNHN 1925-5-61 | — | — | — | — | — | — |
| MNHN 1908-32-24 | — | — | — | — | — | — |
| MNHN 1908-21-6 | — | — | — | — | — | — |
| MNHN 1908-21-14 | — | — | — | — | — | — |

(figs. 3, 5). Because of the position of the manus, the ulna lies parallel and medial to the radius, and has its anterior face turned upwards. The lateral side of the radius is usually seen from above. The femora tend to be directed outward (figs. 3, 4, 6) with the posterior surface facing upward. The foot is turned so that the dorsal surface remains up, but the outer digit (V) lies closer to the tail than digit I. The tibia was strongly attached to the femur by ligaments and retains its proper orientation with that bone. However, the distal attachments of the fibula were stronger than the proximal so the bone tends to lie closer to the tail than the tibia and is exposed in anterior aspect. There appears to be little or no post-mortem contortion of the spinal column such as commonly happened to crocodiles, dinosaurs and smaller reptiles and birds (Sternberg 1970).

The most conspicuous diagnostic character of *Hovasaurus* is the presence of abundant pebbles in the abdominal cavity (figs. 3, 5, 6, 7). The majority of these are quartz and have a water-worn appearance. Some of the stones are larger than the vertebrae of the animal in which they are found. Four specimens have pebbles up to 2*x* long, although the widths do not exceed 1,5*x*. The larger pieces are surrounded by smaller ones, most of which are 0,5–2 mm in diameter (fig. 7). These are still much coarser than the fine-grained silts that buried the specimens.

The pebble mass is completely enclosed within the abdominal cavity of most specimens. The ribs cover the mass dorsally, and the articulated gastralia underlie the mass. The pebble mass has a characteristic shape that tapers anteriorly and caudally. It does not fill the abdominal cavity, but in 14

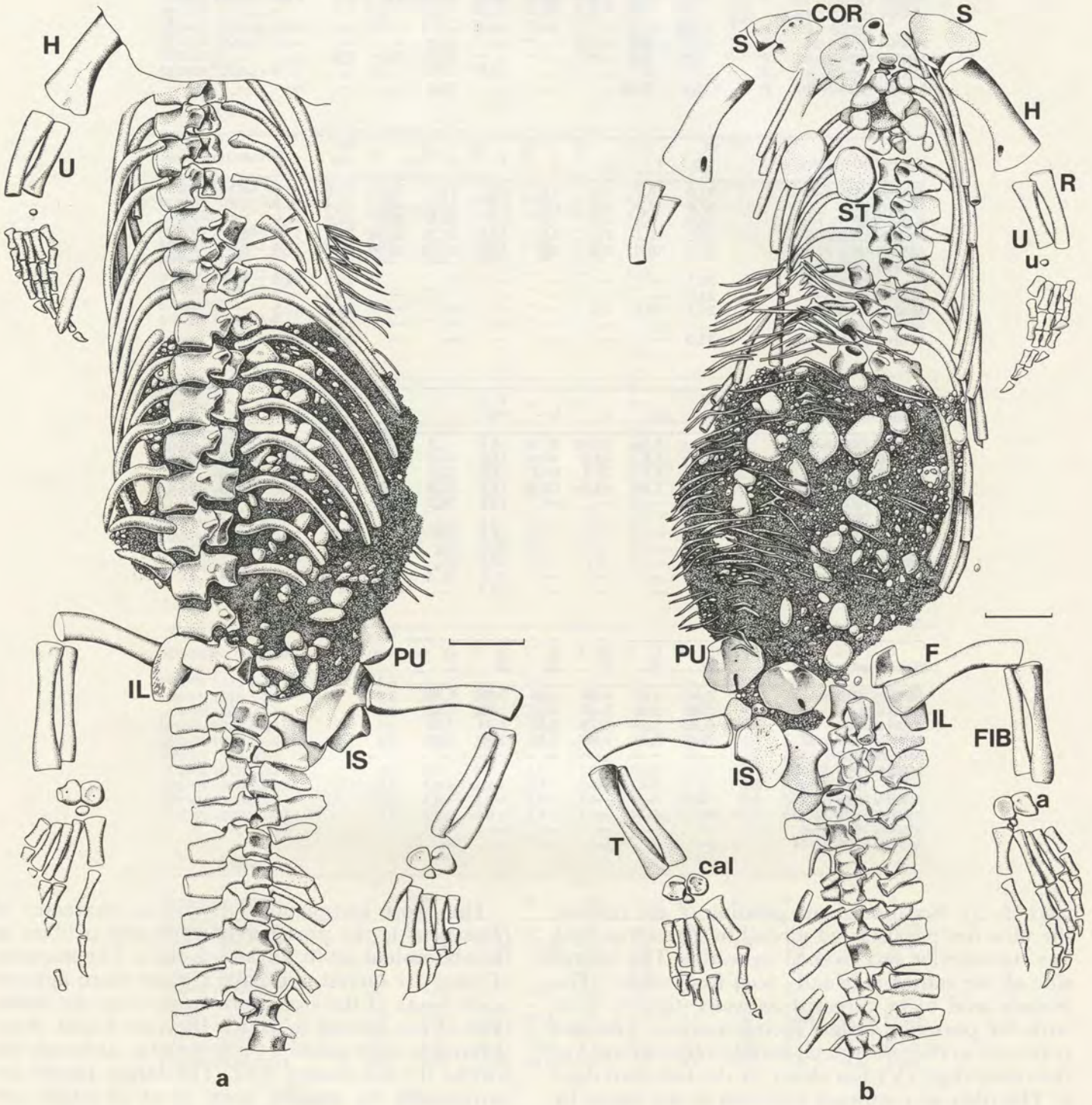



Figure 3. *Hovasaurus boulei*, lectotype. a, MNHN 1908-21-2; b. MNHN 1908-21-7; counterpart of MNHN 1908-21-2. Scale = 1 cm.

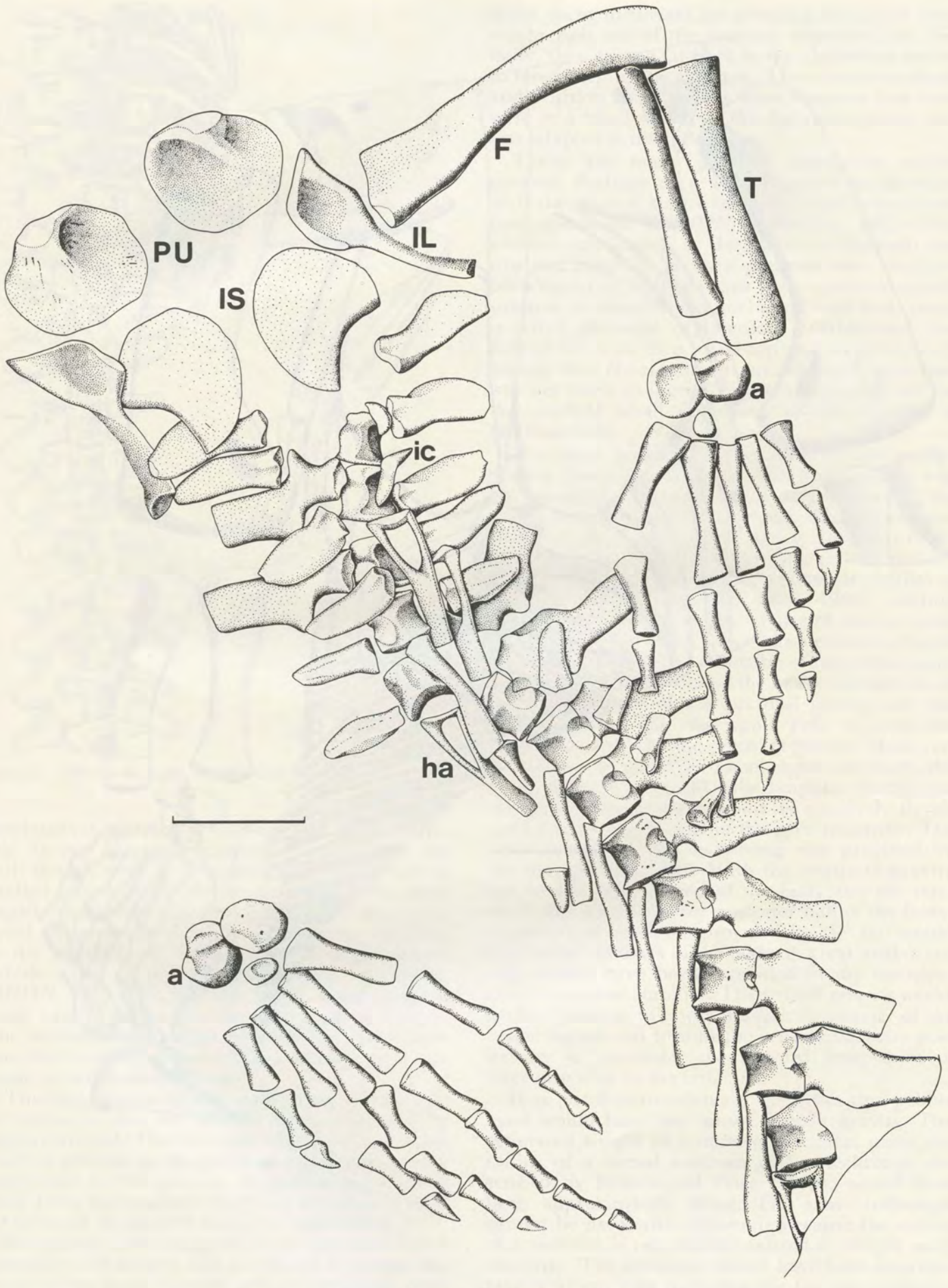



Figure 4. *Hovasaurus boulei*, MNHN 1908-32-77. Scale = 1 cm.

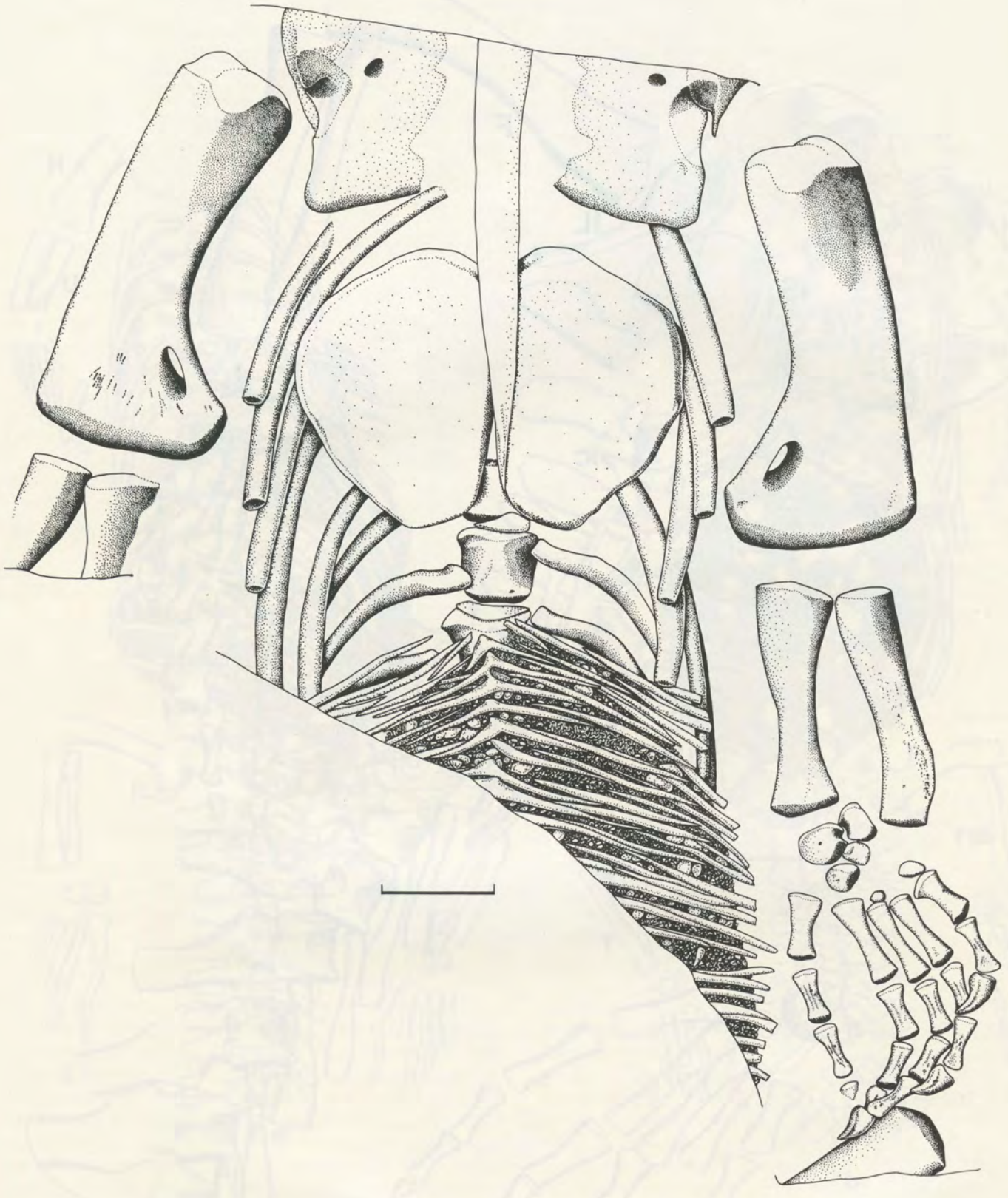


Figure 5. *Hovasaurus boulei*, MNHN 1925-5-12. Scale = 1 cm.

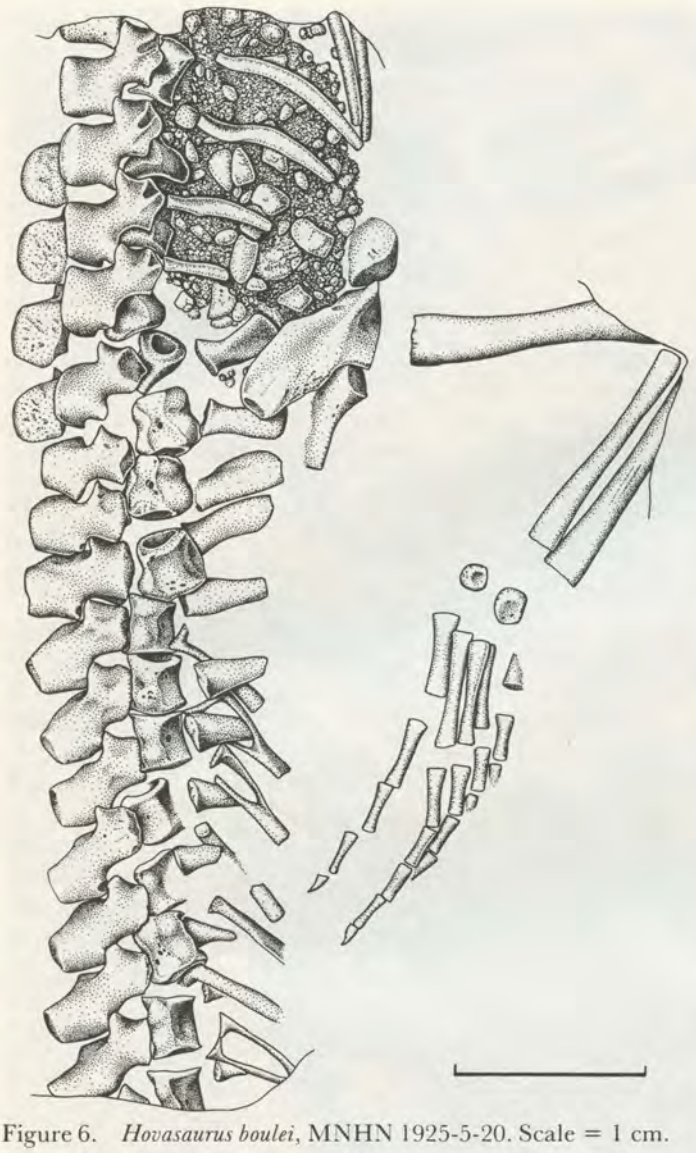


Figure 6. *Hovasaurus boulei*, MNHN 1925-5-20. Scale = 1 cm.

specimens is confined behind the 16th dorsal vertebra. In one specimen it extends anteriorly to the 12th dorsal, and in the balance of the specimens studied the anterior limit cannot be seen. Posteriorly the pebble mass usually enters the pelvic canal dorsal to the pubis, but can extend caudally to the back of the ischium. The sausage-shaped pebble mass of one of the smallest specimens, MNHN 1925-5-25, fills the pelvic canal and extends back to the level of the third caudal vertebra. The well-defined margins of the pebble mass indicate that it was enclosed within a membrane of soft tissue before decomposition.

The most logical explanation in light of the observations is that the pebbles were swallowed by the live animal. The lectotype (fig. 3b) has a small mass of pebbles in the pectoral region that it may have been in the process of swallowing when it died. Even the largest pebbles are less than a third the width of the skull in any of the individuals.

Haughton (1930) suggested that the stones were gastroliths. However, this is difficult to accept because of the large number present and their close packing. The small size of most would probably make them inefficient for grinding food, and they would pass out of the stomach with the food. Finally, they are too far back in the abdominal cavity to have been in the stomach. The consistent shape and position of the pebble mass suggests that they were in a blind sac along the digestive system that was adapted to hold them.

There are many possible alternative explanations. Perhaps they were ingested accidentally with the normal source of food. There are at least two specimens (MNHN 1908-21-6, 1925-5-60) without any stones in the abdomen between the ribs and gastralia, so their presence may not have been essential. Still, it seems that accidental acquisition of so many stones, including such large ones, is not a plausible explanation. Furthermore, the palatal teeth are slender, sharp and recurved, suggesting that *Hovasaurus* was an active predator that was not likely to ingest large amounts of gravel for the possible small organisms or detritus that it might include.

The most probable explanation for the pebble mass is that it functioned as ballast. *Hovasaurus* was an animal that spent a great deal of time in the water, using its long tail for propulsion. The symmetry of the tail suggests that it did most of its swimming underwater rather than on the surface. On the average, the specific gravity of reptiles is about 1,025 (Romer and Price 1940), slightly denser than fresh water; the centre of gravity tends to be high in the body, which has a tendency to roll over in the water. The reduction of the ossified portion of the scapular blade, the heavy ossification of the ventral part of the pectoral girdle, and the pachyostosis of the ribs would help to lower the specific gravity and the centre of gravity. However, the ribs in the posterior dorsal region are short, the ilium is not reduced like the scapular blade, and the puboischiatic plate is not as massively developed as the ventral part of the pectoral girdle. The main propulsion for swimming was provided by the long powerful tail. With the centre of gravity low in the anterior end of the body and the relatively low density of the posterior half of the body, a portion of the force provided by the tail would tend to lift the back of the body. A great deal of energy would have been expended in the maintenance of vertical stability. The pebble mass is in the perfect position to lower the specific gravity of the pelvic region and to shift the centre of gravity posteriorly to maximize the forward component of force provided by the tail.

It is possible to calculate the effect this pebble mass would have had on the specific gravity. The estimated weight of a mature specimen, using the radius of a dorsal centrum and a technique described by Romer and Price (1940), would have been approximately 10 kg. The same technique cannot be used with a juvenile because the radius of a centrum is not directly related to weight until maturity. The lectotype would have been approximately 40 cm long including the tail. By multiplying the weight of the adult by the cubed ratio of ju-



Figure 7. *Hovasaurus boulei*, MNHN 1925-5-29. Ingested pebbles. Magnification approximately X3,7.

venile to adult length, a crude weight estimate of 300 to 500 g is reached for the lectotype. A cast was made of the three dimensional pebble mass of MNHN 1908-21-2/7 and the volume calculated by liquid displacement. The weight of the mass was calculated using the specific gravity of quartz (2,5), and amounted to 25 g. This is enough to raise the specific gravity of the animal by five to ten per cent, to the lower end of the specific gravity range of aquatic turtles (Zug 1971).

The use of ingested stones for ballast is not a new idea. Cott (1961) presented data to show that the "gastroliths" function to lower the specific gravity and the centre of gravity in the Nile crocodile. Large masses of ingested stones, similar in abundance to *Hovasaurus*, are found in the abdomens of many plesiosaur specimens, and were probably used for ballast (Darby and Ojakangas 1980).

Stomach stones are found in at least two specimens of *Thadeosaurus* (MNHN 1908-11-5, Piveteau 1926: pl. XI; MNHN 1908-5-1, Piveteau 1926: Pl. XII, fig. 1) but are few in number and probably did serve as gastroliths. When present, the relative abundance of stomach stones is a quick way to distinguish *Hovasaurus* and *Thadeosaurus*.

Absence of stones in the abdomen of *Tangasaurus* does not necessarily mean that this genus did not swallow pebbles. The gastralia have been lost, and the pebbles could have been lost by post-mortem rupture of the abdominal cavity.

## Skull

*General.* The skull of *Hovasaurus* is poorly known. Only nine of the hundreds of specimens of this genus that have been collected have partial skulls. Two of the best specimens figured by Piveteau (1926: Pl. VII, fig. 3 and Pl. XIV, fig. 1) could not be relocated for study.

The most complete skull studied is that of MNHN 1925-5-34 (fig. 8). The skull has been disarticulated, and the skull roof is visible in ventral view only. Maxilla, jugal, frontal, postfrontal, parietal, pterygoid, epipterygoid and quadrate bones are represented. Elements of the lower jaw are present but are crushed and incomplete so that only the right surangular could be identified.

MNHN 1925-5-30 (fig. 9) includes part of the basisphenoid-parasphenoid complex, a prootic, opisthotics, a basioccipital and exoccipitals. The posterior ends of two hyoid bones are preserved.

Portions of the skull roof and occiput are visible in MNHN 1925-5-36 (fig. 10). Parietals, a postorbital, a squamosal, a quadrate, a supratemporal, a supraoccipital and a hyoid have been identified.

The same region is exposed in MNHN 1908-32-99 (fig. 11) where parietals, a postfrontal, a postorbital, a squamosal, a supratemporal, an opisthotic and a stapes can be seen.

Three specimens, MNHN 1908-32-1, 1908-32-23 and 1925-5-49, have only portions of the most posterior bones of the skull and mandibles preserved.

The bones of all known skulls were disarticulated after death, suggesting that none of these animals was mature enough for the bones to have been firmly sutured. The largest specimen with a skull (MNHN 1925-5-36) is only three-quarters of the maximum known size, and it is possible that

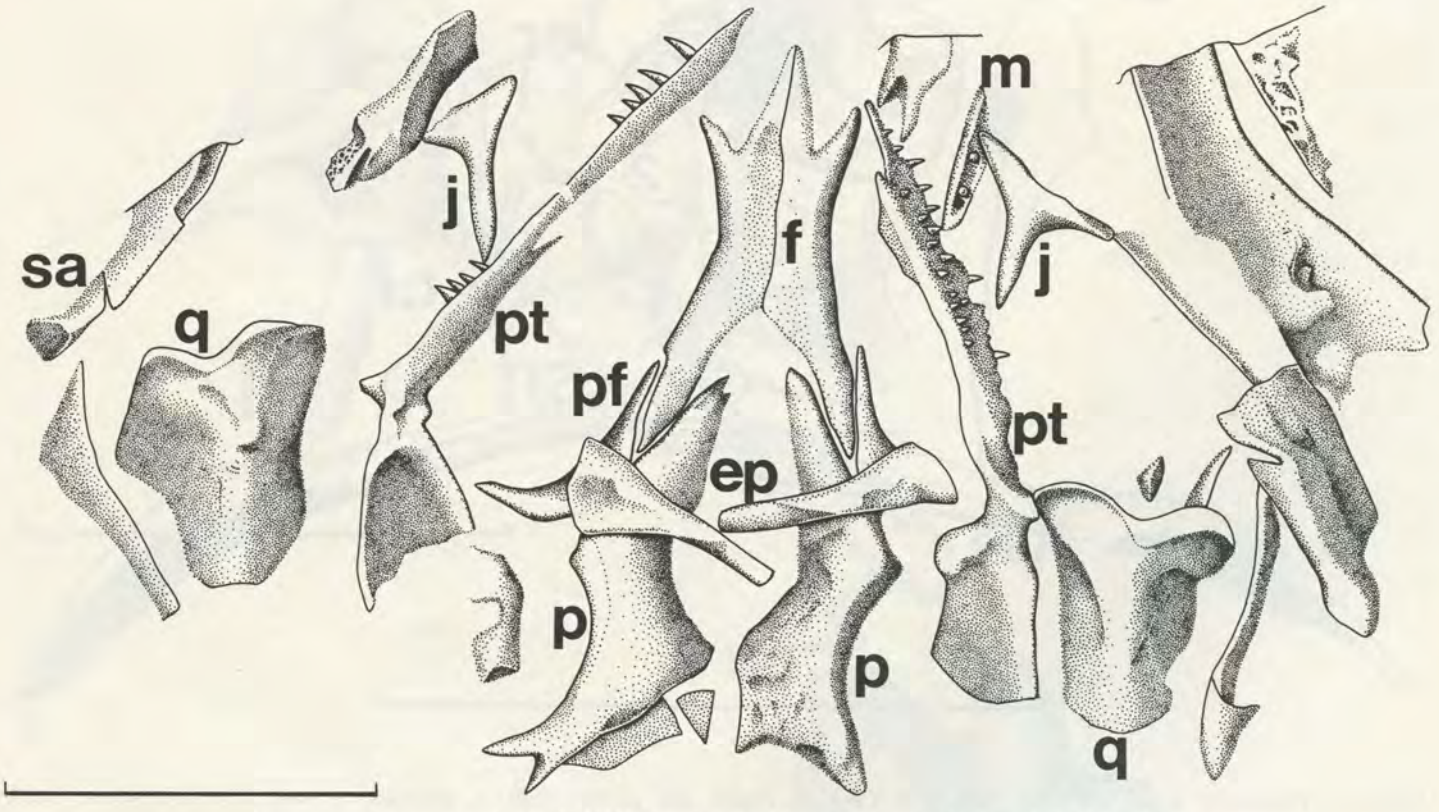



Figure 8. *Hovasaurus boulei*, MNHN 1925-5-34. Ventral view of skull roof. Scale = 1 cm.

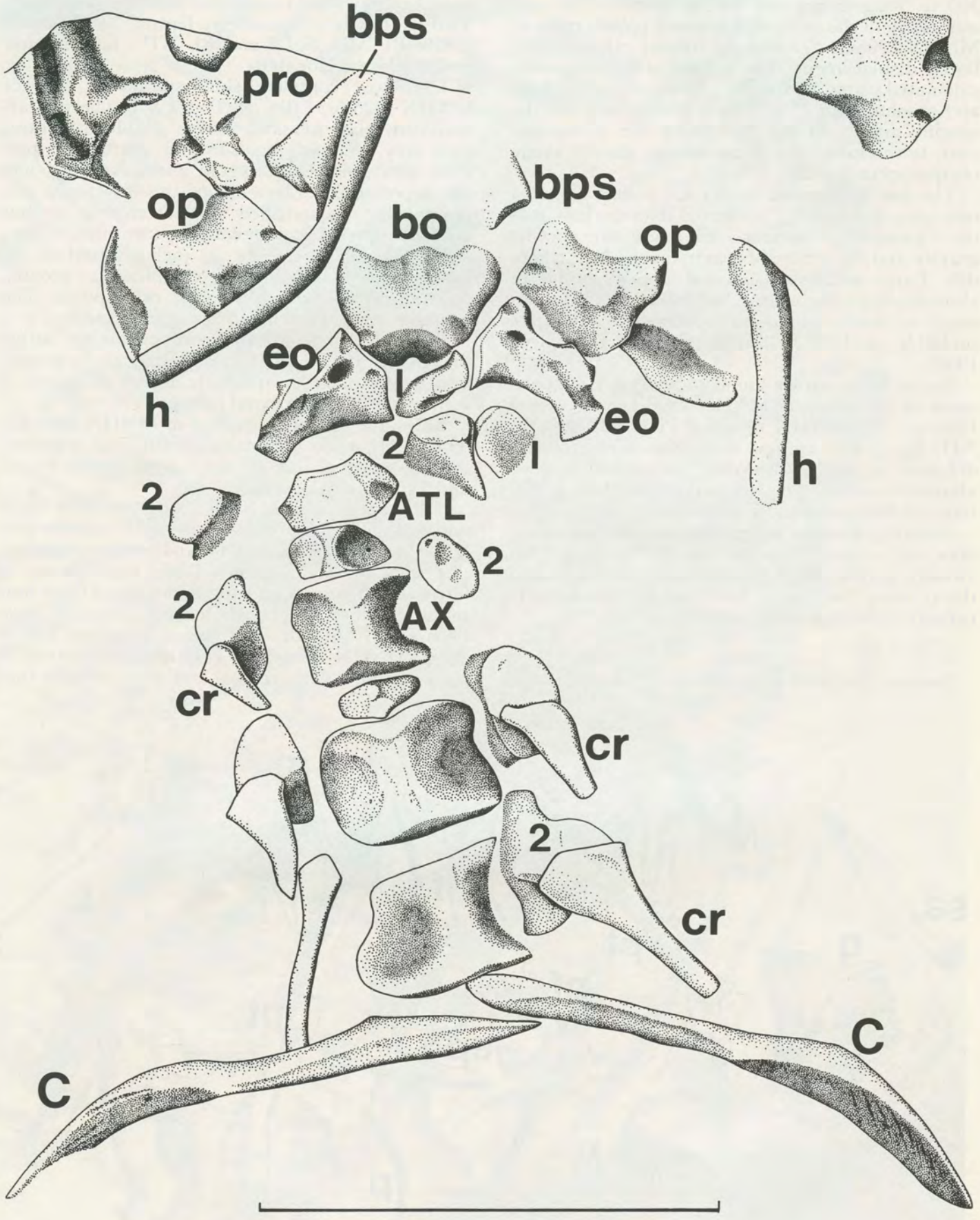



Figure 9. *Hovasaurus boulei*. MNHN 1925-5-30. Cervical region and partial skull, 1, proatlas; 2, base of neural spine. Scale = 1 cm. Upper right, reconstruction of left opisthotic (posterior view).

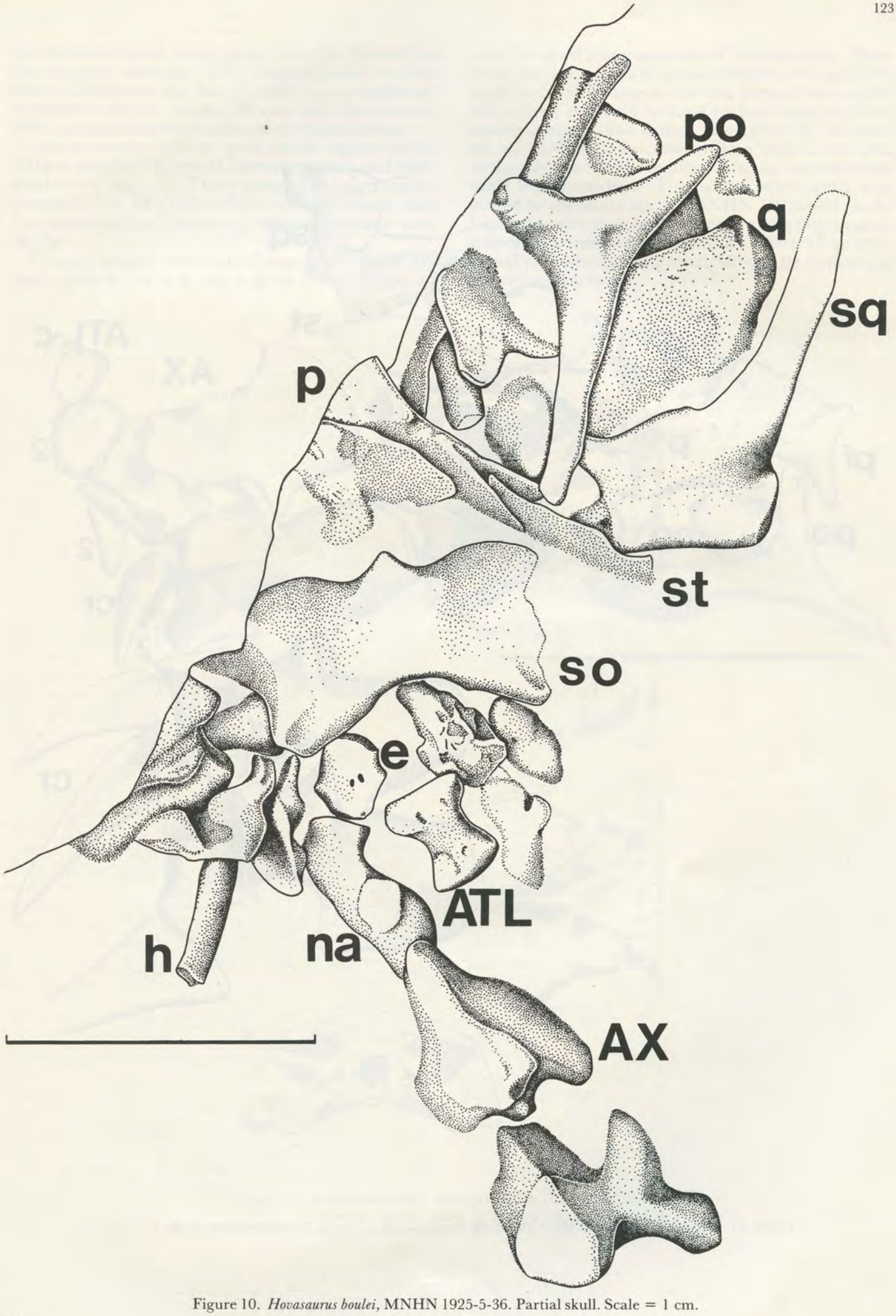



Figure 10. *Hovasaurus boulei*, MNHN 1925-5-36. Partial skull. Scale = 1 cm.

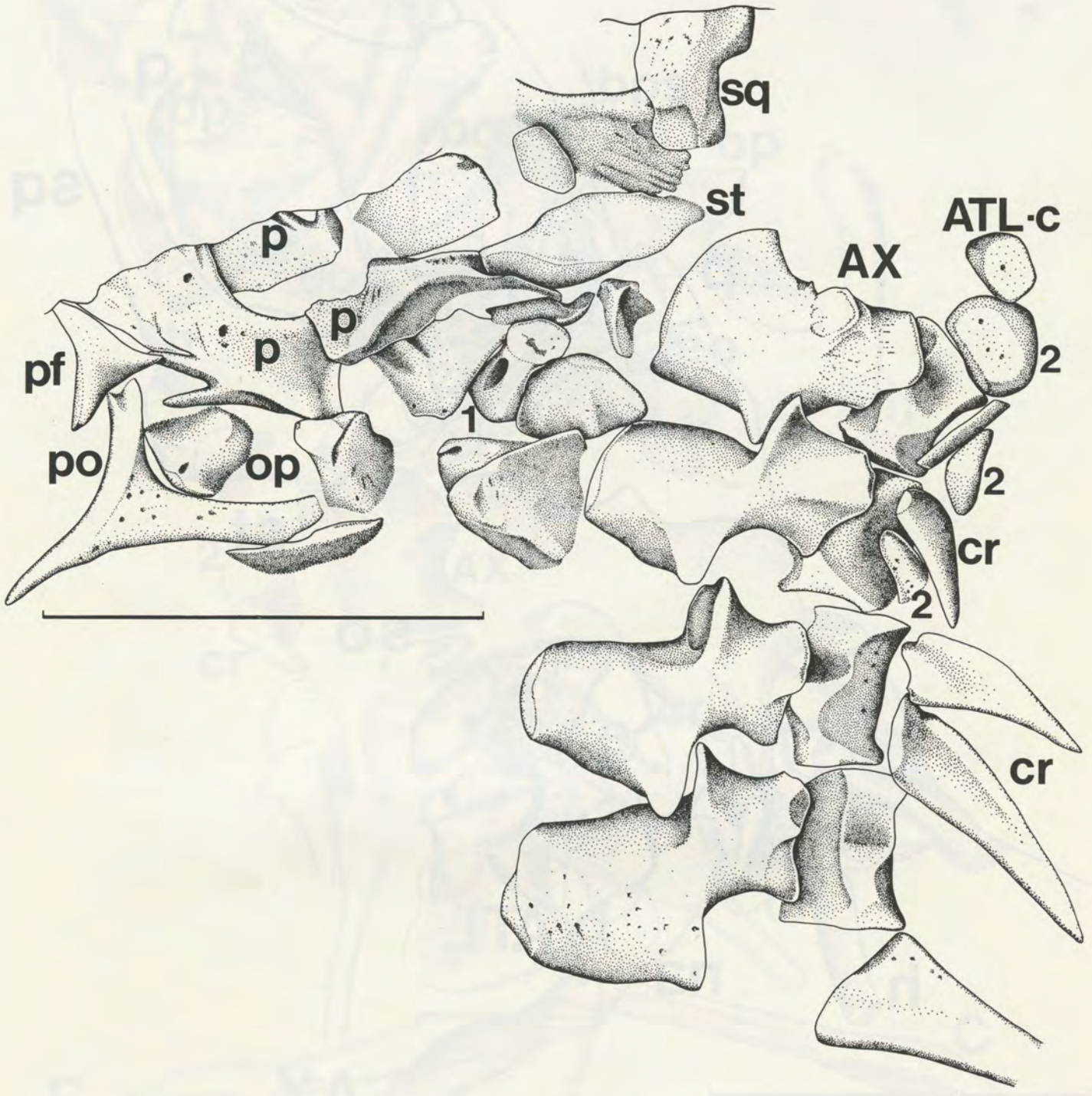



Figure 11. *Hovasaurus boulei*, MNHN 1908-32-99. Partial skull. 1, stapes; 2, intercentrum. Scale = 1 cm.

the dermal bones were more strongly sutured in the largest animals. The endochondral cranial bones, which are the last to ossify in the ontogeny of modern reptile skulls (Howes and Swinnerton, 1901), are well formed in the smallest specimens.

Reconstruction of the postorbital region of the skull is possible in dorsal, lateral, ventral and occipital views (fig. 12). These restorations were based primarily on MNHN 1925-5-34, an animal that was intermediate in size to other specimens with skulls.

Cranial proportions can change during ontogenetic growth, so it is not a good policy to reconstruct a skull using animals of different ages. However, not enough data are available to calculate the coefficient of allometry for the postorbital region. Growth of the skull is more or less isometric in at least some reptilian genera (Currie 1979). Furthermore, the largest specimen with a skull is less than twice the size of the smallest, and the reconstructed skull is intermediate. Finally the other skulls were scaled to the same size as MNHN 1925-5-34 on the basis of bones they have in common rather than on postcranial measurements. The effect of proportional changes due to growth should be minimal in the reconstruction.

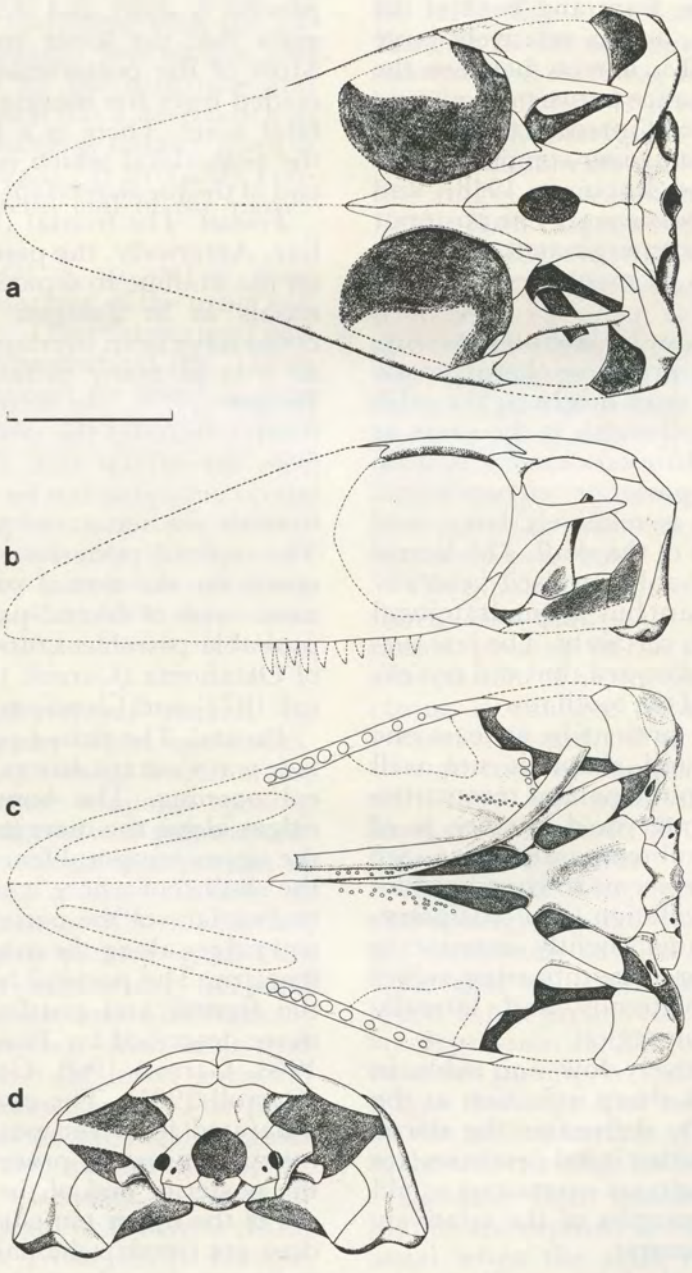



Figure 12. *Hovasaurus boulei*. Reconstruction of skull. a, dorsal view; b, lateral view; c, palatal view; d, occipital view. Scale = 1 cm.

The antorbital region of the skull is unknown. Piveteau (1926) stated that the skull was probably elongate as in *Mesosaurus*, but had no supportive evidence. A skull figured by Piveteau (1926: Pl. XIII, fig. 5, Pl. XIV, fig. 1) is missing the anterior end, but appears to be tapering anteriorly at an angle that suggests there was no elongate snout.

As reconstructed, the skull is about 30 mm wide for an animal with a 6,4 mm long dorsal centrum. This is very close to the width of the skull of *Heleosaurus* (SAM 1070), an eosuchian with an average length of 6,5 mm for the dorsal centra. In dorsal aspect (fig. 12a), the skull seems to have been broader in the quadrate region than immediately behind the orbits. Both temporal openings are visible in dorsal view. The pineal opening is approximately equidistant from the front and back of the parietal along the midline, and is relatively large for an eosuchian. The skull is narrow between the orbits compared to the distance between the upper temporal fenestra. The ratio of interorbital to intertemporal width is 0,4 in *Hovasaurus* compared with 1,1 in *Youngina* (Broom and Robinson 1948), and an estimated 1,0 in *Acerosodontosaurus*. The posterior margin of the skull table is emarginated centrally, but not to the degree seen in many Permian reptiles.

The skull is relatively low in lateral view (fig. 12b) which is considered a primitive characteristic (Reisz 1981). The ratio of skull height in the orbital region to maximum skull width is the same as in the reconstruction of *Acerosodontosaurus* (Currie 1980). The dorsal and posterior circumorbital bones show that the orbit is relatively large, and occupies most of the height of the skull. The lateral temporal fenestra was probably enclosed ventrally by a complete temporal bar, but a quadratojugal has yet to be identified with certainty. The jaw suspension apparently sloped forward, but did not extend much below the level of the tooth row.

Suborbital fenestrae are present in at least one specimen but their size and shape is not well enough known to include in the palatal reconstruction (fig. 12c). The interpterygoid vacuity is of moderate size and the subtemporal fossae are large. The occipital condyle seems to have been located behind the jaw articulation. The basipterygoid articulation was located slightly anterior to the transverse process. Three toothbearing ridges radiate anteriorly, anterolaterally and laterally across the pterygoid from this region.

The skull appears relatively low and wide in occipital view (fig. 12d). A sharp inflection at the back of the parietal clearly delineates the dorsal limit of the occiput. The paroccipital processes are relatively short, but cartilaginous entensions would have formed the ventral margins of the relatively large posterior temporal fenestra.

*Maxilla.* The posterior end of the maxilla can be seen in ventral view in two specimens. The bases of several posterior teeth are preserved and have diameters of less than 1 mm. At least nine maxillary teeth can be seen in the partial maxilla figured by Piveteau (1926, Pl. XIV, fig. 1), but the total maxillary tooth count must have been more than double this number. The maxilla extended posteriorly to the back of the orbit.

*Jugal.* The jugal is triradiate and seems to be relatively smaller than the same element in any other eosuchian known. The suborbital ramus is short, and could not have extended anteriorly for more than half the length of the orbit. The bone is not thickened medially as the other circumorbital bones are. The ventral margin is straight below the orbit, but is inflected ventrally in the region of the subtemporal ramus. There is no evidence of a ventromedial tuberosity such as in *Heleosaurus* (Carroll 1976a) and many other primitive reptiles (Romer and Price 1940, Heaton 1979). The subtemporal process is short and slender, but its presence suggests that the lower temporal bar was complete. Most of the postorbital ramus of the jugal is excluded from the margin of the orbit by the postorbital bone. There is a long diagonal contact with the postorbital which is twisted so that the dorsal end of the jugal overlaps the suture.

*Frontal.* The frontal (fig. 8) is distinctive in outline. Anteriorly, the paired frontals taper to a point on the midline to separate the posterior ends of the nasals as in *Youngina* (Gow 1975). The frontal could have been overlapped externally by the nasal as it is in many primitive reptiles (Currie 1977, Heaton 1979). An anterolateral projection of the frontal excludes the posterior end of the prefrontal from the orbital rim. There is a narrow posterolateral emargination for the postfrontal. The paired frontals are separated posteriorly by the parietals. The tapered posterior end of the frontal fits into a notch on the dorsal surface of the parietal. The same type of frontal-parietal suture is found in a probable petrolacosaurid from the Lower Permian of Oklahoma (Carroll 1968) and in *Youngina* (Carroll 1977) and *Claudiosaurus* (Carroll, 1981).

*Parietal.* The paired parietals meet in a longitudinal, wavy suture anterior and posterior to the pineal opening. The bone is thickened into dorsal ridges along the margins of the pineal opening and the upper temporal fenestra. Another ridge borders the skull roof where it meets the occiput. The ventral surface of the parietal is vaulted between ventral ridges along the margins of the upper temporal fenestra. The parietal has distinctive contacts with the frontal and postfrontal that are identical to those described for *Youngina* (Broom and Robinson 1948, Carroll 1968, Gow 1975) and *Claudiosaurus* (Carroll 1981). The posterior end of the frontal is separated from the postfrontal by the parietal. A rostrally directed process of the parietal excludes the posterior end of the postfrontal from the margin of the upper temporal fenestra. The postfrontal does not overlap the parietal. This pattern appears to be primitive because it is found in protorothyridids. The similarity is particularly striking in *Protorothyris* (Clark and Carroll 1973; fig. 2)

The posterolateral corner of the parietal is notched on its dorsal surface for the attachment of

the supratemporal (figs. 10, 11). The posterior margin of the skull is embayed medially, and the parietals apparently extended onto the occiput for a short distance (fig. 11).

*Postparietal, tabular.* These bones are not seen clearly in any of the specimens. Fragments of one or both elements are present between the parietal and supraoccipital of MNHN 1925-5-36 (fig. 10), so they have been included as a single outline in the reconstruction on the basis of information from the surrounding bones.

*Supratemporal.* The supratemporal is an elongate bone that tapers at both ends (fig. 11). It is relatively larger than in any other eosuchian or protorothyridid. There is no apparent adaptive significance for the enlargement of this bone in *Hovasaurus*, but it could be correlated with the anterior position of the mandibular articulation and the change in orientation of the quadrate and squamosal. The supratemporal fills a deep notch in the parietal (fig. 10), but becomes thinner when it overlaps the squamosal distally. It probably contacted the cartilaginous lateral end of the paroccipital process.

*Postfrontal.* The postfrontal is an arched bone that forms portions of the margins of the orbit and the upper temporal fenestra. The ventrolateral end is tapered and overlaps the postorbital (fig. 11) as in most primitive reptiles except for *Petrolacosaurus* (Reisz 1981). The postfrontal is not excluded from the margin of the upper temporal fenestra by the parietal and postorbital.

*Postorbital.* The postorbital is a triradiate bone with a long intertemporal ramus (fig. 11) that contacts the squamosal posteriorly in an overlapping suture. The weak curvature of the bone shows that both temporal fenestrae would be visible in lateral view.

*Quadratojugal.* The quadratojugal cannot be identified with certainty in any of the specimens. In the reconstruction, the postorbital length of the skull and the size of the lower temporal opening were determined by the skull roof and palatoquadrate elements. If the quadratojugal was present in *Hovasaurus*, it was apparently a large element, at least as long as that of *Heleosaurus* (Carroll 1976a). Although the quadratojugal is present in all Permian eosuchians, it has lost contact with the jugal in the prolacertids, paliguanids and *Claudiosaurus*. The close relationship between *Hovasaurus* and *Youngina* is weak evidence that the lower temporal arch was complete in the tangasaurid. The presence of a subtemporal ramus on the jugal suggests that this bone contacted the quadratojugal, although a similar posterior extension of the jugal does not meet the quadratojugal in *Prolacerta* (Robinson 1967) or *Tanystropheus* (Wild 1973). Haughton (1930) examined one of the missing skulls of *Hovasaurus* (Piveteau 1926: Pl. VI, fig. 3) and felt that the lower temporal bar was complete on the left side of the specimen. Finally, Camp (1945) examined a cast of another specimen described by Piveteau (1926: Pl. IX, fig. 1) and tentatively identified a long, slim bone as the quadratojugal.

*Squamosal.* The posterior margins of the upper and lateral temporal openings are formed by the squamosal. There is an almost rectangular dorsal region with a distinct posterior process (fig. 10). This process is present, although it is not as prominent, in *Youngina*. This is the only portion of the squamosal of *Hovasaurus* that extends onto the occiput, where it possibly would have met the paroccipital process. A distinct, almost rod-like descending process of the squamosal is inclined anteroventrally, one indication that the jaw articulation has shifted anteriorly from its primitive position behind the occiput.

*Palate.* The palate illustrated by Piveteau (1926: Pl. XIV, fig. 1) is basically the same as that of *Youngina* in the configuration of the suborbital and subtemporal fenestra, and the interpterygoid vacuity. The palatine is present but lacks a visible suture with the pterygoid (Piveteau 1926).

The palatal ramus of the pterygoid has two ventral ridges separated by a low vault (Haughton 1930). Both ridges are tooth bearing, and the teeth on the medial ridge of MNHN 1925-5-34 are up to 0,8 mm long. The palatal teeth are randomly distributed on the crests of the ridges. Both pterygoids of MHNH 1925-5-34 can be seen in medial view (fig. 8). The medial edge of the palatal ramus of the pterygoid turns sharply dorsad anterior to the interpterygoid vacuity, and forms a low, vertical plate of bone.

The basipterygoid articulation is located anteromedial to the pronounced but low transverse process of the pterygoid.

The quadrate ramus of the pterygoid is relatively short, less than half the length of the palatal ramus, because of the anterior position of the jaw articulation. The medial surface of the quadrate ramus is concave above the medially thickened ventral margin. The anterodorsal border is strengthened by another ridge that terminates dorsally in a low process. The epipterygoid would have covered most of the anterodorsal margin of the quadrate process.

*Epipterygoid.* The epipterygoid has a broad base and a long, rod-like dorsal extension. The base is not completely ossified in MNHN 1925-5-34 (Fig. 8) because of immaturity, so its basicranial articulation is not preserved. There is a distinct triangular depression on the medial surface of the base, bounded anteriorly and posteriorly by ridges. The ridges converge and meet dorsally, and continue up the medial surface of the columella to terminate at the anterior edge halfway up.

*Quadrate.* Both quadrates of MNHN 1925-5-34 (fig. 8) are exposed in external aspect, which is unusual when the skull roof is exposed in ventral view. In most disarticulated reptile skulls from the Paleozoic, the quadrates lie behind the skull with the condyles facing caudad. The position of the quadrates in this specimen with the condyles oriented anteriorly suggests that in life the ventral

end of the quadrate was anterior to the dorsal end. The condyles of the right quadrate of MNHN 1925-5-36 (fig. 10) are anterior to the squamosal, the ventral ramus of the squamosal is directed anteroventrally, and the quadrate ramus of the pterygoid is short, all of which supports the concept of the jaw articulation being anterior to the occiput.

The quadrate is a broad, relatively low bone that terminated ventrally in a pair of condyles for articulation with the mandible. The width to height ratio is 0,9, compared with 0,8 in *Thadeosaurus* and 0,4 in *Youngina* (Olson 1936), although the dorsal end was unossified at death in MNHN 1925-5-34. The quadrate of *Thadeosaurus* is indistinguishable from that of *Hovasaurus* in shape, size and position. A ridge on the external surface of the quadrate extends from the medial condyle to the dorsal edge as in *Youngina* (Olson 1936) and *Thadeosaurus*. Medial to the ridge is an extensive sutural surface for the pterygoid. A stapedial boss protrudes from the ridge above the condyles, and the cartilaginous distal end of the stapes would have passed dorsal to this knob. The quadrate of *Hovasaurus* is basically the same as those of *Youngina*, *Thadeosaurus*, *Acerosodontosaurus* and *Heleosaurus*.

*Braincase*. The parasphenoid and basisphenoid are fused (Piveteau 1926: Pl. XIV, fig. 1) and will be treated as a unit. The maximum width of the complex is 28 per cent of the total length. The elongate cultriform process makes up approximately two thirds of the total length. Anterior to the basipterygoid tubercles the rostrum is narrow at its base, expands somewhat anteriorly, and then tapers to a point. In *Thadeosaurus* it is swollen anterior to the tubercles. A low ridge runs along the midline of the cultriform process, and ends posteriorly between the basipterygoid processes. The basipterygoid tubercles are oriented anteriorly, ventrally and laterally, and are not fused to the palate. No carotid foramina are visible on the ventral surface (Piveteau 1926). The complex is concave ventrally in transverse section between the crista ventrolateralis, and this region would have been lined in life by the pharyngeal membrane. There is a low, ventral ridge along the midline in the region where the complex overlaps the basioccipital. The crista ventrolateralis does not extend as far beyond the posterior margin of the bone on the midline as it does in *Thadeosaurus*.

The supraoccipital is a large, platelike bone (fig. 10). There is a crest along the midline of the posterior surface, extending from the foramen magnum to a pronounced medial process on the dorsal margin of the bone. Lateral to the margin of the foramen magnum, the ventral margin of the supraoccipital has an oblique, overlapping suture with the exoccipital. A ventrolaterally facing process abuts the dorsomedial portion of the opisthotic. A well-developed lateral ascending process extends dorsolaterally to contact the dermal roofing bones. Ventrolateral to this process, a concave region would have been continuous with the crista alaris of the prootic.

The exoccipital (fig. 9) is excavated medially by the foramen magnum and laterally by the vagus foramen. It is perforated by a single foramen for the hypoglossal nerve ventromedial to the vagus foramen. The vagus and hypoglossal foramina are separated by a well-defined ridge. There is a sharp inflection on the ventral margin of the exoccipital where it contacts the basioccipital. The exoccipital does not take part in the occipital condyle, and there is no facet visible for the articulation with the proatlas. The lateral margins dorsal and ventral to the vagus foramen are thickened for a strong suture with the opisthotic. The dorsal suture for the supraoccipital is relatively small, and the exoccipitals do not meet at the midline.

The basiocciptal (fig. 9) forms the hemispherical occipital condyle. It is concave dorsomedially where it forms the floor of the foramen magnum. A semicircular notochordal "pit" indents the posterodorsal margin of the occipital condyle. A pair of basioccipital tubercles diverge anterolaterally from the occipital condyle along the ventral surface. A pair of small concavities on the posterolateral surfaces of the tubercles possibly represent the insertions of the M. longissimus capitis transversalis cervicus. The basioccipital is thin and vaulted (except for a slight midline ridge) between the basioccipital tubercles. The region is overlapped ventrally by a thin posterior extension of the basisphenoid.

A partially exposed prootic can be seen in MNHN 1925-5-30 (fig. 9) in posterior view. Portions of two shallow grooves could have been for the vena capitis lateralis on the external surface and the subarcuate fossa on the posteromedial face.

The opisthotic is visible in posterior view in MNHN 1925-5-30 (fig. 9) and MNHN 1908-32-99 (fig. 11), and in anterodorsal view in MNHN 1925-5-36 (fig. 10). The exoccipital sutures and lateral margin of the vagus foramen cannot be seen in any of the specimens but can be reconstructed from the exoccipital (fig. 9). As in *Thadeosaurus*, there is almost no development of an osseous paroccipital process in MNHN 1925-5-30. The distal end of the process is unfinished bone and would have been continued in cartilage. The paroccipital process would have been more extensive in large animals, and probably extended to the region where the supratemporal, squamosal and quadrate converge. A bony protuberance occupies a central position on the posterior surface of the opisthotic at the intersection of two low ridges. The external surface of the bone is convex, whereas in most other reptiles it is concave posteriorly when viewed dorsally or ventrally. This is further evidence indicating an anterior position for the quadrate in relation to the occipital condyle. There is a conspicuous but small foramen ventrolateral to the intersection of the opisthotic, exoccipital and basioccipital in all specimens that show this region. A branch of the fourth cranial nerve emerges from this region in crocodiles (Iordansky 1973). The anterodorsal view of the opisthotic (fig. 10) shows broad sutural

surfaces for the prootic and supraoccipital, and confirms that this bone enclosed portions of the posterior ampulla and posterior semicircular canal.

*Stapes*. The right stapes of MNHN 1908-32-99 (fig. 11) protrudes through the fragments of other bones. It is 2,8 mm in length, has a shaft diameter of less than 1 mm and expands distally to 1,5 mm. The footplate is partially obscured and cannot be measured. As in *Youngina* and most other primitive reptiles, the shaft is perforated by the stapedial foramen. There is no evidence of an osseous dorsal process. The distal end of the columella is unfinished bone, and must have been extended in cartilage to the quadrate.

*Mandible*

Details of only two bones of the mandible can be seen. The dorsal margin of the surangular is visible in one specimen (fig. 8). It is thickened medially into a ridge that forms the upper margin of the adductor foramen. Anteriorly this ridge is excavated dorsally for the coronoid. Posteriorly it becomes a prominent buttress where it supports a short, wide, posteromedially oriented facet that connects to the articular.

Piveteau (1926) noted that there was a short retroarticular process on the articular.

*Hyoid*

*Hovasaurus* has a pair of hyoid (ceratobranchial I) bones (figs. 9, 10; Piveteau 1926: Pl. XIV, fig. 1) similar to those of *Thadeosaurus*, and many other primitive reptiles. The hyoid is a long, slender curved rod of bone. The anterior portion is almost parallel to the longitudinal axis of the skull, and the posterior portion is inflected posterolaterally. The posterior end is cupped and probably had a cartilaginous extension (epibranchial I). The central region of the bone is somewhat flattened. A low ridge extends along the ventromedial surface of the anterior half of the bone, separating the insertion regions of two sets of hyoid musculature. The hyoid of MNHN 1925-5-30 is more than 9 mm (2,4*x*) in length with a shaft diameter of about 1 mm.

## Vertebrae

*General*. The vertebrae of *Hovasaurus* have notochordal centra (figs. 13, 15b) as do most primitive reptiles.

Piveteau (1926: Plate VII, fig. 3) counted 24 presacral vertebrae in one specimen of *Hovasaurus*. A number of specimens, including MNHN 1908-32-99 (fig. 11) show that there are five cervical vertebrae, whereas others, such as MNHN 1908-32-24 (Piveteau 1926: Pl. XIII, fig. 1) have 20 dorsals. This suggests that the presacral count is 25, which is confirmed by the complete preserved presacral series of MNHN 1908-32-1. The number of presacral vertebrae falls within the range known for other genera of primitive eosuchians. Numerous specimens of *Hovasaurus* are known to have two sacral vertebrae (figs. 3, 5). It would be easy to misinterpret the first caudal rib as a third sacral rib because it curves slightly anteriorly and almost touches the ilium. Most primitive reptiles have between 50 and 70 caudal vertebrae (Romer 1956), but the total number is known in few eosuchians. Gow (1975) has shown only 30–35 caudals in his reconstructions of *Youngina*. However, none of the specimens he examined has a caudal series preserved in its entirety, so it can be assumed that the tail as reconstructed is too short. Carroll (1975a) estimated that the caudal count of *Saurosternon* approaches 70. Fifty-six caudals are preserved in *Kenyasaurus* (Harris and Carroll 1977) and 47 in *Thadeosaurus* (Carroll 1981). In one specimen of *Hovasaurus*, MNHN 1908-32-58, the eighth to 53rd caudals are preserved, but do not include any distal caudals. SAM 9546 includes 14 distal caudals, none of which is the terminal caudal. An estimate of 70 caudal vertebrae is probably conservative for *Hovasaurus*.

The presacral series can be divided into cervical and dorsal sections. Piveteau (1926) distinguished the cervicals by the absence of ribs. However, there are cervical ribs in *Hovasaurus*, which must have been inconspicuous in the specimen he was looking at. This specimen has been misplaced, and could not be relocated for study. Ribs have been disarticulated from the sterna in all known specimens of *Hovasaurus*, so relationship to the sternum cannot be used to define the dorsal region. The ribs of the sixth presacral segment are considerably longer than those of the fifth, and have the same basic form as more posterior ribs. For this reason, the sixth presacral vertebra is considered to be the first dorsal.

*Cervical Vertebrae*. The atlas-axis complex is preserved in ventral (fig. 9), dorsal (fig. 10) and lateral (fig. 11) views.

The proatlas is a small, paired element. The articulation with the exoccipital is at right angles to the articular facet for the atlas and is separated from it anteroventrally by a small area of finished bone (fig. 10). A small process on the dorsoposterior surface may represent a rudimentary neural arch.

The atlas centrum cannot be seen clearly in any specimens. It is preserved in dorsal view in MNHN 1925-5-36 (fig. 10) and possibly lateral view in MNHN 1908-32-99 (fig. 11). Unfortunately, the atlas-axis complex of the latter specimen is disarticulated, and the orientation of the atlas centrum is questionable. The close articulation between the centra of the atlas and axis suggests that the former is being viewed in dorsal aspect. However, the bone exposed in this view is finished, suggesting that it is a lateral surface. The bone interpreted as the atlantal centrum in MNHN 1925-5-36 (fig. 10) is about 75 per cent the length of the axial centrum, and shows articular facets on the dorsolateral surfaces for articulation with the neural arch. The atlantal neural arch is paired as in all primitive reptiles. There is a caudally directed spine, and an anterolateral facet that articulates

with the proatlas (fig. 10). The atlantal intercentrum is large, about 50 per cent of the length of the axis centrum. The atlantal and axial intercentra meet ventrally, thereby exlcuding the atlantal centrum from the ventral margin of the vertebral column. In ventral aspect, the anterior margin of the intercentrum of the atlas is concave for its articulation with the occipital condyle. The centrum of the axis is relatively short, about 60 per cent of the length of a dorsal centrum. More than half of the central length is excluded from the ventral margin of the vertebral column by the intercentra. There is a pronounced ventral keel (fig. 9), and the lateral walls of the centrum are concave. The suture between the axial neural arch and centrum is typical for most of the presacral column of primitive reptiles (fig. 11). The anterior edge of the neural spine curves strongly anterodorsally (figs. 10, 11). There is a pronounced facet for articulation with the neural arch of the atlas. The articular facet of the posterior zygapophysis is inclined only slightly from the horizontal plane. The facet on the neural arch for the attachment of the rib is inconspicuous in the specimens examined, and must have been minute. The neural spine is blade-like, with a thin anterior margin and a thick posterior edge (fig. 10). The axial intercentrum is a large element with a conspicuous mid-ventral, longitudinal ridge (fig. 9). In MNHN 1925-5-30, the bone is unfinished on the ventral midline. In lateral view, the intercentrum tapers dorsally and is not fused to the atlantal centrum in MNHN 1925-5-30 (fig. 9) and MNHN 1908-32-99 (fig. 11).

The centrum of the third cervical is longer than that of the axis, but is only 75 per cent of the length of the average dorsal. The rib facet is found near the front of the neural arch. It is relatively small, oval in shape, and faces ventrally. The transverse process is weak, and is located ventral to the zygapophyses. The neural spine curves posteriorly in large animals (MNHN 1925-5-49) and is relatively wide and anteroposteriorly short distally (fig. 10). The third intercentrum is the last one ossified in immature specimens. The midventral ridge is prominent anteriorly, and much weaker posteriorly. A slight posteroventral protuberance would have fitted snugly into a depression at the anterior end of the ventral ridge of the third centrum (fig. 9). This suggests that the third intercentrum and centrum were firmly attached and functioned as a unit.

The centrum of the fourth vertebra is about 85 per cent of the length of a dorsal centrum. The transverse process has become more prominent, and the neural spine is approximately two thirds the length of one of the dorsal spines. The transverse process is strengthened by strong anteroventral and posteroventral ridges, and a weaker dorsal process (MNHN 1925-5-49).

The fifth cervical is transitional in morphology between the more anterior cervicals and the dorsals. The centrum is almost the same length as a dorsal centrum. The transverse process has a longer articular facet for the rib, and is oriented more laterally. The neural spine is almost 75 per cent of the length of the neural spine of a mid-dorsal vertebra.

*Dorsal Vertebrae.* The basic structure of a notochordal centrum is hourglass shaped, constricted at the centre and expanding anteriorly and posteriorly into round, hollow ends that form the intervertebral articulations. The narrow waist is strengthened ventrally by a longitudinal ridge of bone. When viewed laterally, there is little curvature along the ventral ridge. The ventral edge of this ridge tends to be developed into a sharp keel in the cervicals, but becomes well rounded in the dorsals.

The width of a dorsal centrum is approximately 83 per cent of its length (table 2), whereas the height of the centrum is only 65 per cent of the length.

There is a pair of strong dorsolateral ridges for the attachment of the neural arch. The centrum is widest dorsally across the ridges, and tapers ventrally. As in pelycosaurs (Romer and Price 1940) and most other primitive reptiles, the dorsal part of each side of the posterior rim of the centrum is bevelled so that the surface faces somewhat dorsolaterally as well as posteriorly (fig. 13). The anterior edge has complementary dorsolateral expansions that articulate with the bevelled surface of the adjacent centrum. The ventral rims of both anterior and posterior ends of the centrum are bevelled for the intercentra.

The articulation for the rib does not appear to extend from the neural arch to the centrum in the dorsals. A strong ridge extends posterodorsally on the centrum to support the ventral edge of the transverse process (fig. 13). In large specimens, this ridge is longitudinally striated, presumably for ligaments that hold the rib in position.

The centrum forms the floor and part of the lateral walls of the neural canal. Between the supporting buttresses for the neural spine, the centrum is deeply excavated in young specimens, and the hourglass shape of the notochordal sheath can be made out clearly (figs. 3, 6). In more mature specimens, the region is only shallowly excavated, and there tend to be distinct pits close to the centre of the longitudinal axis. It appears that the bottom of the neural canal was nearly flat when viewed laterally in adult specimens (fig. 15b).

The neural arch does not co-ossify with the centrum until late in life. In the smallest specimens, the right and left halves of each neural arch disassociated after death.

From the anterior margin of the centrum, the ventral edge of each pedicel of the neutral arch curves posteroventrally to a point approximately one third the longitudinal distance of the centrum from the anterior edge of the centrum (figs. 3, 6). Posterior to this point, the ventral edge curves posterodorsally until it reaches the dorsal limit of the centrum. The suture cannot be seen in large specimens (fig. 13).

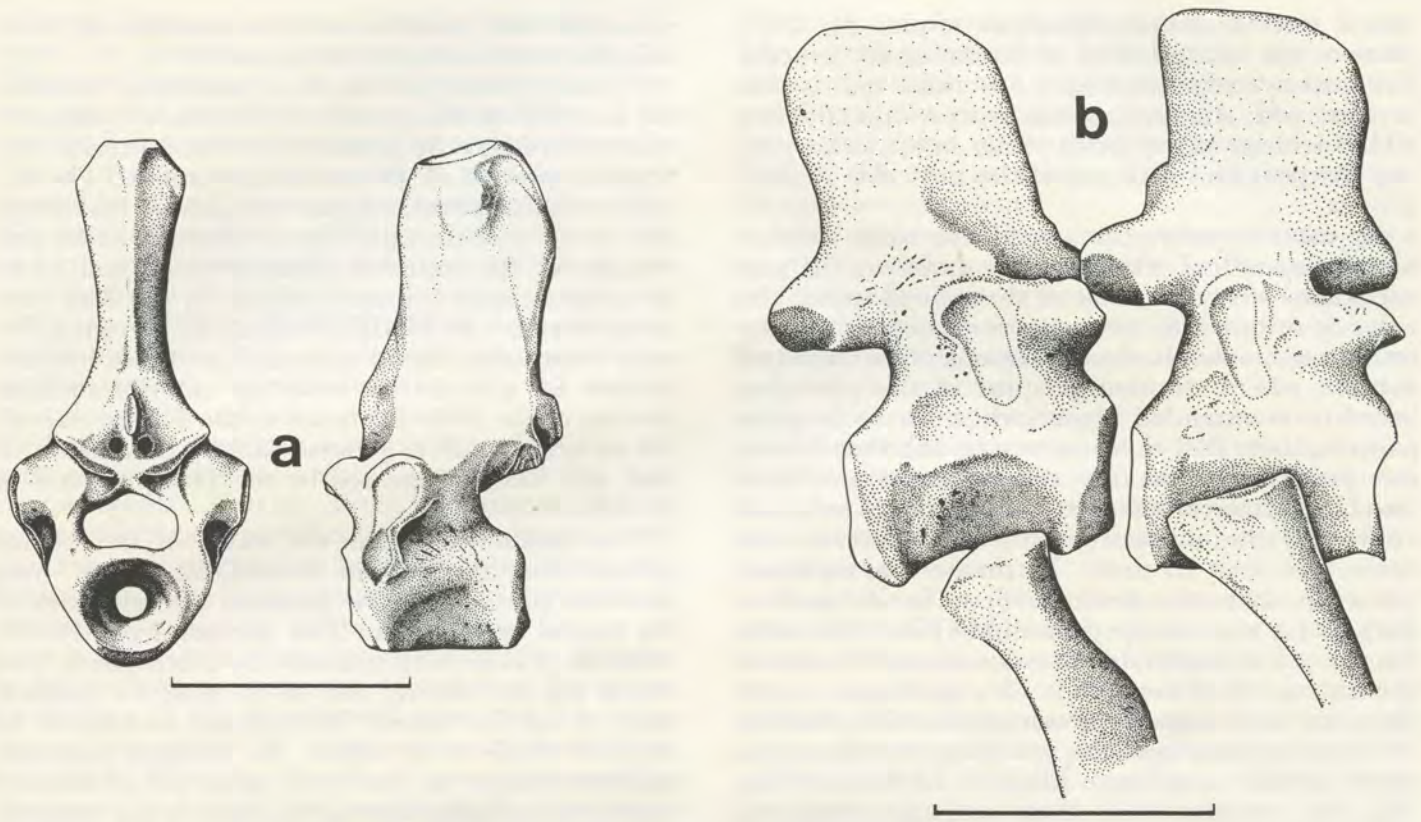



Figure 13. *Hovasaurus boulei*, dorsal vertebrae. a, SAM 9463, partially restored, posterior and lateral views of 13th dorsal vertebra; b, MNHN 1908-32-60, 16th and 17th dorsal vertebrae. Scale = 1 cm.

The anteroventral corner of each pedicel seems to reach the anterior edge of the centrum, and could have taken a limited part of the intervertebral articulation. Between this point and the base of the anterior zygapophysis, the anterior margin of the pedicel is shallowly concave, and forms the posterior margin of the intervertebral opening. The posteroventral corner of the neural arch is well forward from the posterior limit of the centrum; it curves anterodorsally and then posterodorsally to the posterior zygapophysis. This rim forms the anterior margin of the intervertebral opening.

There is an extra intervertebral articulation between the pairs of zygapophyses. The terms zygosphene and zygantrum are inappropriate for these articulations for a number of reasons. In the sense used by Romer (1956), a zygosphene bears slanting articular surfaces on either side of an anteriorly projecting process. The accessory articulation is variable in *Hovasaurus*, but never bears ventrolaterally oriented facets, and is most prominent on the posterior edge of the neural spine.

The accessory articulation is variable throughout the vertebral column (fig. 13), and apparently in different individuals as well. It could be that some of this variability is age specific, but more probably is just individual variation. However, throughout the vertebral column there is some form of contact of the neural spines, and in some cases this contact can extend vertically far up the neural spine. Because most specimens are split along the midline, details of the midline processes are poorly preserved in general. It is not possible to follow the changes undergone through the column for any single specimen.

In the cervical region, it appears that the neural spines are in contact along the midline near the base of the neural spines, but there is no specialized articulation in this region.

There is a distinct process on the posterior surface of the neural spine in the dorsals. It does not seem to have extended caudally beyond the posterior limit of the posterior zygapophyses in the anterior dorsals. In the sixth presacral of SAM 9463, the process is represented by a low ridge that does not extend dorsally or caudally beyond the zygapophyses. The process is prominent in the ninth presacral of SAM 9461, but lies below the dorsal limit of the posterior zygapophyses. The size of the process increases progressively, and is equally well-developed in the 11th and 12th vertebrae of MNHN 1908-32-59. The largest rectangular process observed was in about the 13th presacral vertebra of SAM 9463 (fig. 13). It is relatively long dorsoventrally, extending dorsally above the articular sufaces of the zygapophyses. The rectangular process extends farther caudally than the posterior zygapophyses. Generally in more posterior dorsals, the process is reduced to a low ridge. By the 18th presacral of MNHN R146a it is very small. The process seems to persist throughout the dorsal series; the 25th presacral neural spine of MNHN 1908-21-19 has a minute nubbin of bone on the midline of its posterior surface.

There is a deep pit on the posterior surface of the neural spine on each side of the rectangular process

in the anterior dorsals. This pair of pits (fig. 13) is close to the ventral level of the accessory process. The pits are separated by a low ridge that is continuous with the rectangular process dorsally, and which widens out ventrolaterally into a ridge joining the posterior margins of the posterior zygapophyses.

In most vertebrae, a prominent ridge extends along the midline of the anterior surface of the neural spine. Near the base of the neural spine, this ridge is anterior to the posterior limits of the anterior zygapophyses. In the regions of the vertebral column where the neural spine of the preceding vertebra is extended posteriorly by a rectangular process, there had to be some way to accommodate the process or else the centra would not have touched. Most vertebrae are exposed only in lateral view, and the anterior view of this midline ridge cannot be seen in them. Fortunately some specimens do show the anterior view. In an anterior dorsal of a juvenile specimen (MNHN 1925-5-28), there is a longitudinal depression along the crest of the anterior midline ridge. This depression is the right size and shape to accommodate the posterior rectangular process of the preceding vertebra. In a more mature specimen, MNHN 1908-32-24 (fig. 14), the complexity of these articulations is revealed. There is a distinct pit at the base of the anterior midline ridge of the 12th presacral. It is higher than it is wide, and is large enough for the posterior rectangular process of the 11th presacral to fit inside. Ventrolateral to the depression there are two bony protuberances that would have inserted into the pits ventrolateral to the posterior rectangular process of the preceding vertebra. Ventromedial to these protuberances is a shallow depression into which fits the ventral expansion of the ridge that is continuous dorsally with the rectangular process. The complex of anterior midline depressions and protuberances is symmetrical as a unit, but offset to the left of the midline.

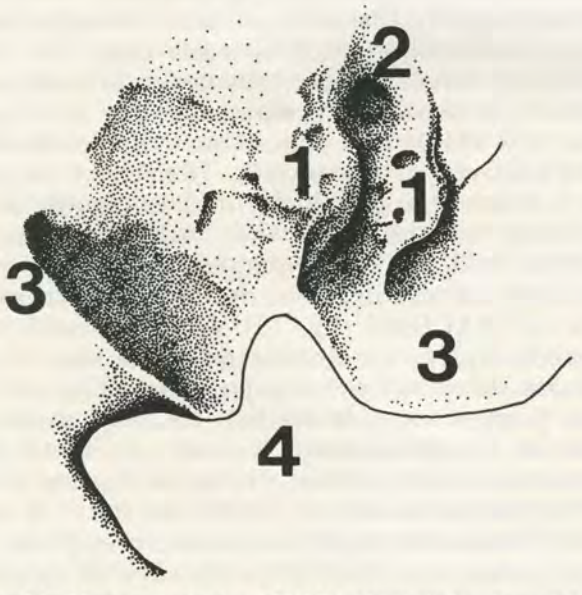



Figure 14. *Hovasaurus boulei*, MNHN 1908-32-24. Accessory articulations on anterior surface of 12th neural spine. 1, processes; 2, pit; 3, anterior zygapophyses; 4, neural canal. X9.

In more posterior dorsals, a prominent process, the anterior midline process of the neural spine, develops dorsal to the contact with the posterior rectangular process of the preceding vertebra. The anterior midline process seems to reach its maximum size in the mid-dorsals. Here it extends as far anteriorly as the anterior zygapophyses, and looks like a prominent tubular process. In the 18th presacral vertebra of MNHN 1908-32-24 there is a circular depression dorsal to a small posterior midline process for articulation with the anterior midline process of the 19th. Posterior to the 21st presacral, the anterior midline process rapidly diminishes in size, and has disappeared by the 24th presacral in MNHN 1908-32-24.

The contact between the bases of the neural spines along the midline is variable in the most posterior presacrals. The posterior midline ridge of the neural spine of the 25th presacral of MNHN 1908-32-24 is divided ventrally by a depression into which fits the ventral end of the anterior midline ridge of the first sacral. The contact is different in MNHN 1908-21-19 where the minute posterior midline process of the 25th presacral articulates with a minute, flat facet at the base of the anterior midline ridge of the first sacral.

The presence of accessory articulations along the midline of the neural spines of presacral vertebrae is clearly a derived character that is not found in ancestral protorothyridids (Carroll and Baird 1972), nor in most lines of eosuchians. In re-examining the type of specimen of *Youngina capensis*, it was discovered that accessory articulations are present (Currie 1981a). *Kenyasaurus* (Currie, in press) seems to have an anterior midline process of the neural spine in the mid and posterior thoracics, as does *Thadeosaurus*. *Tangasaurus*, although badly preserved, seems to show the same adaptation.

In juvenile specimens the anterior outline of the neural arch between the anterior zygapophyses and the posterior outline in the same plane are deeply embayed medially. This occurs because the ossification of the midline ridges cannot begin until the two halves of the neural spine co-ossify into a single unit.

The anterior zygapophyses are supported by a buttress oriented dorsomedially and slightly anteriorly from the base of the transverse process. The buttress of each side is joined by a thin shelf of bone above the neural canal. The articular surfaces extend onto this shelf, but do not meet. They are separated anteriorly by a medial notch, and posteriorly by the ventral end of the anterior midline ridge of the neural spine (fig. 14).

The posterior zygapophysis is supported by a strong ridge that extends dorsomedially, and to a lesser extent anteriorly, to the neural spine. The dorsolateral surface of this ridge is convex along its longitudinal axis, but concave where it meets the neural spine and near the posterolateral tip of the zygapophysis. In most dorsal vertebrae of mature

animals, there is a narrow shelf of bone that connects the posterior zygapophyses ventromedially. The posterior edge of the articular surface is almost straight and perpendicular to the midline of the vertebral column in the anterior and mid dorsals. The articular surface is widest near its ventromedial limit and tapers as it extends dorsolaterally. The articular surface, on the average, is 60 per cent as long anteroposteriorly as it is in the plane perpendicular to it. In the most posterior dorsals, the articular surface is diamond shaped with its widest expansion about half way between the lateral and medial borders. In end view (fig. 13), the ventrolateral outline of the zygapophysis is convex medially, but becomes concave laterally. The degree of curvature is variable throughout the presacral column. Because of the curvature of the articular surfaces, it is difficult to determine the angle that the articular surface has been rotated from the horizontal. This is particularly true in the cervicals and anterior dorsals where the medial convex region is broad and the curvature is gentle. If a line is drawn from the ventromedial edge of the articular surface to the dorsolateral edge, this line is on the average about 35° from horizontal, but can be as high as 45° in the dorsals of some specimens. In the posterior dorsals, the average inclination to the horizontal is somewhat lower — about 25°. In *Youngina* (Gow 1975), the inclination is less than 30° in the anterior dorsals, whereas the inclination in most other primitive reptiles is closer to the condition seen in *Hovasaurus*.

The longest neural spines of the presacral column are found in the vicinity of the 19th to 22nd vertebrae. In large specimens, the neural spines in this region can be more than 50 per cent greater than the maximum length of the centrum (table 2). The shortest neural spine of the vertebral column is that of the axis, which in MNHN 1908-32-1 is less than half the height of the longest dorsal neural spine. The height of the neural spine increases gradually between the axis and mid dorsals, and then decreases in the posterior dorsals and sacrals.

Among closely related genera, the presacral neural spines of *Youngina* and *Kenyasaurus* are relatively low, while those of *Thadeosaurus* and *Tangasaurus* are higher but still not as well developed as the neural spines of *Hovasaurus*.

The neural spines are constricted anteroposteriorly above the level of the midline processes of the neural spine. In mature specimens there is a slight expansion dorsal to this level. The maximum anteroposterior length of a neural spine of the mid and posterior dorsals is approximately 80 per cent of the greatest length of the corresponding centrum. Above this expansion, the neural spine tapers negligibly and ends in a plateau of unfinished bone (fig. 13).

The lateral thickness of the neural spines varies throughout the column. The neural spines of posterior dorsals, sacrals and caudals tend to be relatively thin. In the posterior dorsals of large animals (central length greater than 8 mm), the distal width of the spines is consistently almost 3 mm. The neural spines of the anterior and mid dorsals are greatly thickened distally by lateral ridges that end dorsally in mammilary processes. The width of the neural spine of the tenth presacral of MNHN 1908-32-59 is 4,5 mm, more than half the length of the associated centrum.

*Sacral Vertebrae.* The sacral centra are the same length as the posterior dorsals. In the two sacral vertebrae, the large articulations for the sacral ribs are found on both the neural arches and the centra. Because of these massive articulations, the ventral ridge of the centrum is pronounced. The average ratio of sacral spine height to maximum dorsal spine height for six specimens is 0,85. Neural spine length increases in the second sacral, and continues to increase through the proximal caudals. The sacrals do not co-ossify into a single unit in any of the specimens examined.

*Caudal Vertebrae.* The anterior caudal centra are either the same length as the dorsals, or are slightly shorter. The reduction in the length of the caudal centra is gradual. In the series of 45 caudals of MNHN 1908-32-58, the distal centra are only 10 per cent shorter than the proximal centra.

The shape of a caudal centrum is different from that of a dorsal centrum. The anterior and posterior edges, as seen in lateral view, are nearly straight (fig. 15). The centrum is longest dorsally, and noticeably shorter along the ventral margin. The ventral edges of the rims are bevelled where they articulate with the haemal arches. The width of the centrum is greatest dorsally, but tapers quickly below the level of the notochordal canal.

The midline ventral ridge is conspicuous in the anterior caudals, but becomes less prominent posteriorly, and disappears towards the end of the rib-bearing series. A pair of ventrolateral ridges appear on the centra of the rib-bearing caudals, become prominent by the end of the rib-bearing series, and continue on the remaining caudals.

The articular facets for the caudal ribs are found mainly on the centra, but also extend onto the neural arches (fig. 4).

The ventrolateral outline of the pedicel of the neural arch is essentially the same in the cervical, dorsal, sacral, and proximal caudal vertebrae. The outline changes in the anterior caudals, however, and before the end of the rib-bearing series has taken on a more symmetrical form (fig. 4). The ventral margin is almost horizontal in lateral view, but close to the centre of the centrum there is a ventral process on each pedicel that fits into a corresponding socket in the centrum. The lateral surface of this process forms a relatively small part of the sutural facet on the vertebra for the caudal rib. The base of the pedicel of the neural arch does not take part in the intervertebral articulation.

The caudal neural spine is one of the most highly specialized features of *Hovasaurus*. It was tall to boost the force that the tail would produce in the water by its lateral undulations when swimming. Of the specimens examined, the highest ratio of

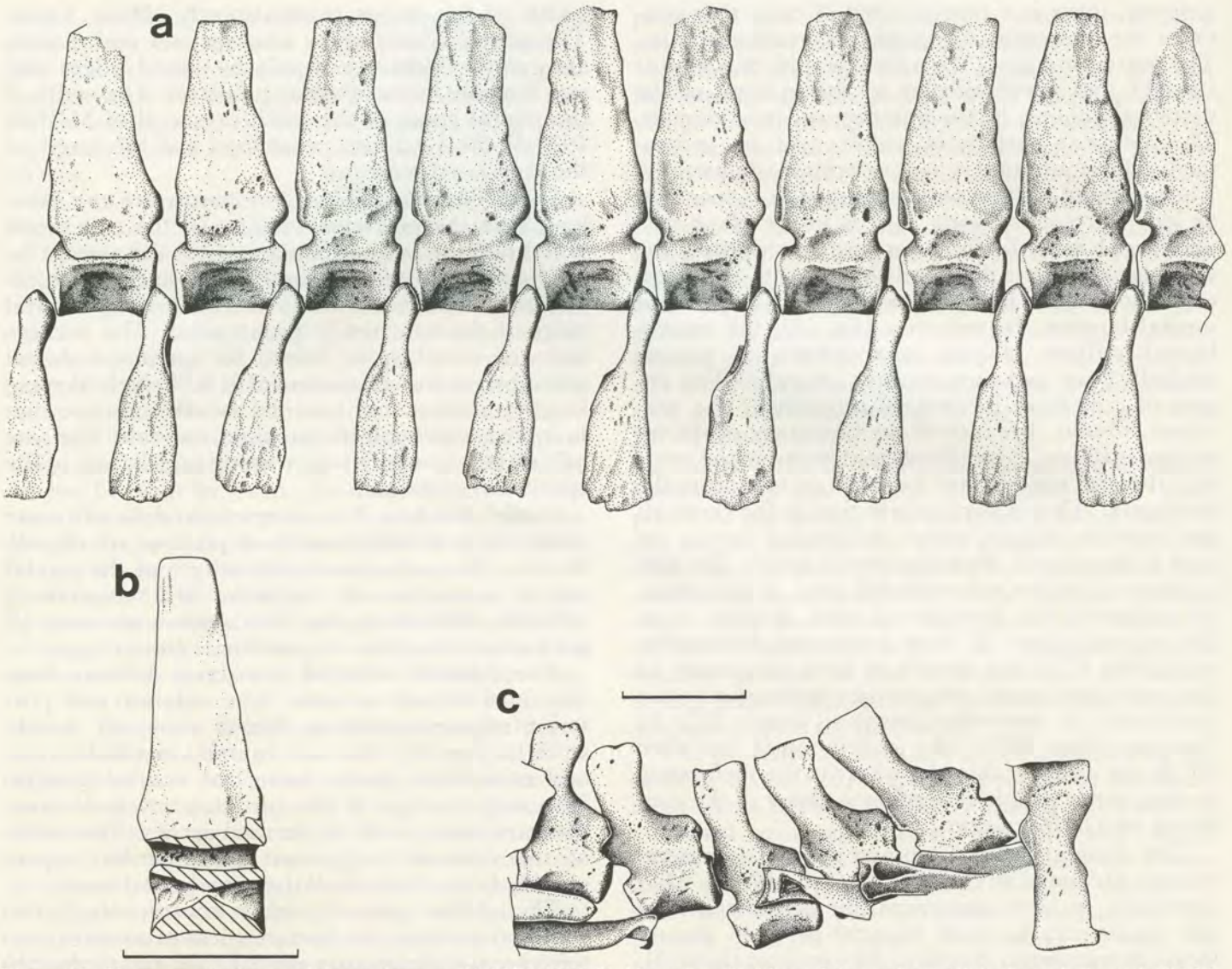



Figure 15. *Hovasaurus boulei*, caudal vertebrae. a, MNHN 1908-21-11, series of mid-caudal vertebrae (right lateral view); b, SAM 9462, mid-caudal vertebra, broken open to show neural and notochordal canals; c, SAM 9456, distal caudals, approximately 58th–63rd. Scale = 1 cm.

caudal neural spine height to length of associated centrum was 2,7 and the ratio of maximum neural spine height to average length of a dorsal centrum is at least 2,5. In comparison, the same ratio in *Tangasaurus* is 1,35. The neural spines of the tail of *Hovasaurus* grow with high positive allometry (table 2). Because the coefficient of allometry is higher in the caudals (1,43) than in the dorsal neural spines (1,34), the ratios of lengths of caudal neural spine to dorsal neural spine are 1,07 in juveniles and 1,19 in large animals. At all ages, the neural spines of the mid caudals are higher than the tallest presacral neural spines.

The neural spine of the first caudal is taller than that of the second sacral, but is shorter than the highest neural spine of the presacral series. The second caudal has a neural spine taller than that of the first caudal, and, in all but the smallest specimens, taller than any dorsal spines. Neural spine height continues to increase from the third caudal to the mid caudal region. In MNHN 1908-32-58 and MNHN 1908-32-64/73, the tallest neural spines are those of the 12th to 24th caudals. Neural spine height diminishes by seven per cent over the next ten caudals (MNHN 1908-32-64/73). No specimen shows a complete caudal series. However, on the basis of morphological comparisons with MNHN 1908-32-58, it can be concluded that the first caudal preserved in SAM 9456 could not be more proximal than the 50th segment. In this region of the tail, neural spine height is reduced by 35 per cent over the series of 13 caudals preserved in SAM 9456. The height of the last neural spine preserved, estimated to be about the 63rd caudal, is 1,3 times the length of the associated centrum.

Three regions can be defined in the tail on the basis of morphology of the neural arch and spine. Proximal caudals can be defined by the presence of zygapophyses, but there is no sharp distinction between the mid caudal and distal caudal regions.

As in more anterior vertebrae, the posterolateral margin of the neural arch forms the largest portion of the border of the intervertebral opening in the proximal caudals. Proximal caudals (figs. 3, 4, 6)

have distinct zygapophyses. In MNHN 1908-32-64/73, the most caudad pair of posterior zygapophyses is found on the 14th caudal and the last anterior zygapophyses are on the 15th caudal. There is a pronounced anterior midline ridge at the base of the neural spine that contacts the base of the neural spine of the preceding vertebra in a simple butt joint. Above this contact, the anterior margin of the neural spine curves posterodorsally, the amount of curvature decreasing until the margin is almost vertical distally. The posterior margin of the neural spine is almost straight, and is posterior to the centrum. The anteroposterior length of the distal end of the neural spine is about 70 per cent of the length of the centrum, and double the lateral width of the neural spine.

The mid caudals (fig. 15a, b) are more symmetrical in lateral view than the anterior and distal caudals. In contrast with the presacrals, sacrals and proximal caudals, the anterolateral margin of the neural arch forms as much of a border of the intervertebral opening as does the posterolateral margin of the preceding neural arch. The neural spines continue to articulate above the neural canal. This articulation, laterally wide at the base and tapering dorsally, can extend as much as 20 per cent of the height of the neural spine. In lateral view, the articular surface of the anterior midline ridge tends to be slightly convex, and the posterior margin tends to be concave. The neural spine tapers distally, and becomes laterally thin. The anterior margin of the neural spine tends to be slightly concave in lateral view and the posterior margin tends to be slightly convex. The centre of the neural spine is only slightly posterior to the centre of the centrum.

The intervertebral articulation at the base of the neural spine persists in the distal caudals, and can make up to 25 per cent of the height of the neural spine. Above the midline articulations, the margins of the neural spine are concave in lateral view, but the curvature is more pronounced on the anterior margin (fig. 15c). The distal end expands to about 65 per cent of the length of the associated centrum. The centre of the neural spine lies over the posterior quarter of the centrum. The terminal caudals are presently unknown.

*Intercentra*

Intercentra ossify early in the life of *Hovasaurus* in the first three cervicals and in the caudals. It would appear that the remaining intercentra remained cartilaginous until the animal was more than half grown. In mature animals, they are present throughout the vertebral column.

The atlantal intercentrum is the largest of the series. Ossified intercentra of mature specimens of *Hovasaurus* (fig. 5) are long in an anteroposterior direction, and can be up to 45 per cent of the length of a dorsal centrum in large animals. They broadly overlap the ventral surfaces of the adjacent centra, and extend dorsally more than halfway up the outer rims of the centra. The shape of the intercentra is basically the same as that of all primitive reptiles. The ventral surface is convex, both longitudinally and transversely.

Normal intercentra are found in the sacral segments (MNHN R146), and in association with the first two caudals (MNHN 1908-32-77). The third caudal vertebra is preceded by a crescentic intercentrum with a pair of parallel plates of bone projecting posteroventrally (MNHN 1908-21-7, MNHN 1908-32-77, SAM 9460). These plates do not meet distally, and each plate is less than two thirds of the length that is required to enclose the haemal canal. The fourth caudal section is the first to bear a complete chevron.

There is no indication of separate centres of ossification in the chevrons of *Hovasaurus* such as seen in *Sphenodon* (Howes and Swinnerton 1901). Furthermore, the crescentic basal portion of the chevron is found throughout the tail (figs. 3, 4, 6, 15c).

In lateral view, the chevron is pointed proximally, with two facets for articulation with the adjacent centra. The haemal arch is oriented slightly posteriorly as well as ventrally (fig. 15a). In young specimens the haemal canal occupies at least half of the dorsoventral length of the chevron in the proximal part of the tail. In more mature specimens, the haemal spine makes up a relatively larger percentage of the total length of the chevron. The dimensions of the haemal canal grow with negative allometry, whereas the haemal spine exhibits positive allometric growth (table 2). Regardless of the age of the animal, the haemal canal decreases in size posteriorly in the tail. This feature was found to be useful in determining whether isolated series of caudal vertebrae were from proximal or distal parts of the tail.

The haemal spine expands posteriorly and to a lesser extent anteriorly from the haemal arch to form a large, distinctive plate of bone with a vertical axis (figs. 3, 4, 15a). The distal expansion of the haemal spine has the same anteroposterior length as the distal end of the neural spine of the same segment.

In mature specimens, the haemal arch and spine are the same dorsoventral length (2,6*x*) as the neural arch and spine of the associated vertebra. This relationship is consistent throughout the tail.

## Ribs

Ribs are present in all but the atlantal segment of the presacrum, both sacrals, and the proximal caudals.

The second rib is short, somewhat less than the length of the associated axial centrum (figs. 9, 11), and tapers distally to a point. There are distinct tubercular and capitular heads (MNHN 1925-5-49), the latter extending to the intercentrum. The rib of the third cervical is longer than its centrum, recurved (fig. 11) and dichocephalous (fig. 9) (MNHN 1925-5-49). The fourth cervical rib is one third longer than the associated centrum and about twice the length of the axial rib. The capitular

head is still distinct but is very small relative to the tubercular head (MNHN 1925-5-49). There is a flange extending from the tubercular head along the outside curve of the rib shaft (fig. 11). The next rib is apparently holocephalous, with a continuous, dumbell-shape articular surface that articulated with the transverse process of the fifth cervical (MNHN 1925-5-49). The fifth rib is approximately double the length of the associated centrum, is not as strongly curved as the more anterior cervicals, but still tapers to a point distally.

The rib of the sixth vertebra is the first dorsal. The head has a larger circumference than any other region of the rib, and is distinct in outline from more anterior ribs (fig. 11). The articular surface is continuous, but is constricted in the centre so that capitular and tubercular portions of the head can be distinguished. This pattern is found in all but the last dorsal. The primitive condition, as exemplified by *Hylonomus* (Carroll 1964), is to have a notch separating the capitular and tubercular heads. The shaft of the sixth rib of *Hovasaurus* is almost straight, and is more than five times the length, *x*, of the dorsal centrum in MNHN 1908-32-1.

The anteroposterior length-to-height ratio of the proximal rib articulation increases from one third in the anterior dorsals to more than half in the posterior dorsals.

There is a progressive increase in length from the sixth to tenth dorsal ribs. The 11th to 17th ribs are approximately 7,5*x*, measured along the outside of the curvature. The maximum rib length is 7,8*x* in *Acerosodontosaurus* (Currie 1980), and 7,0*x* in *Thadeosaurus* and *Tangasaurus*. In *Hovasaurus* there is a gradual reduction in length of more posterior ribs up to the 21st, and a rapid reduction in length from the 22nd to 25th dorsals (figs. 3, 5). The last dorsal rib is only about 1,5*x* in length.

The anterior dorsal ribs are curved for the proximal third of the shaft, and almost straight distally. Ribs of the mid and posterior dorsal regions are curved throughout their length, suggesting that *Hovasaurus* was a relatively broad bodied animal like *Acerosodontosaurus* (Currie 1980), *Youngina* (Gow 1975), *Kenyasaurus* (Harris and Carrol 1977) and *Tangasaurus* (Currie, in press). The 25th rib does not curve ventrally, but extends laterally and curves slightly anteriorly (fig. 5, MNHN R146, MNHN 1908-32-4, MNHN 1908-32-24, MNHN 1908-32-67).

The dorsal ribs of *Hovasaurus* juveniles are indistinguishable from those of other younginoid genera. The ribs of the adults are visibly pachyostotic although not to the degree seen in *Champsosaurus* and *Mesosaurus*. The distal expansion of the 20th dorsal rib of a juvenile (MNHN 1908-21-2/7) is 0,30*x* whereas in MNHN 1908-32-67, an adult, the diameter of the same rib is 0,43*x*. The maximum shaft diameter of a dorsal rib in *Tangasaurus* is 0,30*x*. Pachyostosis is more discernible in the posterior dorsals, which are banana-shaped ribs in adults. The maximum shaft diameter is 12 per cent of the length of the 23rd rib in a juvenile (MNHN 1908-32-21) and 16 per cent in an adult (MNHN 1908-32-67).

The distal ends of the sixth to 24th ribs are concave and probably continued in cartilage. It is possible that the cartilaginous extensions of the 11th to 15th ribs attached directly to the sternum, while an unspecified number of pairs of more posterior ribs would have been connected to the sternum by cartilaginous mesosternal elements.

The sacral ribs have the same shape and orientation as most primitive reptiles. The proximal suture covers most of the lateral surface of the centrum and extends onto the neural arch. A small, anteroventral extension of the proximal sutural surface does not reach the intercentrum, but represents the primitive capitular head. The first sacral rib extends laterally, ventrally and anteriorly and meets the ilium in a broad contact. The distance between the first sacral vertebra and the ilium is 1,6*x*. The diameter of the shaft is 0,5*x* at its narrowest point, and it is anteroposteriorly longer than the centrum at the distal end. Most of the distal expansion is anteroventral to the longitudinal shaft of the sacral rib.

The orientation is almost the same in the second sacral (MNHN 1908-32-24), although it curves anteriorly to a lesser extent. The head of the second sacral is larger than that of the first sacral, and the measurement between the proximal and distal sutures is five to ten per cent greater than the shaft length of the first sacral rib (figs. 3a, 6) (MNHN R146). The distal expansion is flat and bladelike, and is anteroposteriorly shorter than the centrum. The nature of contact between the distal ends of the sacral ribs cannot be seen in any of the specimens examined. The distal end does not bifurcate as it does in *Youngina* (Gow 1975).

The number of pairs of caudal ribs is variable in *Hovasaurus*. There is a minimum of ten pairs (MNHN 1908-32-29) and a maximum of twelve (MNHN 1908-21-5). Ten pairs of caudal ribs are preserved in MNHN 1908-32-73, but there are facets on the 11th caudal vertebra for another caudal rib pair. In MNHN 1908-32-58, the 10th caudal rib is minute and resembles a smaller projection of bone on the 11th caudal vertebra. However, the 11th is clearly an outgrowth of the vertebra, does not have a separate centre of ossification, and is therefore not a rib. Ten pairs of ribs are preserved with MNHN 1908-32-77 (fig. 4), but articular facets on the 11th and 12th caudal vertebrae show that the animal had 12 pairs of caudal ribs. There is a pronounced transverse process on each side of the 13th caudal vertebra, and a smaller process on the 14th.

It is difficult to distinguish fused caudal ribs from transverse processes in the mid caudal region of many primitive reptiles. The fact that all but one or two of the lateral processes of the caudal vertebrae of *Hovasaurus* are true caudal ribs suggests that the majority of such processes in the tails of other eosuchians are caudal ribs rather than transverse

processes. For simplicity, all lateral processes of caudal vertebrae will be referred to as caudal ribs.

The anterior caudal ribs are constricted distal to the vertebral suture, but expand distally into horizontal plates of bone in *Hovasaurus* (figs. 3, 4, 6). A distinct proximoventral groove divides the rib head into capitular and tubercular portions (figs. 3b, 4). The distal ends of the first two caudals are concave regions of unfinished bone in all but the largest specimens. The remaining caudal ribs taper distally. The first four caudals extend 1,5*x* laterally, and the first has a maximum expansion of approximately 0,75*x*.

The proximal caudals of *Thadeosaurus*, *Kenyasaurus* and probably *Tangasaurus* have slender, tapering caudal ribs, as in all other eosuchians.

The first caudal rib of *Hovasaurus* is oriented slightly anteriorly as well as laterally (figs. 3b, 4, 6), and seems almost to reach the ilium. The unfinished bone on the distal end suggests there was a cartilaginous or at least ligamentous attachment to the distal end of the ilium. It probably represents the first stage of incorporation of a third rib into the sacrum, and is present in *Tangasaurus* (Currie, in press) and *Kenyasaurus* (Harris and Carroll 1977).

## Pectoral Girdle and Limb

*Scapulocoracoid*

The scapula and a single coracoid fuse into a single element, the scapulocoracoid, in mature specimens. In contrast to most primitive reptiles, eosuchians have one rather than two coracoids. The coracoid foramen is found in the anterior coracoid of pelycosaurs (Romer and Price 1940), and ossification of the posterior coracoid was often delayed. The presence of the coracoid foramen in *Hovasaurus* suggests that the single element is the homologue of the anterior coracoid of more primitive reptiles.

The scapular blade is extremely low (fig. 16b, c), even in mature animals, and the almost horizontal ventral plate is massive. The orientation of the scapulocoracoid can be reconstructed with little chance of serious error because of associated bones of the pectoral girdle. The posterior width across the paired scapulocoracoids would have been the same as the maximum width of the sternum, and the anterior width was delimited by the clavicles and interclavicle. As reconstructed (fig. 17a), the ossified scapular blade extends less than halfway up the side of the body. The clavicle and cleithrum extend slightly farther dorsally, but are still lower than expected. The posterior margin of the scapular blade lies above the glenoid, and is higher than the anterior margin. The anterodorsal rim of the scapula is longitudinally striated, indicating that there was a cartilaginous suprascapula. For maximum advantage of the serratus musculature (Holmes 1977), the suprascapular blade would have been extensive.

The scapula and coracoid do not fuse into a single unit until stage E (fig. 18), as in *Thadeosaurus*.

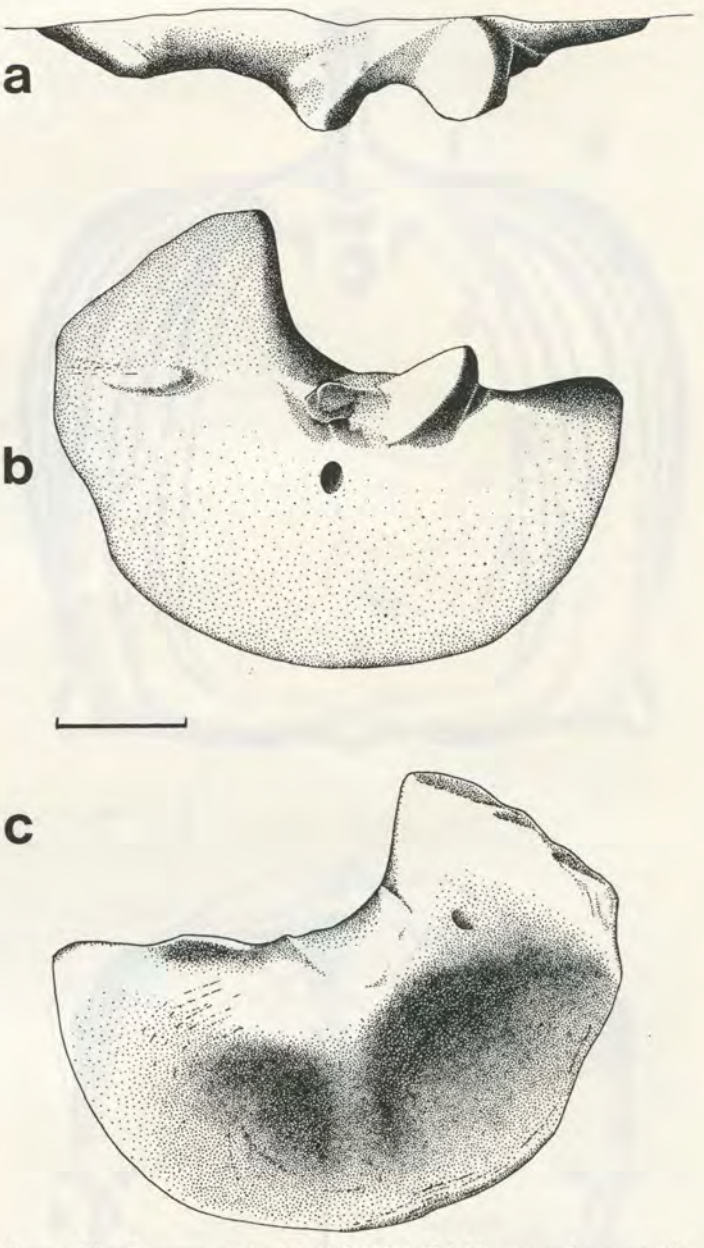



Figure 16. *Hovasaurus boulei*, MNHN R147, scapulocoracoid. a, lateral view; b, ventral view; c, dorsal view. Scale = 1 cm.

The ventral, horizontal portion of the scapula was apparently larger than the ossified scapular blade.

In contrast to most primitive reptiles, there is no supraglenoid ridge in *Hovasaurus*. The anterior facet of the glenoid is supported by an anteroventral ridge. The supraglenoid foramen has also been lost. In several specimens, there is a depression in the ridge anterior to the glenoid (fig. 18b, d). This depression has a more dorsal position in larger specimens (fig. 18g), where it is comparable to a similar pit in *Champsosaurus* (Sigogneau-Russell 1979). Carroll (1981) noted the presence of a similar depression in *Thadeosaurus* and speculated that it may have been the opening for the supraglenoid foramen, although this is unlikely. The depression could have served as part of the origin of the subcoracoscapularis.

The vertical and horizontal plates of the scapula

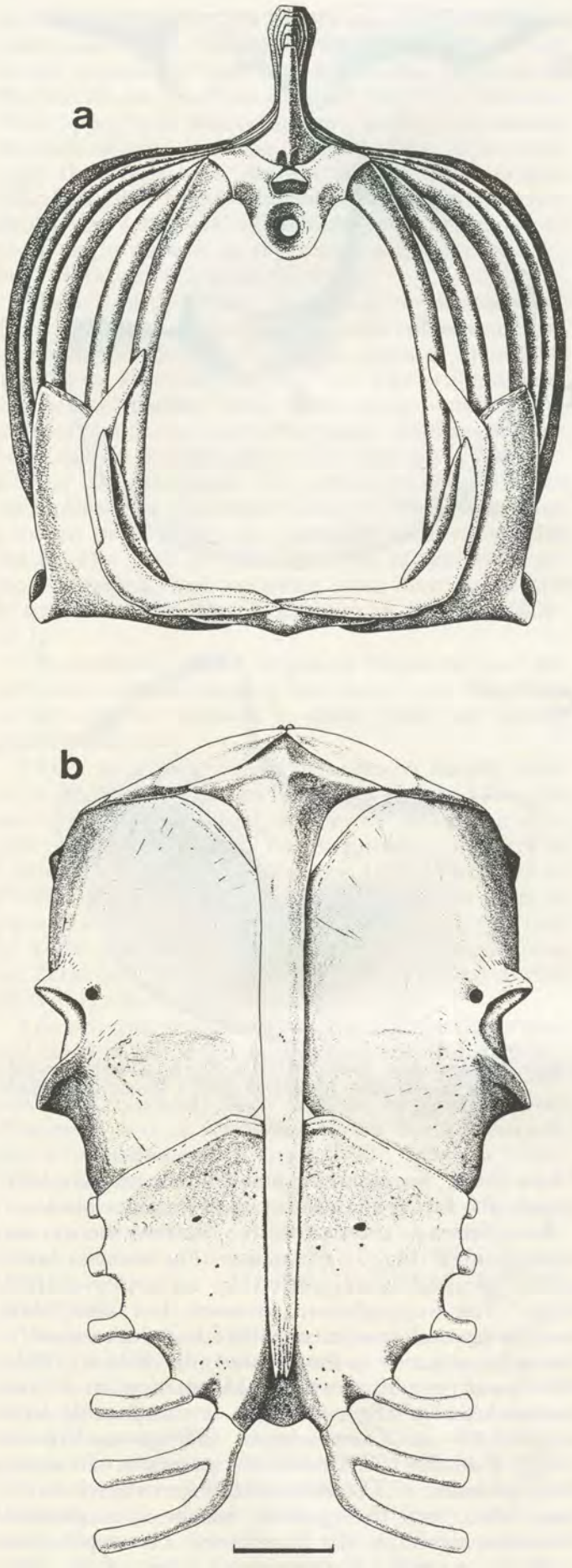



Figure 17. *Hovasaurus boulei*, reconstruction of pectoral region, a, anterior view; b, ventral view. Scale = 1 cm.

meet almost at right angles. Anteriorly there is a well-defined process along the inflection. The position of the process anterodorsal to the glenoid suggests that it served as the origin for the long head of the triceps lateralis. In living reptiles this muscle often originates from an area of the same relative size and position by means of a tendon.

The glenoid is formed by both scapula and coracoid (fig. 18a–e), and is the primitive "screw-shaped" type common to nearly all primitive reptiles. The anterior facet is strongly convex in transverse section, and faces more posteriorly than laterally. Centrally the glenoid is low, extending into a pit on the ventral surface of the coracoid. The posterior facet is broad and relatively flat. It extends as far laterally as the anterior facet, and faces anterolaterally and somewhat dorsally. The glenoid is indistinguishable from that of *Thadeosaurus*, the study of which suggested to Carroll (1981) that:

> — *Thadeosaurus* could move its humerus more under the body than *Captorhinus*, and therefore could have had a more lizard-like posture;
>
> — the humerus had greater freedom of motion than *Captorhinus*, especially ventrally, and was capable of moving in an arc greater than 60°;
>
> — posteriorly, the humerus could approach the body wall.

The base of the strong, lateral ridge on the coracoid that supports the posterior glenoid facet is heavily scarred (fig. 18m), probably in part for the long head of the triceps medialis, but mainly for the joint ligaments. The biceps and coracobrachialis muscles would have originated on the external surface of the coracoid medial to the glenoid. The coracoid foramen is represented by a notch in the coracoid at stage A (fig. 18b), but closes anteriorly early in life (fig. 18d).

The scapulocoracoid is preserved in internal view in MNHN R147 (fig. 16). The concave medial surface has some muscle scarring centrally for insertion of the sternocoracoideus and costosternocoracoideus musculature. Anteriorly the inner surface has been damaged and muscle scarring cannot be seen. A distinct ridge on the medial surface of the lateral edge of the coracoid posterior to the glenoid may be the origin of part of the subcoracoscapularis, which in lizards and *Sphenodon* inserts onto the proximal head of the humerus. The ridge extends ventromedially to strengthen the scapulocoracoid.

The scapulocoracoid of *Thadeosaurus* has the same features as that of *Hovasaurus*, including the limited dorsal extent of the scapular blade and an identical glenoid. Proportions are slightly different in mature specimens of *Thadeosaurus* and *Hovasaurus*. In the former genus, the distance from the anterior margin of the glenoid to the posterior margin of the coracoid is 55 per cent of the total length of the complex and the length of the glenoid is 25 per cent of the total length. These figures in *Hovasaurus*

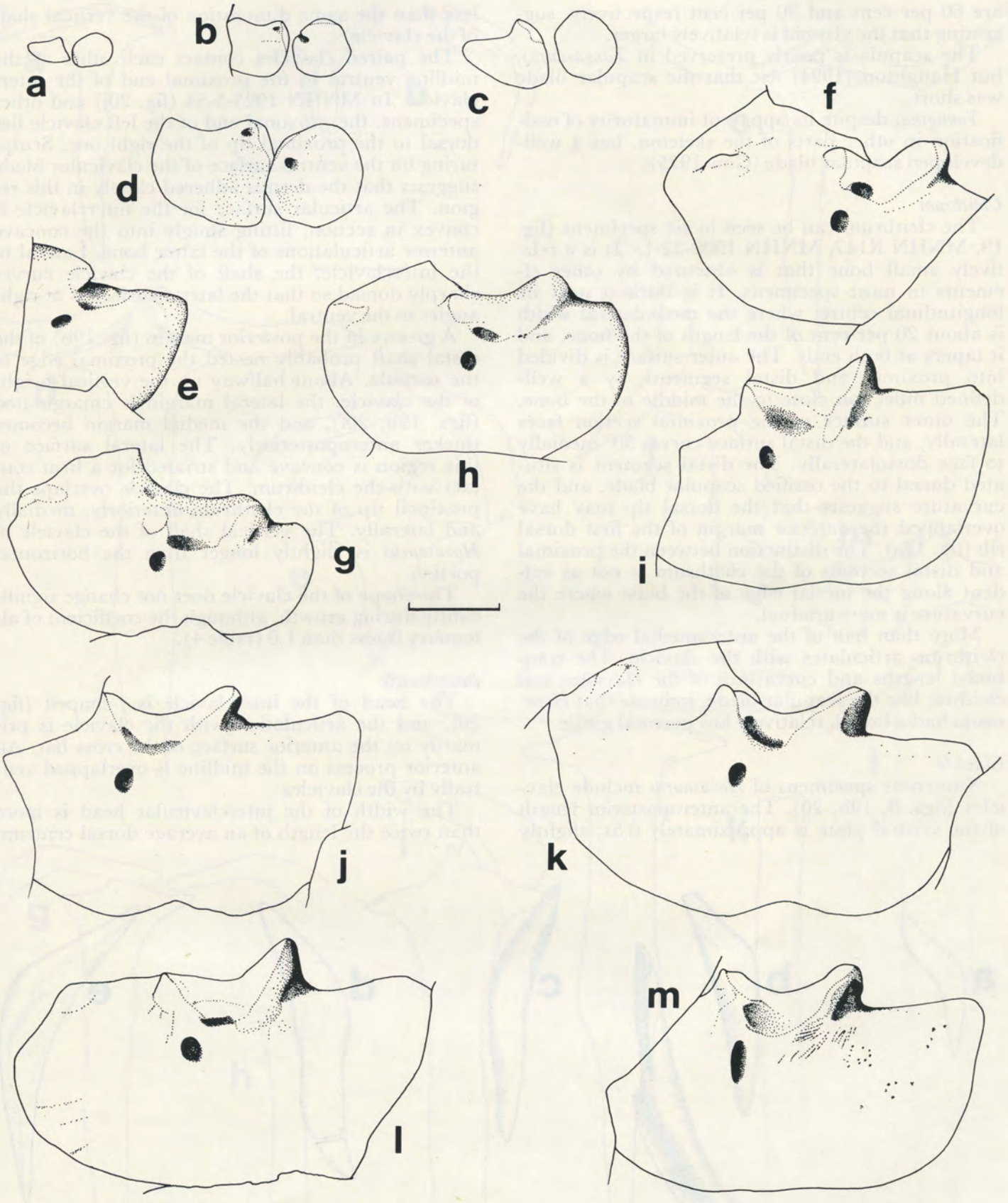



Figure 18. *Hovasaurus boulei*, scapulocoracoid, ventral view. a, MNHN 1908-21-8; b, MNHN 1925-5-30; c, MNHN 1908-21-7; d, MNHN 1908-32-23; e, MNHN 1925-5-12; f, MNHN 1925-5-49, partially restored from right side; g, MNHN 1908-32-26; h, MNHN 1908-32-27; i, MNHN 1925-5-56; j, MNHN 1908-21-18; k, MNHN 1908-32-67, partially restored from right side; l, MNHN 1925-5-54, partially restored from right side; m, MNHN 1925-5-38, reversed image. Scale = 1 cm.

are 60 per cent and 30 per cent respectively, suggesting that the glenoid is relatively larger.

The scapula is poorly preserved in *Tangasaurus*, but Haughton (1924) felt that the scapular blade was short.

*Youngina*, despite its apparent immaturity of ossification in other parts of the skeleton, has a well-developed scapular blade (Gow 1975).

*Cleithrum*

The cleithrum can be seen in six specimens (fig. 19, MNHN R147, MNHN 1908-32-1). It is a relatively small bone that is obscured by other elements in most specimens. It is thickest near its longitudinal centre, where the mediolateral width is about 20 per cent of the length of the bone, and it tapers at both ends. The outer surface is divided into proximal and distal segments by a well-defined inflection close to the middle of the bone. The outer surface of the proximal section faces laterally, and the distal surface curves 50° medially to face dorsolaterally. The distal segment is situated dorsal to the ossified scapular blade, and the curvature suggests that the dorsal tip may have overlapped the anterior margin of the first dorsal rib (fig. 17a). The distinction between the proximal and distal sections of the cleithrum is not as evident along the mesial edge of the bone where the curvature is more gradual.

More than half of the anteromedial edge of the cleithrum articulates with the clavicle. The combined lengths and curvatures of the clavicles and cleithra, like the scapular blade, indicate that *Hovasaurus* had a broad, relatively low pectoral girdle.

*Clavicle*

Numerous specimens of *Hovasaurus* include clavicles (figs. 9, 19b, 20). The anteroposterior length of the ventral plate is approximately 0,5*x*, slightly less than the same dimenstion of the vertical shaft of the clavicle.

The paired clavicles contact each other at the midline ventral to the proximal end of the interclavicle. In MNHN 1925-5-54 (fig. 20j) and other specimens, the proximal end of the left clavicle lies dorsal to the proximal tip of the right one. Sculpturing on the ventral surface of the clavicular blade suggests that the dermis adhered closely in this region. The articular surface for the interclavicle is convex in section, fitting snugly into the concave anterior articulations of the latter bone. Lateral to the interclavicle, the shaft of the clavicle curves sharply dorsad so that the lateral surface is at right angles to the ventral.

A groove in the posterior margin (fig. 19b) of the distal shaft probably nested the proximal edge of the scapula. About halfway up the vertical height of the clavicle, the lateral margin is emarginated (figs. 19b, 20f), and the medial margin becomes thicker anteroposteriorly. The lateral surface of this region is concave and striated for a firm contact with the cleithrum. The clavicle overlaps the proximal tip of the cleithrum anteriorly, medially and laterally. The vertical shaft of the clavicle of *Hovasaurus* is slightly longer than the horizontal portion.

The shape of the clavicle does not change significantly during growth, although the coefficient of allometry is less than 1,0 (table 4).

*Interclavicle*

The head of the interclavicle is t-shaped (fig. 20), and the articulation with the clavicle is primarily on the anterior surface of the cross bar. An anterior process on the midline is overlapped ventrally by the clavicles.

The width of the interclavicular head is more than twice the length of an average dorsal centrum

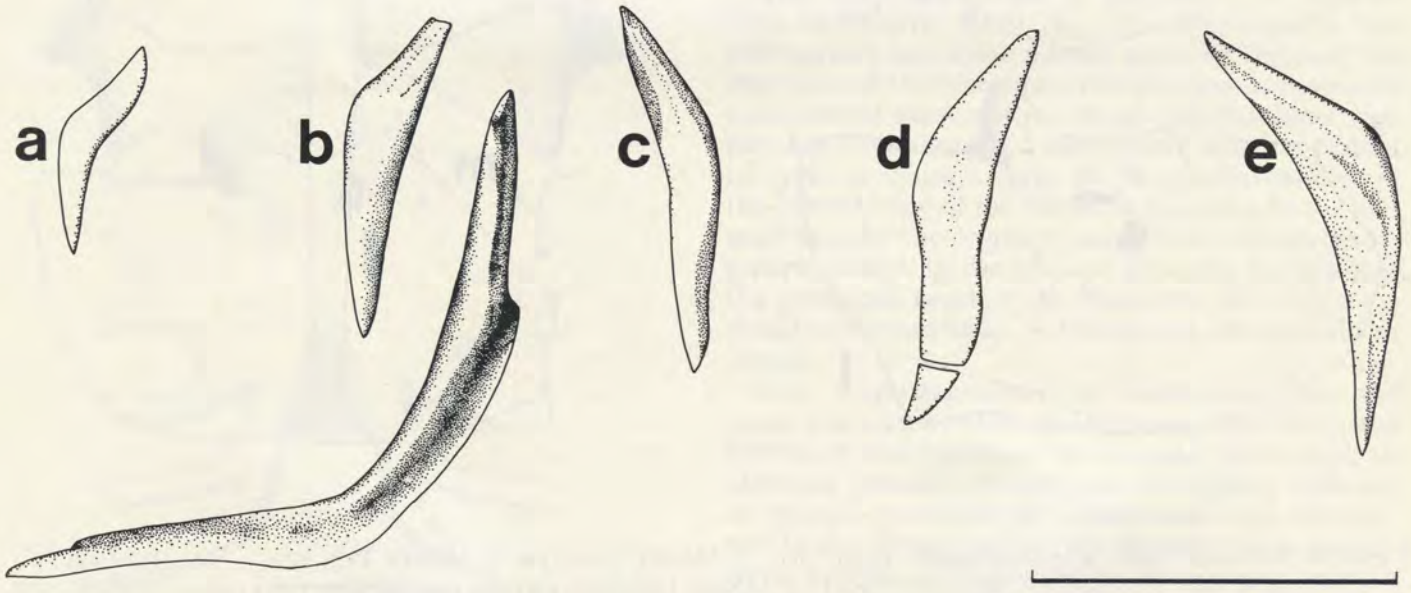



Figure 19. *Hovasaurus boulei*, cleithrum. a, MNHN 1908-21-8, posterior view of left cleithrum; b, MNHN 1908-32-99, anterior view of right cleithrum and posterior view of right clavicle; c, MNHN 1908-32-99, anterior view of left cleithrum; d, MNHN 1908-32-23, anterior view of right cleithrum; e, MNHN 1925-5-34, posterior view of right cleithrum. Scale = 1 cm.

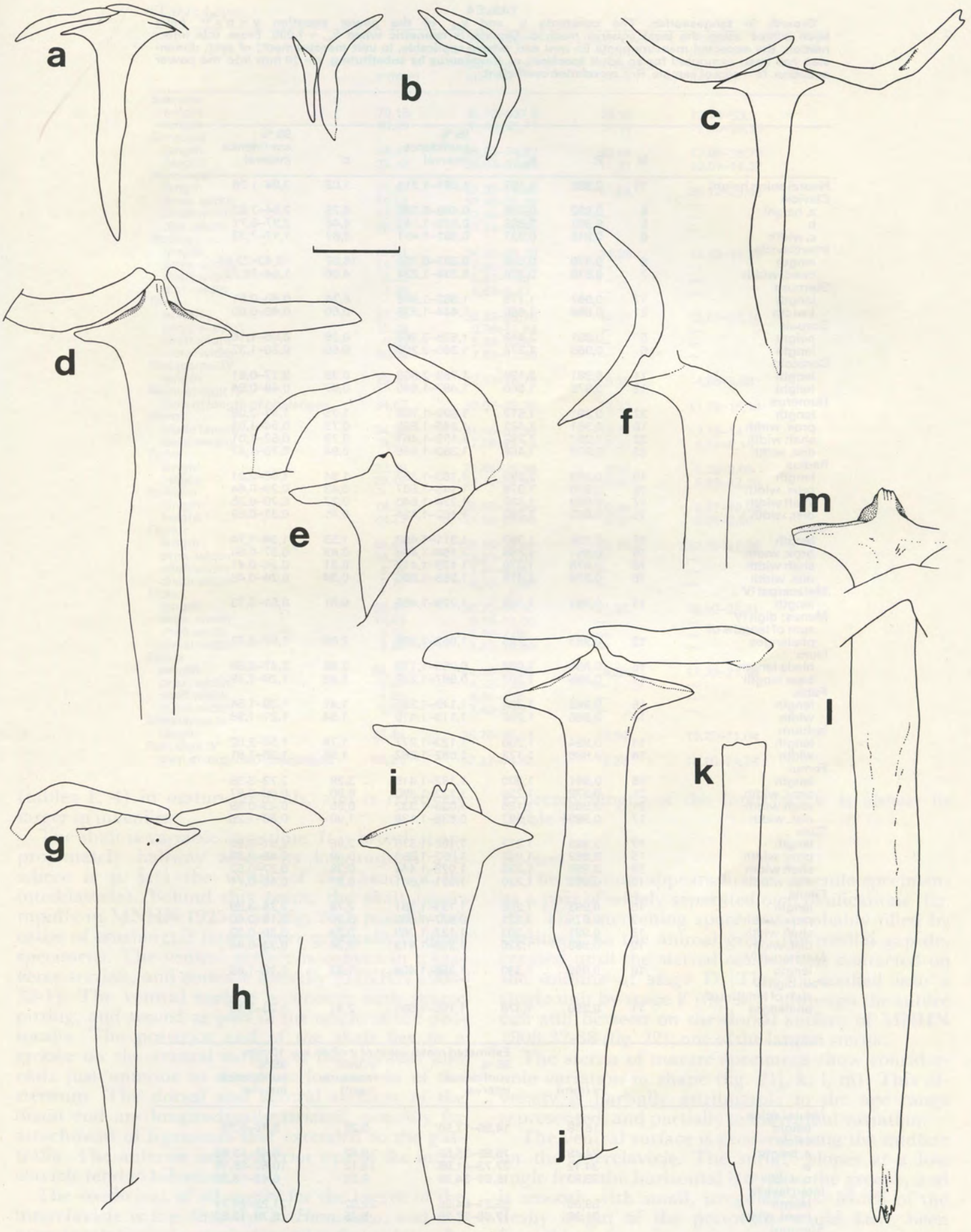



Figure 20. *Hovasaurus boulei*, dermal elements of pectoral girdle. a, MNHN 1925-5-30, interclavicle and clavicles; b, MNHN 1908-32-99, clavicles and cleithra; c, MNHN 1908-32-23, interclavicle and clavicles; d, MNHN 1925-5-38, interclavicle and clavicles; e, MNHN 1925-5-49, interclavicle and clavicles; f, MNHN 1925-5-34, interclavicle, clavicle; g, MNHN 1908-32-26, interclavicle, clavicles; h, MNHN 1908-21-24, interclavicle; i, MNHN R147, interclavicle, clavicle; j, MNHN 1925-5-54, interclavicle, clavicle; k, MNHN 1908-32-25, interclavicle; l, MNHN 1908-21-18, interclavicle; m, MNHN 1908-32-67, head of interclavicle. Scale = 1 cm.

**TABLE 4**

**Growth in tangasaurids. The constants b′ and $k_{yx}'$ of the power equation $y = b'x^{k_{yx}'}$ have been solved using the least squares method. Growth is isometric when $k_{yx} = 1{,}000$. From this information, the expected measurements (in mm and, where applicable, in unit measurement) of each dimension has been computed for an adult specimen of *Hovasaurus* by substituting $x = 10$ mm into the power equation. N = size of sample. R = correlation coefficient.**

| | N | R | $k_{yx}'$ | 95 % confidence interval | b′ | 95 % confidence interval |
|---|---|---|---|---|---|---|
| Neural spine height | 11 | 0,992 | 1,197 | 1,081–1,311 | 1,03 | 0,84–1,26 |
| Clavicle | | | | | | |
| a, height | 6 | 0,932 | 0,708 | 0,469–0,893 | 4,79 | 2,94–7,82 |
| b | 5 | 0,993 | 0,883 | 0,626–1,140 | 4,46 | 2,97–6,71 |
| c, width | 6 | 0,915 | 0,921 | 0,381–1,461 | 2,87 | 1,12–7,33 |
| Interclavicle | | | | | | |
| length | 6 | 0,979 | 0,548 | 0,387–0,709 | 16,87 | 12,42–22,91 |
| head, width | 7 | 0,878 | 0,734 | 0,234–1,234 | 4,06 | 1,54–10,72 |
| Sternum | | | | | | |
| length | 17 | 0,987 | 1,775 | 1,662–1,888 | 0,74 | 0,60–0,91 |
| ½ width | 21 | 0,968 | 1,660 | 1,444–1,876 | 0,60 | 0,40–0,90 |
| Scapula | | | | | | |
| height | 5 | 0,991 | 2,448 | 1,528–3,368 | 0,25 | 0,05–1,16 |
| length | 6 | 0,963 | 1,874 | 1,360–2,388 | 0,60 | 0,26–1,37 |
| Coracoid | | | | | | |
| length | 11 | 0,981 | 2,194 | 1,786–2,602 | 0,38 | 0,17–0,81 |
| height | 13 | 0,978 | 1,666 | 1,487–1,845 | 0,67 | 0,48–0,94 |
| Humerus | | | | | | |
| length | 22 | 0,991 | 1,612 | 1,520–1,704 | 1,75 | 1,47–2,08 |
| prox. width | 18 | 0,981 | 1,421 | 1,246–1,596 | 0,73 | 0,54–1,01 |
| shaft width | 22 | 0,957 | 1,282 | 1,103–1,461 | 0,73 | 0,52–1,01 |
| dist. width | 23 | 0,979 | 1,488 | 1,390–1,586 | 0,94 | 0,79–1,27 |
| Radius | | | | | | |
| length | 15 | 0,993 | 1,285 | 1,183–1,387 | 1,94 | 1,63–2,31 |
| prox. width | 15 | 0,970 | 1,378 | 1,149–1,607 | 0,43 | 0,29–0,64 |
| shaft width | 17 | 0,979 | 1,387 | 1,234–1,540 | 0,27 | 0,20–0,35 |
| dist. width | 15 | 0,969 | 1,263 | 1,102–1,424 | 0,41 | 0,31–0,53 |
| Ulna | | | | | | |
| length | 17 | 0,995 | 1,387 | 1,311–1,463 | 1,53 | 1,34–1,74 |
| prox. width | 19 | 0,981 | 1,345 | 1,194–1,496 | 0,49 | 0,37–0,64 |
| shaft width | 18 | 0,978 | 1,270 | 1,123–1,417 | 0,31 | 0,24–0,41 |
| dist. width | 15 | 0,974 | 1,479 | 1,268–1,690 | 0,34 | 0,24–0,49 |
| Metacarpal IV | | | | | | |
| length | 13 | 0,992 | 1,342 | 1,229–1,455 | 0,61 | 0,51–0,73 |
| Manus; digit IV | | | | | | |
| sum of lengths of phalanges | 13 | 0,983 | 1,225 | 1,062–1,388 | 2,06 | 1,57–2,72 |
| Ilium | | | | | | |
| blade length | 15 | 0,996 | 1,064 | 0,955–1,173 | 2,96 | 2,47–3,56 |
| base length | 11 | 0,986 | 1,107 | 0,987–1,227 | 1,49 | 1,24–1,79 |
| Pubis | | | | | | |
| length | 15 | 0,989 | 1,200 | 1,149–1,251 | 1,41 | 1,30–1,54 |
| width | 14 | 0,986 | 1,260 | 1,110–1,410 | 1,54 | 1,21–1,98 |
| Ischium | | | | | | |
| length | 14 | 0,994 | 1,200 | 1,123–1,277 | 1,79 | 1,58–2,02 |
| width | 14 | 0,988 | 1,172 | 1,082–1,262 | 1,56 | 1,35–1,81 |
| Femur | | | | | | |
| length | 18 | 0,991 | 1,300 | 1,182–1,418 | 3,28 | 2,73–3,95 |
| prox. width | 21 | 0,972 | 1,256 | 1,132–1,380 | 0,80 | 0,66–0,97 |
| shaft width | 21 | 0,969 | 1,185 | 1,038–1,332 | 0,55 | 0,43–0,69 |
| dist. width | 17 | 0,969 | 0,987 | 0,836–1,138 | 1,00 | 0,80–1,26 |
| Tibia | | | | | | |
| length | 17 | 0,993 | 1,272 | 1,166–1,378 | 2,96 | 2,51–3,50 |
| prox. width | 15 | 0,982 | 1,243 | 1,092–1,394 | 0,60 | 0,48–0,76 |
| shaft width | 19 | 0,958 | 1,236 | 1,028–1,444 | 0,38 | 0,27–0,52 |
| dist. width | 19 | 0,972 | 1,226 | 1,091–1,361 | 0,57 | 0,46–0,71 |
| Fibula | | | | | | |
| length | 15 | 0,993 | 1,256 | 1,131–1,381 | 2,78 | 2,28–3,39 |
| prox. width | 7 | 0,975 | 1,221 | 0,877–1,565 | 0,34 | 0,19–0,60 |
| shaft width | 19 | 0,991 | 1,203 | 1,137–1,269 | 0,29 | 0,26–0,33 |
| dist. width | 16 | 0,986 | 1,326 | 1,239–1,413 | 0,38 | 0,33–0,44 |
| Metatarsal IV | | | | | | |
| length | 16 | 0,995 | 1,330 | 1,256–1,404 | 1,33 | 1,18–1,50 |
| Pes; digit IV | | | | | | |
| sum of lengths of phalanges | 11 | 0,990 | 1,378 | 1,195–1,561 | 2,31 | 1,73–3,10 |

| | Estimated mean value of y when x = 10 mm | | | |
|---|---|---|---|---|
| | y (mm) | 95 % confidence interval | y (unit measurement) | 95 % confidence interval |
| Neural spine height | 16,18 | 14,96–17,50 | 6,22 | 5,75–6,73 |
| Clavicle | | | | |
| a, height | 24,49 | 16,85–35,56 | 9,42 | 6,48–13,68 |
| b | 34,12 | 27,73–41,98 | 13,12 | 10,67–16,15 |
| c, width | 23,93 | 16,69–34,36 | 9,21 | 6,42–13,22 |
| Interclavicle | | | | |
| length | 59,60 | 55,21–64,25 | 22,92 | 21,23–24,71 |
| head, width | 21,98 | 17,66–27,35 | 8,45 | 6,79–10,52 |
| Sternum | | | | |
| length | 44,26 | 41,21–47,51 | 17,02 | 15,85–18,27 |
| ½ width | 27,23 | 24,03–30,83 | 10,47 | 9,24–11,86 |

(Table 4 cont.)

| | y (mm) | Estimated mean value of y when x = 10 mm 95 % confidence interval | y (unit measurement) | 95 % confidence interval |
|---|---|---|---|---|
| Scapula | | | | |
| height | 70,15 | 35,73–137,7 | 26,98 | 13,74–53,0 |
| length | 45,29 | 31,19–65,77 | 17,42 | 12,00–25,30 |
| Coracoid | | | | |
| length | 58,61 | 45,92–74,82 | 22,54 | 17,66–28,78 |
| height | 31,12 | 26,03–37,24 | 11,97 | 10,01–14,32 |
| Humerus | | | | |
| length | 71,61 | 67,92–75,49 | 27,54 | 26,12–29,03 |
| prox. width | 19,63 | 17,46–21,49 | — | — |
| shaft width | 13,90 | 12,45–15,52 | — | — |
| dist. width | 28,97 | 27,23–30,84 | — | — |
| Radius | | | | |
| length | 37,41 | 34,67–40,36 | 14,39 | 13,33–15,52 |
| prox. width | 10,35 | 8,83–12,13 | — | — |
| shaft width | 6,49 | 5,37–7,83 | — | — |
| dist. width | 7,48 | 6,61–8,47 | — | — |
| Ulna | | | | |
| length | 37,24 | 35,32–39,26 | 14,32 | 13,57–15,10 |
| prox. width | 10,79 | 9,76–11,94 | — | — |
| shaft width | 5,83 | 5,28–6,46 | — | — |
| distal width | 10,35 | 7,67–13,96 | — | — |
| Metacarpal IV | | | | |
| length | 13,40 | 12,17–14,76 | 5,15 | 4,68–5,68 |
| Manus; digit IV | | | | |
| sum of length of phalanges | 34,67 | 30,57–39,36 | 13,33 | 11,76–15,14 |
| Ilium | | | | |
| blade length | 34,36 | 31,55–37,38 | 13,22 | 12,13–14,38 |
| base length | 19,01 | 17,08–21,18 | 7,31 | 6,57–8,15 |
| Pubis | | | | |
| length | 22,39 | 21,48–23,34 | 8,61 | 8,26–8,98 |
| height | 28,12 | 24,77–31,92 | 10,82 | 9,53–12,28 |
| Ischium | | | | |
| length | 28,31 | 25,50–31,40 | 10,89 | 9,81–12,08 |
| height | 23,23 | 21,53–25,06 | 8,93 | 8,28–9,64 |
| Femur | | | | |
| length | 65,46 | 59,16–72,44 | 25,18 | 22,75–27,86 |
| prox. width | 14,39 | 13,23–15,67 | — | — |
| shaft width | 8,36 | 7,41–9,43 | — | — |
| distal width | 9,73 | 8,53–11,09 | — | — |
| Tibia | | | | |
| length | 55,46 | 50,70–60,60 | 21,33 | 19,50–23,31 |
| prox. width | 10,49 | 9,18–12,00 | — | — |
| shaft width | 6,50 | 5,42–7,80 | — | — |
| distal width | 9,62 | 8,82–10,50 | — | — |
| Fibula | | | | |
| length | 50,12 | 44,98–55,85 | 19,28 | 17,30–21,48 |
| prox. width | 5,64 | 4,32–7,35 | — | — |
| shaft width | 4,69 | 4,44–4,95 | — | — |
| distal width | 8,00 | 7,43–8,61 | — | — |
| Metatarsal IV | | | | |
| length | 28,44 | 26,70–30,27 | 10,94 | 10,27–11,64 |
| Pes; digit IV | | | | |
| sum of lengths of phalanges | 55,21 | 47,32–64,42 | 21,23 | 18,20–24,78 |

(tables 1, 4) in mature animals, and is relatively larger in juveniles.

The shaft is variable in outline. It is broadest approximately halfway along its longitudinal axis where it is $\frac{2}{3}x(\frac{1}{3}$ the width of the head of the interclavicle). Behind this point, the shaft tapers rapidly in MNHN 1925-5-54 (fig. 20j), possibly because of crushing; it tapers more gradually in most specimens. The ventral surface is convex in transverse section, and concave dorsally (MNHN 1908-32-1). The ventral surface is smooth with sparse pitting, and served as part of the origin of the pectoralis. The posterior end of the shaft lies in a groove on the ventral surface of the sternum and ends just anterior to the posterior margin of the sternum. The dorsal and ventral surfaces of the distal end are longitudinally striated, possibly for attachment of ligaments that extended to the gastralia. The anterior and posterior tips of the interclavicle tend to bifurcate.

The coefficient of allometry for the length of the interclavicle is less than 1,0 in *Hovasaurus*, and the bone is relatively longer in juveniles than adults. In an animal with a dorsal vertebra 10 mm long, the expected length of the interclavicle is almost 6*x* (table 4).

*Sternum*

The sternum appears first in juvenile specimens as a pair of widely separated oval ossifications (fig. 21). The intervening space was probably filled by cartilage. As the animal grew, the medial gap decreased until the sternal ossifications contacted on the midline at stage D. They co-ossified into a single unit by stage F (fig. 21i), although the suture can still be seen on the dorsal surface of MNHN 1908-32-38 (fig. 22), one of the largest sterna.

The sterna of mature specimens show considerable variation in shape (fig. 21j, k, l, m). This diversity is partially attributable to the age range represented, and partially to individual variation.

The ventral surface is grooved along the midline for the interclavicle. The surface slopes at a low angle from the horizontal lateral to the groove, and is smooth with small, irregular pits. Much of the fleshy origin of the pectoralis would have been from this region.

The anteroventral margin is notched on the mid-

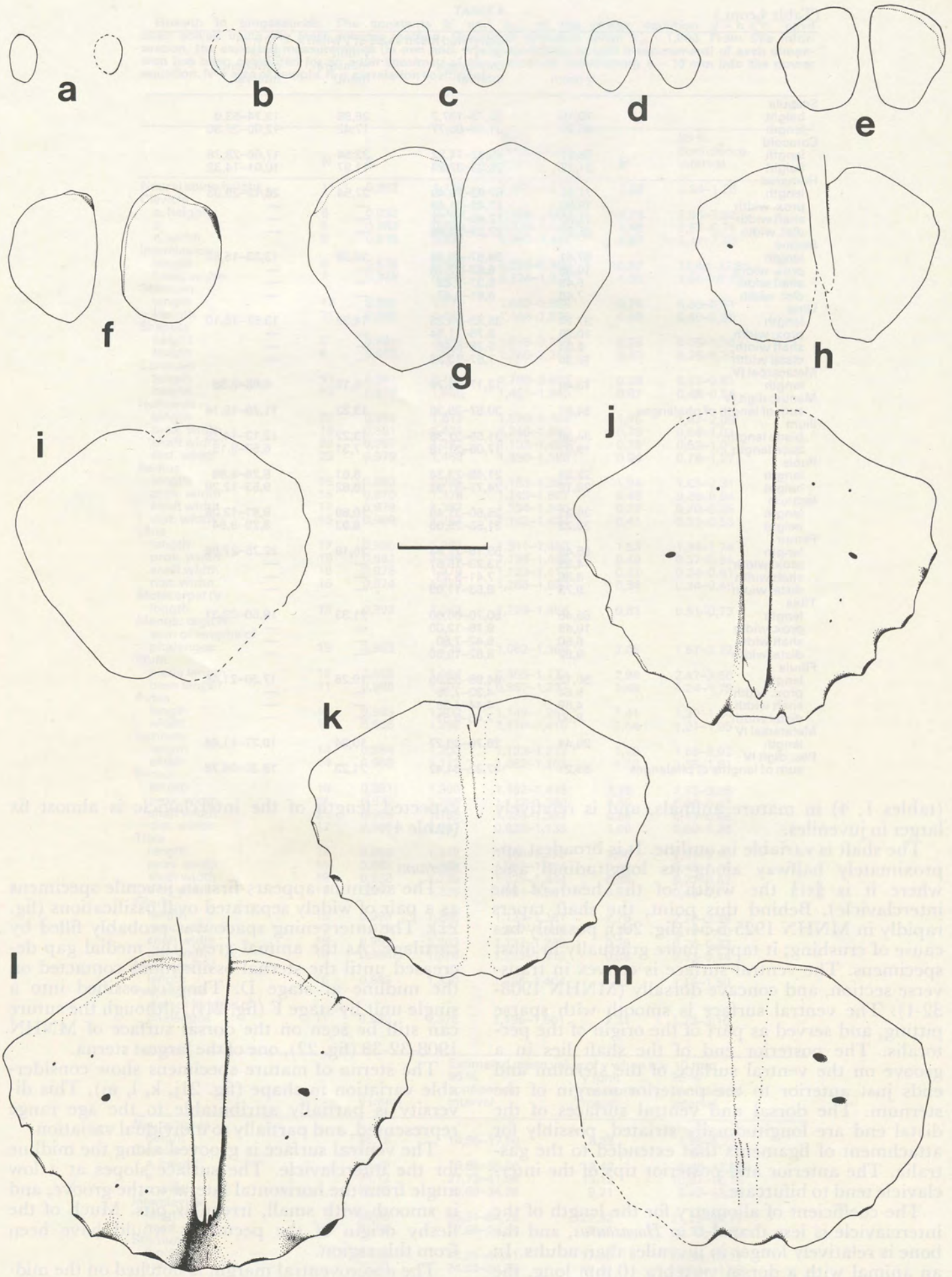



Figure 21. *Hovasasaurus boulei*, sternum, ventral view. a, MNHN 1908-21-8; b, MNHN 1908-32-29; c, MNHN 1925-5-30; d, MNHN 1908-21-7; e, MNHN 1908-32-77; f, MNHN 1908-32-23; g, MNHN 1925-5-12; h, MNHN 1925-5-29; i, MNHN 1908-32-26; j, MNHN 1908-21-24; k, MNHN R147; l, MNHN 1908-21-18; m, MNHN 1908-32-67. Scale = 1 cm.

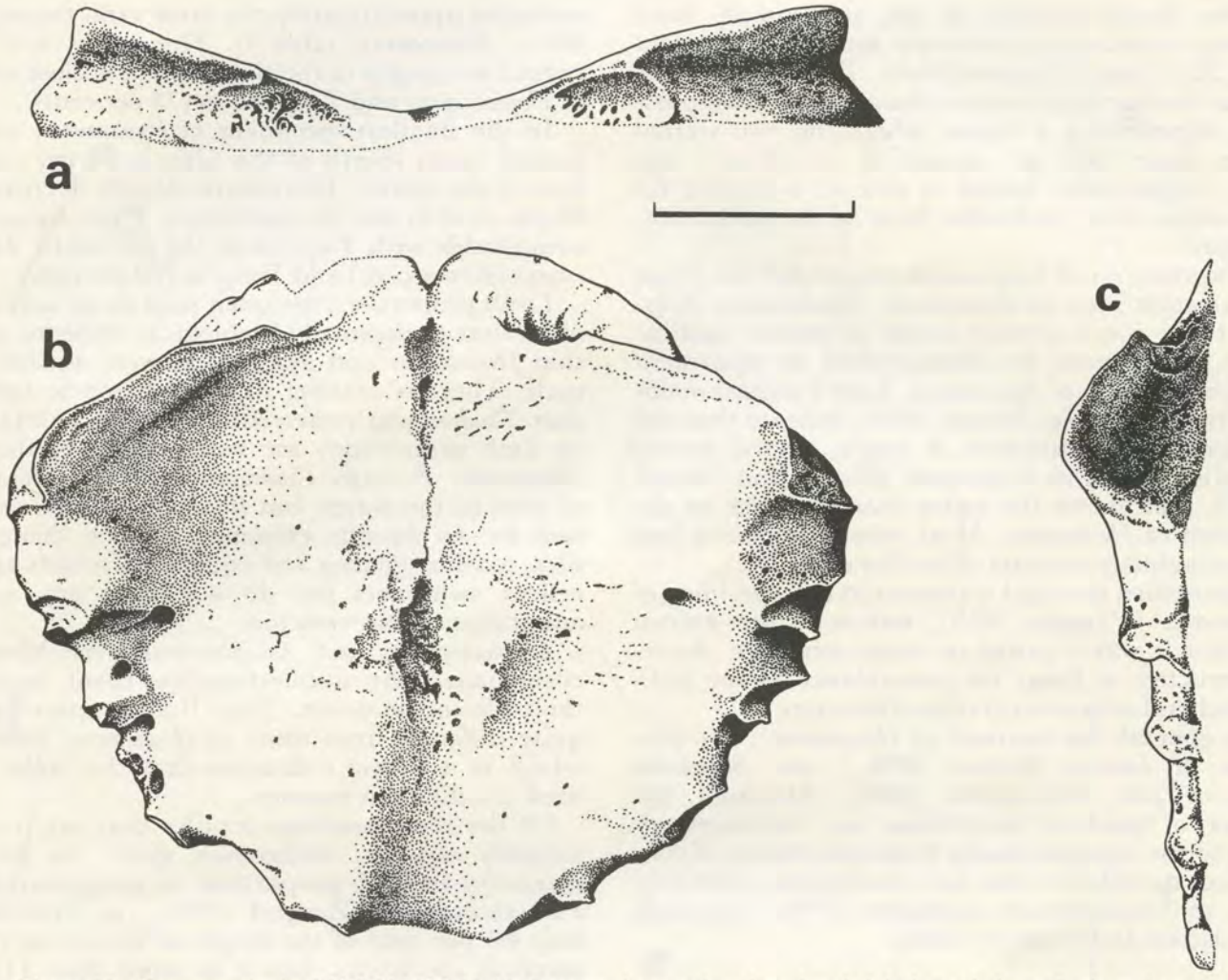



Figure 22. *Hovasaurus boulei*, MNHN 1908-32-38. Sternum in anterior, dorsal and right lateral views. Scale = 1 cm.

line. In ventral view, the anterior margin between the notch and the point where the sternum meets the inner edge of the coracoid faces anteriorly or anteromedially. The sternum is dorsoventrally thin on the midline but becomes thicker laterally (fig. 22a). In this region the ventral surface of the sternum underlies a pair of anterodorsally oriented facets, one on each side of the midline, that are heavily scarred, finished bone. As the coracoids are separated from each other posteromedially, there is an open area anterior to the facets. The superficial layer of the sternocoracoideus would have originated from the scarred facets on the sternum and passed through this open area onto the internal surface of the scapulocoracoid as in *Sphenodon* and *Iguana* (Holmes 1977).

Lateral to the origin of the sternocoracoideus superficialis is a laterally elongate, anterolaterally oriented trough with a surface of unfinished bone. The coracoid would have articulated with this surface of the sternum. The greatest thickness (fig. 22c) and width (fig. 22b) of the sternum is at the lateral edge of the articulation with the coracoid.

The sternum has four or possibly five costal connections on each side. There appears to be a dorsolaterally oriented facet immediately behind the lateral limit of the coracoid articulation (fig. 22b), to which the 11th rib was probably connected via cartilage. Four concave facets of unfinished bone are found on short projections along each side of the sternum. The sternum is thicker anteriorly and would have been almost directly ventral to the distal end of the ribs. The first unquestionable costal facet therefore is dorsoventrally high and faces somewhat dorsally. The last facet is on the thin posterior edge of the sternum close to the midline (fig. 22c) and consequently is low with a horizontal orientation. The intervening two facets are intermediate in height and dorsolateral orientation. With the exception of the last facet, all points of attachment for the ribs are oriented primarily laterally when viewed from above (fig. 22b) and all have about the same anteroposterior length. It appears that only one rib would have attached to each of these facets by means of a cartilaginous extension (fig. 17b). The last facet is anteroposteriorly longer and is oriented more posteriorly than laterally. At least two ribs would have been connected to this facet via a mesosternal element (fig. 17b) of cartilage.

Posteriorly the sternum has an extension along the midline in most mature specimens (fig. 21), which is separated from the last facet for the ribs by a shallow emargination.

The dorsal surface of the sternum is more strongly concave in transverse section at the front (fig. 22a) than it is posteriorly. The centre of the dorsal surface is excavated along the midline, possibly representing a region where the two sternal plates have not yet co-ossified completely (fig. 22b). A low ridge lateral to this pit is scarred for the origin of the profundus layer of the sternocoracoideus.

The sternum of *Tangasaurus* falls within the range of variation seen in *Hovasaurus*. *Thadeosaurus* (Carroll 1981) has a growth series of sternal ossifications that cannot be distinguished at equivalent ages from those of *Hovasaurus*. Paired sternal ossifications in *Youngina* (Broom 1922), indicate that this specimen was immature. A single, central sternal plate is present in *Kenyasaurus* (Harris and Carroll 1977), and shows the same characteristics as the sternum of *Hovasaurus*. Most other eosuchians had a cartilaginous sternum of smaller size.

An ossified sternum is present in one specimen of *Araeoscelis* (Vaughn 1955), but it is not known whether it was a paired or single structure. As reconstructed, it bears no resemblance to the paliguanid and tangasaurid type of sternum.

In general the sternum of *Hovasaurus* resembles those of *Lacerta* (Romer 1956 ) and *Sphenodon* (Howes and Swinnerton 1901). Although the sterna of modern lacertilians are cartilaginous, each forms ontogenetically from two centres of condensed mesoderm that are continuous anteriorly with the mesodermal rudiments of the coracoids (Gladstone and Wakeley 1932).

## Limb proportions

In the smallest specimens of *Hovasaurus* the humerus is about 20 per cent shorter than the femur (table 1). However, the humerus grows at a higher rate than the femur, and in mature specimens can be 10 per cent longer than the femur (tables 1, 4). The coefficient of allometry of the humerus also exceeds that of the femur in *Tangasaurus* (Haughton 1924) and *Thadeosaurus* (Currie 1981b) and the length of the humerus exceeds that of the femur. This appears to be a characteristic of tangasaurids not found in most other types of reptiles. Compared to the femur, the humerus is relatively shorter in *Youngina* than it is at any life stage in *Hovasaurus*. There is no information available on growth of postcranial elements in *Youngina*, so although the humerus is 32 per cent shorter than the femur in the immature specimens that have been found, the ratio of humerus to femur length could have been higher in larger specimens.

The length of the forearm of *Hovasaurus* is 77 per cent of the length of the humerus in immature specimens, and only 52 per cent in large individuals. The ratio of radius to humerus length is slightly higher in the largest specimens of *Thadeosaurus* (0,59) and *Tangasaurus* (0,62). However, the lengths of the radii are not significantly different in any of the three genera.

The lower segments of the front and back limbs maintain approximately the same ratio throughout life in *Hovasaurus* (table 1). The radius is 67 per cent of the length of the tibia, which is close to that of *Thadeosaurus* and *Tangasaurus* (73 per cent).

In the smallest specimens of *Hovasaurus*, the expected mean length of the tibia is 88 per cent of that of the femur. The relative length decreases to 85 per cent in mature specimens. These figures are comparable with *Tangasaurus* (85 per cent), *Thadeosaurus* (90 per cent) and *Youngina* (89 per cent).

Limb proportions are often used as an indication of habitat preference. Osteological evidence shows that *Hovasaurus* and *Tangasaurus* were aquatic animals. There is nothing in the skeleton to indicate that *Thadeosaurus* preferred an aquatic habitat, yet its limb proportions are very similar to those of *Hovasaurus*. Perhaps *Thadeosaurus* spent a great deal of time in the water, but had not become specialized for an aquatic existence. Among living reptiles, marine iguanas and aquatic varanoids are excellent swimmers but do not show any special adaptations in the skeleton.

*Champsosaurus* and *Askeptosaurus* were Mesozoic eosuchians that unquestionably spent much of their life in the water. Their limb proportions are quite different from those of *Hovasaurus*, however, which is a strong indication that the limbs were used in a different manner.

Of the non-eosuchian reptiles that are unquestionably aquatic, nothosaurs show the greatest similarity in limb proportions to tangasaurids. In *Pachypleurosaurus* (Zangerl 1935), the humerus is only 80 per cent of the length of the femur in the smallest specimens, but it is more than 115 per cent in large animals. The forearm is about 50 per cent of the length of the humerus, as in *Hovasaurus*. The significance of limb proportions will be discussed later.

### *Humerus*

In general configuration, the humerus of *Hovasaurus* is primitive for a reptile. The powerful development of the entepicondyle beyond the elbow joint increased the mechanical advantage of the flexor musculature, indicating that the animals were probably obligatory sprawlers.

The humerus grows with a high coefficient of allometry (1,6). The expected length of a humerus in an animal with a 10 mm long dorsal centrum is 27 mm (27,8 OLU; 7,2*x*). *Hovasaurus* has a relatively long humerus compared with other Permian reptiles. *Palaeothyris* has a humerus 19 OLU (5,0*x*) in length (Carroll 1970). The humerus of the larger specimen of *Tangasaurus* falls close to the expected length of a *Hovasaurus* of similar size (Currie, in press). The humerus of *Thadeosaurus* is significantly shorter (25,8 OLU; 6,7*x*).

In juvenile specimens of *Hovasaurus boulei* (figs. 23a, 24a, b, c), little more than the cylindrical shaft of the humerus was ossified at the time of death. The width of the distal end of the bone is 47 per cent of the length of the bone. The plane of proximal expansion is almost perpendicular to that of

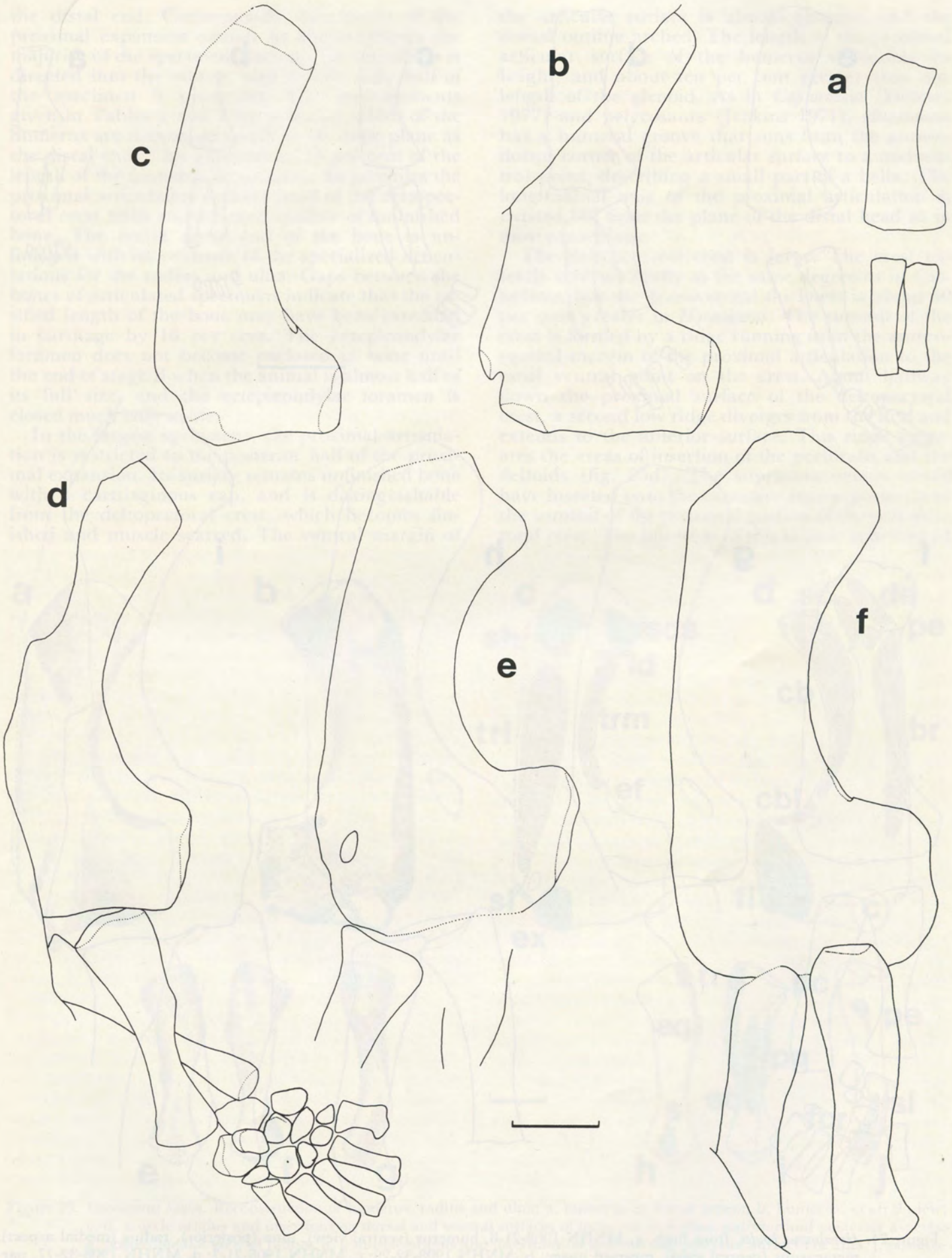



Figure 23. *Hovasaurus bolei*, front limb, a, MNHN 1908-32-1, humerus (dorsal view), radius (anterior view), ulna (anterior view); b, MNHN 1925-5-50, humerus, reversed image; c, MNHN 1908-32-24, humerus, reversed; d, MNHN 1908-32-59, humerus, radius, ulna, carpus, reversed image; e, MNHN 1925-5-46, humerus; f, MNHN 1908-32-60, humerus, radius, ulna, reversed. Scale = 1 cm.

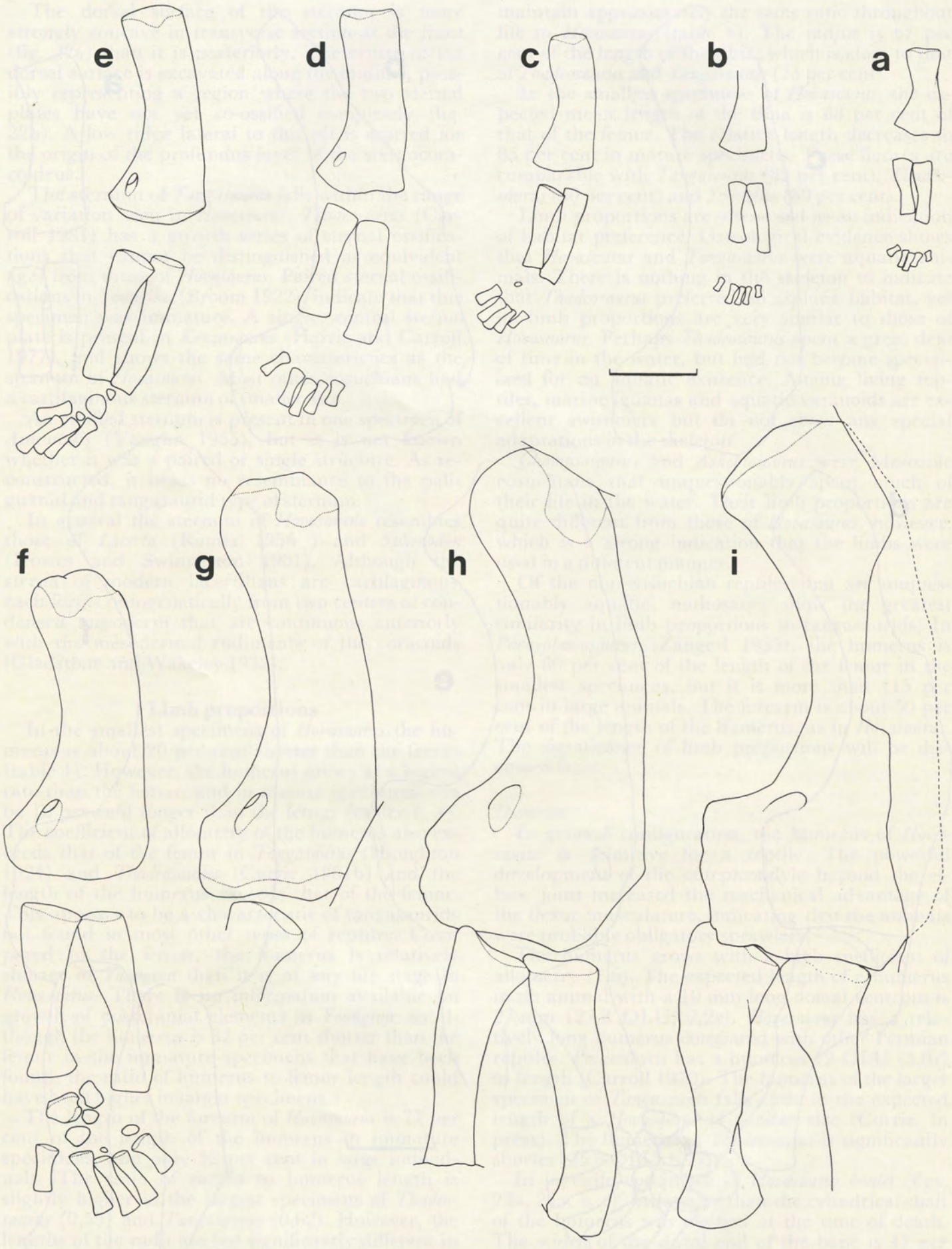



Figure 24. *Hovasaurus boulei*, front limb. a, MNHN 1908-21-8, humerus (ventral view), ulna (posterior), radius (medial aspect), metacarpus (ventral view), reversed image; b, MNHN 1908-32-29; c, MNHN 1908-21-7; d, MNHN 1908-32-77, partially restored from right side; e, MNHN 1908-32-23, reversed; f, MNHN 1925-5-12; g, MNHN 1908-32-25; h, MNHN 1925-5-56; i, MNHN 1908-32-67. Scale = 1 cm.

the distal end. Consequently, the extent of the proximal expansion cannot be determined in the majority of the specimens because the expansion is directed into the matrix, and usually only half of the specimen is preserved. The measurements given in Tables 1 and 4 for proximal width of the humerus are maximum width in the same plane as the distal end. This amounts to 34 per cent of the length of the humerus in juveniles. In juveniles the proximal articulation and the head of the deltopectoral crest form a continuous surface of unfinished bone. The entire distal end of the bone is unfinished with no evidence of the specialized articulations for the radius and ulna. Gaps between the bones of articulated specimens indicate that the ossified length of the bone may have been extended in cartilage by 16 per cent. The entepicondylar foramen does not become enclosed in bone until the end of stage B when the animal is almost half of its full size, and the ectepicondylar foramen is closed much later in life.

In the largest specimens, the proximal articulation is restricted to the posterior half of the proximal expansion. Its surface remains unfinished bone with a cartilaginous cap, and is distinguishable from the deltopectoral crest, which becomes finished and muscle scarred. The ventral margin of the articular surface is almost straight, and the dorsal outline arched. The length of the proximal articular surface of the humerus is double its height, and about ten per cent greater than the length of the glenoid. As in *Captorhinus* (Holmes 1977) and pelycosaurs (Jenkins 1971), *Hovasaurus* has a humeral groove that runs from the anterodorsal corner of the articular surface to a midventral point, describing a small part of a helix. The longitudinal axis of the proximal articulation is twisted 60° from the plane of the distal head as in most eosuchians.

The deltopectoral crest is large. The crest extends ventrolaterally to the same degree as in *Captorhinus*, but the dorsoventral thickness is about 40 per cent greater in *Hovasaurus*. The summit of the crest is formed by a ridge running from the anteroventral margin of the proximal articulation to the most ventral point on the crest. About halfway down the proximal surface of the deltopectoral crest, a second low ridge diverges from the first and extends to the anterior surface. This ridge separates the areas of insertion of the pectoralis and the deltoids (fig. 25d). The supracoracoideus would have inserted onto the canocave region posterior to the summit of the proximal portion of the deltopectoral crest. The insertion of this muscle is delimited

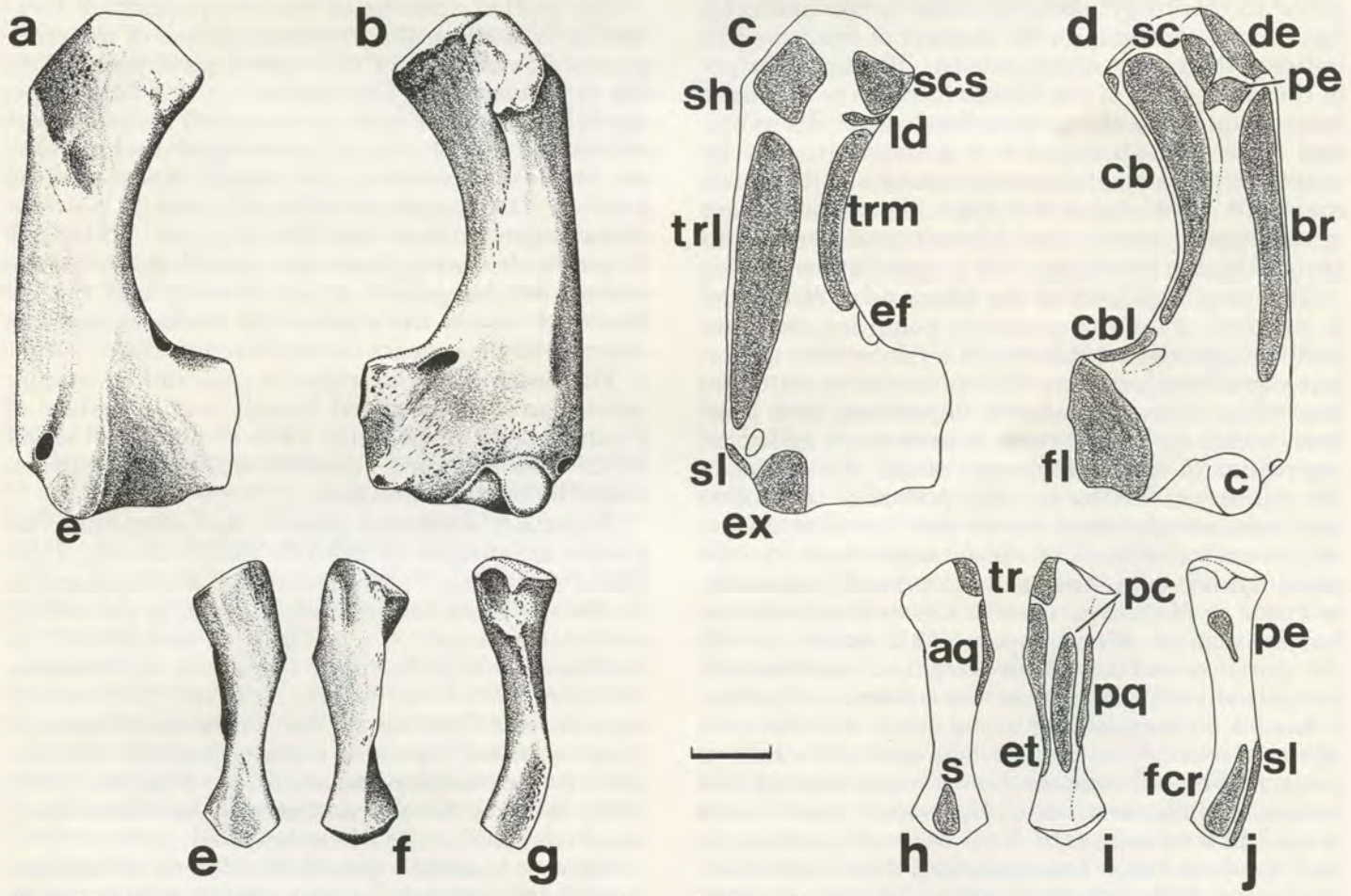



Figure 25. *Hovasaurus boulei*. Reconstruction of humerus, radius and ulna; a, humerus in dorsal aspect; b, humerus, ventral view; c, d, muscle origins and insertions on dorsal and ventral surfaces of humerus; e, f, ulna, anterior and posterior aspects; g, posteromedial view of radius; h, i, muscle origins and insertions on anterior and posterior surfaces of ulna; j, posteromedial areas of muscle origin and insertion of the radius. Scale = 1 cm.

posteriorly by a low ridge extending from the most ventral point of the proximal humeral articulation to the most ventral point of the deltopectoral crest. Scarring on the ventral surface of the proximal head of the humerus posterior to the supracoracoideus marks the insertion of the coracobrachialis brevis. The extent of fleshy attachment cannot be made out, but it probably would have extended down the shaft of the humerus as in living reptiles. A sharply defined ridge extends from the deltopectoral crest onto the anterior margin of the shaft of the humerus, and shows the anterior extent of the proximal portion of the brachialis inferior insertion. The distal extent of this muscle is defined by a tapering concavity near the ventroanterior margin of the distal head of the humerus.

The posterior margin of the proximal head is scarred distal to the articulation for the subcoracoscapularis insertion, which extends onto a scarred region on the dorsal surface. A low ridge distal to the slightly concave, dorsal insertion of the subcoracoscapularis would have been the point of insertion of the latissimus dorsi.

The dorsal surface of the humerus is divided into posterodorsal and anterodorsal regions by a low ridge extending from the posterodorsal corner proximally to the ectepicondyle. The short head of the triceps medialis would have originated posterior to this ridge along the shaft of the humerus, but there is nothing on the humeri of *Hovasaurus* to indicate the extent of this muscle. The fleshy origin of the short head of the triceps lateralis would have been anterior to the longitudinal ridge. Its proximal limit is marked by a prominent, heavily scarred ridge near the anterior margin of the proximal head. Proximal to this ridge, the dorsal surface is excavated above the deltopectoral crest, and scarred for the insertion of the scapulohumeralis.

The proximal head of the humerus of *Hovasaurus* is different from the primitive condition exemplified by *Captorhinus* (Holmes 1977) in several minor, but significant, respects. The proximal articulation has taken a more posterior orientation and position, which by itself would suggest more restricted capability of anterior motion of the distal end of the humerus. However, this potential restriction has been compensated for by the lateral extension of the posterior facet of the glenoid. Similarly the proximal articulation has become more ventrally oriented in *Hovasaurus* than in *Captorhinus*, and cannot be seen in dorsal aspect. This would restrict the dorsoventral arc of movement of the humerus compared with that seen in *Captorhinus*, except that it has been compensated for by increased convexity of the glenoid, plus greater exposure of its ventral surface. The articulation between the glenoid and humerus indicates that *Hovasaurus* was better adapted for bringing the front limb under the body and was somewhat less sprawling than *Captorhinus*. The distal end of the humerus could not have been raised above the proximal end because the proximodorsal rim of the humerus would contact the dorsal margin of the glenoid. *Hovasaurus* would have been able to pull its humerus into a more vertical position than *Captorhinus*. But more importantly, when the humerus was brought under the body in *Hovasaurus*, it would have been beneath the glenoid and not lateral to it. This would have meant that the front limb was thrusting against the bony support of the scapulocoracoid when it was brought underneath the body, rather than against the tendons and ligaments holding it to the scapulocoracoid.

The separation between dorsal and ventral surfaces for muscle insertion is more pronounced in *Hovasaurus* than in *Captorhinus*. The area of insertion of the scapulohumeralis has shifted anteriorly from the position in *Captorhinus* (Holmes 1977) and increased in area. The increased ability of this muscle to pull the distal end of the humerus dorsoanteriorly is correlated with the increased ability of the ventral musculature to pull the humerus ventroposteriorly. The more ventral position of the deltopectoral crest and its increased size shows that more emphasis was placed on pulling the front limb under the body in *Hovasaurus* than in *Captorhinus* and protorothyridids (Reisz 1980).

The distal end of the humerus is primitive in appearance. The entepicondyle is massive for an eosuchian, so that the distal expansion of the humerus is more than double the shaft diameter.

The dorsal opening of the entepicondylar foramen is located on the proximal surface of the entepicondyle rather than the more typical position on the dorsal surface. The ventral wall of the entepicondylar groove is more pronounced than the dorsal wall so that the dorsal groove and opening cannot be seen in anteroventral aspect. Because of its position, the foramen is often not seen in posterodorsal aspect either (fig. 23a, b, d, e). When this happens, the more prominent ventral margin of the entepicondylar groove is not showing and the inflection between the shaft of the humerus and the entepicondyle appears more pronounced.

The ectepicondylar ridge is powerful in mature specimens. It is rounded distally with a surface of finished bone in MNHN 1908-32-60 and AMNH 5333. The extensor musculature of the forearm would have originated here.

A distinct supinator process and ectepicondylar groove are present in MNHN 1925-5-50 (fig. 23b). The distal ends of the supinator and ectepicondyle in this specimen are unfinished bone, so the ectepicondylar foramen was probably closed distally by cartilage. In slightly larger specimens of *Hovasaurus* (MNHN 1925-5-46, fig. 23e; AMNH 5333) the ectepicondylar foramen for the radial nerve and associated blood vessels is enclosed entirely in bone. The ectepicondylar foramen of *Youngina* (Gow 1975) is open distally and shows that these specimens were immature when they died.

There is a shallow groove distolateral to the ectepicondylar foramen on the posterodorsal surface where the supinator process and the ectepicondyle are joined by a bridge of bone. The supinator musculature would have originated here as in modern

lizards (Romer 1944). The presence of this groove in MNHN 1908-32-60 (fig. 23e) indicates that the ectepicondylar foramen was completely encircled by bone in this specimen, even though the foramen itself cannot be seen because of damage.

There is a pronounced ridge of bone on the anteroventral surface of the humerus proximal to the entepicondylar foramen for the insertion of the coracobrachialis longus. The anteroventral surface of the entepicondyle is concave in longitudinal section, and heavily scarred for the origins of the flexor musculature of the forearm and hand. A distomedially oriented ridge bounds this region distolaterally, and has longitudinal muscle scarring along its surface. The ridge terminates where the posterior and distal surfaces of the entepicondyle meet and has a distoventrally oriented depression for muscle insertion. It appears that the ulnar flexors originated on this ridge and in the scarred region between the ridge and the humerus-ulna articulation.

The ectepicondylar foramen emerges from the bone lateral to the capitellum on the distal surface of the humerus and cannot be seen in anteroventral aspect (fig. 24).

There is an almost circular capitellum for articulation with the radius on the anteroventral surface on the distal end. As in other primitive reptiles, the humerus-ulna articulation is medial to the capitellum and includes a convex region posterior to a narrow concavity next to the capitellum.

Except for size, the humerus of *Hovasaurus* is indistinguishable from that of *Thadeosaurus* (Currie 1981b). The prominent development of the entepicondyle is also evident in *Tangasaurus* (Currie, in press). The humerus of *Youngina* is poorly ossified (Gow 1975) and only the base of the entepicondyle is preserved. However, as in tangasaurids it is sharply divergent from the shaft, and the entepicondylar foramen is located close to the proximal margin of the entepicondyle.

*Radius*

The radius shows moderate positive allometry in its growth. At maturity its length is approximately 14,4 OLU, or 3,7$x$. This is not significantly different from the length in *Thadeosaurus* (15,1 OLU; 3,9$x$). The length of the radius of *Tangasaurus* falls within the range of variation for this dimension in *Hovasaurus* (Currie, in press).

The radius is slightly longer than the ulna as in most eosuchians. In *Acerosodontosaurus*, the ulna (excluding the olecranon) is longer than the radius.

In general outline, the radius of *Hovasaurus* has a twisted outline similar to that of *Acerosodontosaurus* (Currie 1980), *Thadeosaurus* (Carroll 1981) and *Champsosaurus* (Erickson 1972). The shaft is straight for the proximal two thirds of the bone, but curves posteriorly at the distal end (fig. 24b, c, d, e, f, h). The anterior and lateral surfaces of the radius are visible in only two juvenile specimens (figs. 3, 23a) where no details are preserved. The remaining specimens are exposed in posterior and medial aspect.

The proximal surface of the radius is concave for articulation with the capitellum. The outline of the articular surface is oblong with a mediolateral longitudinal axis, a flattened posterior margin and a strongly convex medial rim. A slight lip extends over the end of the humerus like a miniature olecranon. The humerus-radius articulation is continuous posteriorly with a limited articular surface for the ulna. This posterior surface forms the dorsal and mediodorsal margins of a distinct concavity in the proximoposterior surface of the radius. Ventromedial to this hollow is a tubercle for insertion of a tendon of the biceps muscle. A ridge twists ventromedial from this process to a point about halfway along the longitudinal axis of the radius where it ends (MNHN 1925-5-56, 1908-32-67). This ridge probably served for insertion of the biceps also.

The distal end of the radius is exposed in medial view in MNHN 1925-5-12 (fig. 5) and posteromedial view in MNHN 1925-5-56 (fig. 24h). A sharp ridge separates the medial and anterior surfaces of the distal half of the radius as in *Thadeosaurus* (Carroll 1981). The supinator longus would have inserted onto the ridge. The radius is flattened and scarred medial to the ridge, probably for the insertion of the flexor carpi radialis. The distal articulation is oval in outline with a convex surface.

*Ulna*

The olecranon process is not ossified in *Hovasaurus*. There is a series of longitudinal grooves and ridges on the lateral, anterolateral and posterolateral surfaces of the proximal end of the radius. A similar series on the olecranon of captorhinids suggested to Holmes (1977) that the triceps would have inserted broadly on this region via a tendinous sheet.

Approximately a third the length of the ulna from the proximal end there is a protuberance of bone on the lateral margin (fig. 23d) that was probably the centre of insertion of the anconaeus quartus as in *Captorhinus* (Holmes 1977) and protorothyridids (Reisz 1980). The distal end of the anterior surface of the ulna is shallowly concave over most of the surface. As in all living reptiles this region would have served as the origin of the supinator manus. It is bordered medially by a low but distinct ridge that runs along the medial edge of the radius in the distal half of the bone.

On the posterior surface of the ulna, the ridge of insertion for the triceps musculature is bounded medially by a shallow trough. There is a ridge along the rim of the articulation. The posteroventral surface of this narrow ridge is rugose, suggesting perhaps that the joint ligaments attached here. A longitudinal ridge originates distal to the proximal articulation on the posterior surface, and becomes prominent distally as the medial edge of the bone (figs. 24i, 25f). The same ridge is present in *Acerosodontosaurus* (Currie 1980), but is not as con-

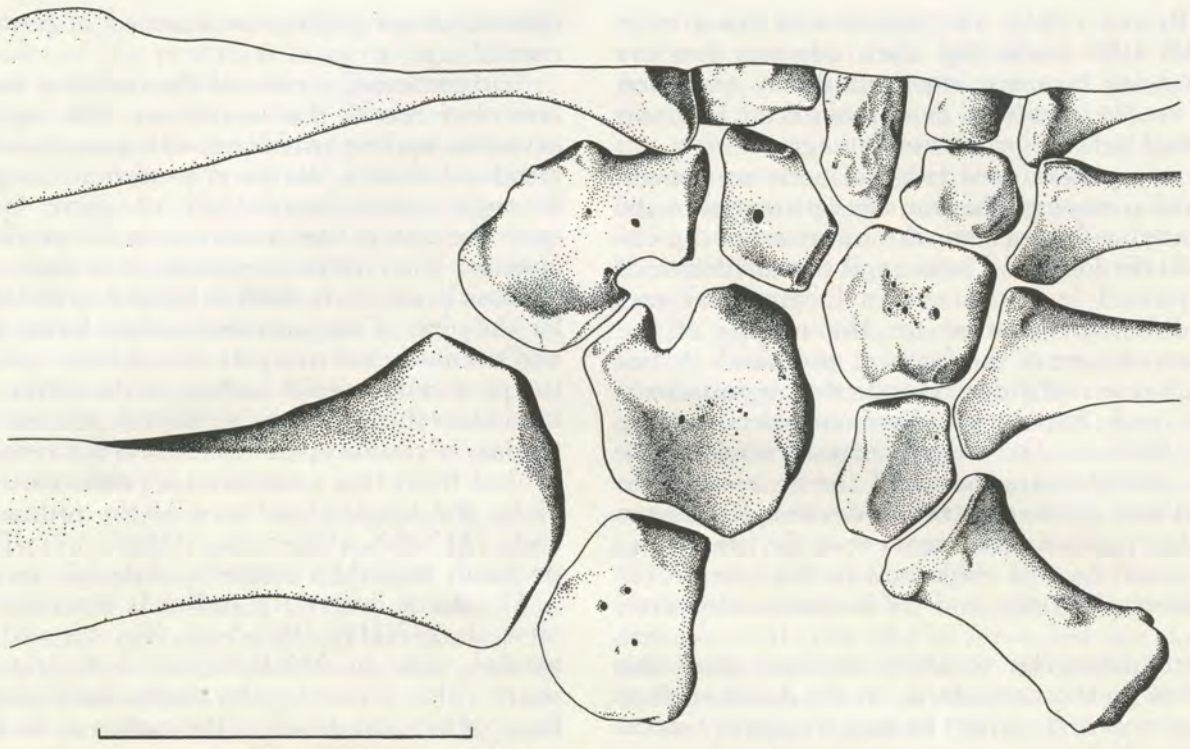


Figure 26. *Hovasaurus boulei*, SAM 9457, manus, ventral aspect. Scale = 1 cm.

spicuous. In *Thadeosaurus* the ridge is as well developed as in *Hovasaurus*. The central area of the ulna is flattened posterolateral to the ridge. One of the profundus heads of the palmaris communis muscle probably would have had its origin here. The pronator quadratus would have originated from the medial edge of the ridge. The ventral end of the ridge is relatively low and terminates posterodorsal to the articulation with the ulnare (fig. 26).

*Manus*

The carpus, like that of most primitive reptiles, has eleven elements (figs. 23d, 26). Each element tends to have a smaller surface area ventrally than it does dorsally. The elements key together to form a dorsally arched carpus.

The carpus is not fully ossified until at least stage D (fig. 24f). In at least one specimen, there is partial ossification of the ulnare at stage B (fig. 24c). Three ossifications can be seen at stage C (fig. 24e). In *Claudiosaurus* (Carroll 1981), the ulnare, intermedium and radiale are the first three bones to have finished surfaces, which suggests that these three bones may have been the first to ossify in *Hovasaurus*.

The radiale is a relatively small element, approximately half the size of the ulnare. The articulation with the radius is broad and slightly concave. The lateral surface of the radiale articulated with the lateral centrale, but unlike *Acerosodontosaurus* (Currie 1980) there is also a small proximolateral articular facet for the intermedium.

The intermedium is at least 50 per cent longer than its maximum width. The proximal articulation with the ulna is extensive and is delimited ventrally by a low ridge where the joint ligaments inserted. The surface of the articulation with the ulnare is flat, and has been expanded by a ridge on the ventral surface. It is doubtful that much movement was possible at this joint. A protuberance on the medial rim of the intermedium (fig. 26) is the most dorsolateral point of origin of the extensor digitorum communis brevis.

The ulnare is the most prominent bone of the carpus. It is wider than it is long as in *Thadeosaurus*, *Youngina*, *Acerosodontosaurus*, and most other eosuchians. The articulation below the perforating foramen with the lateral centrale is broadened ventrally by a ridge, and the articular surface is relatively flat and incapable of much movement. The distal articular surface with the fourth and fifth distal carpals is convex, and is broader than the concave joint surfaces on the distal carpals. Rotation was therefore possible between the proximal and distal carpals. The ventrolateral surface of the ulnare is concave where the digiti minimi inserted. The dorsal surface is flat and featureless (MNHN 1925-5-50).

The pisiform would have projected posterolaterally when articulated properly with the ulna and ulnare. The ventral medial face of the bone is concave for the insertion of the flexor carpi radialis.

The lateral centrale appears to separate the intermedium and ulnare at the base of the perforating foramen, and yet apparently formed little or none of the border of that foramen.

The medial centrale is a wide bone that, as in *Acerosodontosaurus* (Currie 1980), articulated with the first three distal tarsals. In all three specimens of *Hovasaurus* where this region shows, the medial

centrale has extended laterally from the primitive position seen in most Permian reptiles, and contacts the fourth distal tarsal as well. This contact prevents the lateral centrale from articulating with the third distal carpal. This specialized character exists in *Thadeosaurus* (Carroll 1981), and probably in *Tangasaurus* (Haughton 1924: fig. 1).

The first distal carpal is relatively small and contacts only the first metacarpal distally. In several eosuchians, including *Acerosodontosaurus*, the first distal carpal is large enough to articulate with the first two metacarpals. The second distal carpal of *Hovasaurus* is larger than the first, and contacts metacarpals I and II. The fourth distal carpal is large and contacts five of the ten other carpals plus the third and fourth metacarpals. As in *Thadeosaurus*, the fifth distal carpal articulates with the fourth and fifth metacarpals.

The metacarpals and phalanges are known from specimens of all ages (table 3). The first and fifth metacarpals are approximately the same length, and are about 25 per cent shorter than the subequal second, third and fourth metacarpals. These proportions are essentially the same in *Claudiosaurus* and *Champsosaurus*, but in *Thadeosaurus* and *Tangasaurus* the fourth metacarpal is clearly longer than the others. The increase in symmetry of the metacarpals of *Hovasaurus* could be related to the use of the manus as a paddle, which is apparently the case in nothosaurs and crocodiles (Robinson 1975). With the exception of the first metacarpal, each metacarpal is overlapped dorsomedially by its neighbour in *Hovasaurus* and *Thadeosaurus*. Metacarpal IV grows with strong positive allometry (table 4) and at maturity is 13,4 mm (5,2 OLU; 1,3*x*) in length. This bone is the same relative length in *Tangasaurus* (Currie, in press). In contrast, growth in this element in *Thadeosaurus* is isometric, but the mature length is significantly greater (6,1 OLU; 1,6*x*).

The phalangeal formula is 2.3.4.5.3 for the manus. The first digit, including the metacarpal, is 47 per cent of the length of the fourth digit, the second is 68 per cent, the third is 85 per cent and the fifth is 64 per cent. On the average, the fifth digit is 75 per cent of the length of the third. These proportions are about the same at any life stage so all elements probably have approximately the same coefficient of allometry during growth. The coefficient for the phalanges of the fourth digit is 1,2 which is the lowest allometric growth rate in the front limb. At maturity the fourth digit is 93 per cent of the length of the radius, or 13,3 OLU (3,5*x*). The fourth digit of the manus grows with negative allometry in *Thadeosaurus*, but at maturity the relative length of the digit (15,0 OLU; 3,9*x*) is greater than that of *Hovasaurus*.

The ventral surface of each phalanx is flattened with a shallow longitudinal groove for one of the ligaments of the palmaris communis profundus.

The penultimate phalanx of each digit is as long as or longer than the antepenultimate phalanx (or metacarpal in the case of the first digit). This characteristic has been noted in many primitive and extant reptiles, but its significance is not understood at present.

The unguals are recurved and sharply pointed distally. The flexor tubercles are not strongly developed (figs. 3, 4, 5 and 6), and the unguals are indistinguishable from those of most other eosuchians.

## Pelvic Girdle and Limb

*Ilium*

The three pelvic bones are known from all life stages in *Hovasaurus* (fig. 27). In even the largest specimens the three elements are not co-ossified, although the sutures have small interfingering protuberances and pits for strength.

The distal end of the iliac blade has a posteriorly facing, concave facet in juvenile animals (fig. 27a, b, f, h, i), which indicates that the bone was continued distally in cartilage. As an individual matured, the facet became relatively smaller. It has disappeared by stage F. and in the larger specimens the iliac blade terminates caudally in a point (MNHN 1908-32-24).

Two measurements were taken (table 1) — the length of the base (between the anterior limit of the iliopubic suture and the posterior of the ilioischiatic suture) and the length of the iliac blade (between the anterior limit of the iliopubic suture and the most caudad point of the blade). Both dimensions increase isometrically in size during growth ($k_{yx}'$ is not significantly different from 1,0). At maturity the base is 7,3 OLU (1,9*x*) in length, and the blade is 13,2 OLU (3,4*x*). Growth is isometric in *Thadeosaurus* as well for these dimensions, and the base (6,6 OLU; 1,7*x*) and blade (13,1 OLU; 3,4*x*) are not significantly different from those of *Hovasaurus*. Compared with the average length of a dorsal centrum (*x*), the length of the iliac blade is the same in *Acerosodontosaurus*.

The ilium, as would be expected in any element where two of the major dimensions grow at almost the same rate, does not change much in outline through its life history (fig. 27).

As in most eosuchians, the acetabulum is formed mainly by the ilium in *Hovasaurus*. A strong ridge arches over the acetabulum anteriorly and dorsally, and is confluent posteriorly with less prominent ridges from the ilioischiatic contact and the ventral margin of the iliac blade. This ridge system has replaced the supra-acetabular buttress of protorothyridids, and permits a more powerful anterodorsal thrust of the hind limb against the pelvis for greater speed (Brinkman 1979).

The iliac blade extends caudally far beyond the acetabulum at all life stages, and is much more extensive that that of *Youngina* (Gow 1975). The external surface of the blade is concave and the internal is convex. Consequently the internal surface of the blade faces dorsomedially for attachment of the sacral ribs. This region is striated (fig. 27h, l) by ridges and grooves for strong contacts. The length of the sutural surface on the ilium of MNHN R146

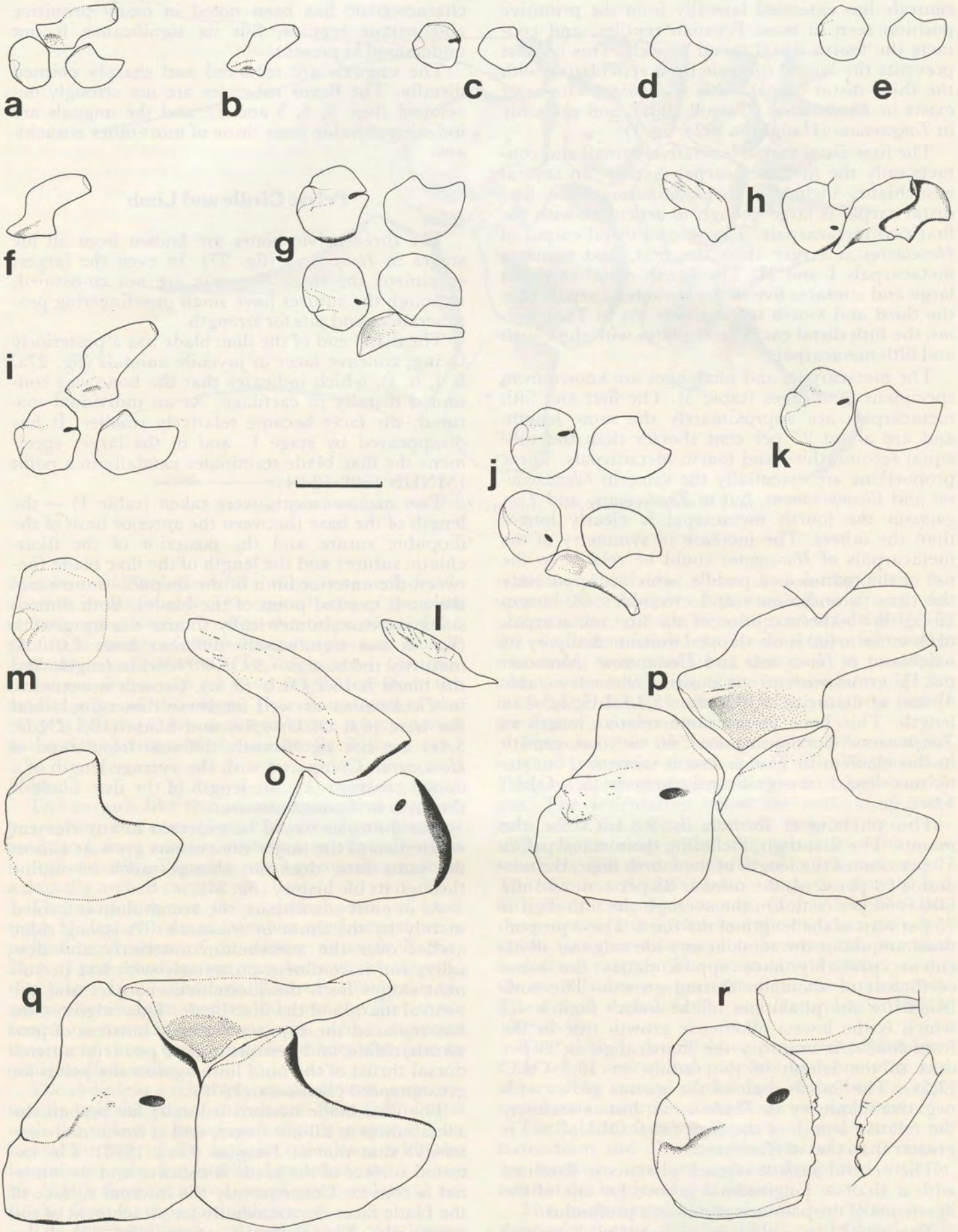



Figure 27. *Hovasaurus boulei*, pelvic girdle. a, MNHN 1925-5-10, composite drawing from right and left sides; b, MNHN 1925-5-20, reversed image; c, MNHN 1925-5-25; d, MNHN 1908-21-8, reversed; e, MNHN 1908-32-29, composite; f, MNHN 1908-32-21, reversed; g, SAM 9460; h, MNHN 1908-32-4, ilium (medial view), ilium (lateral view, reversed image), pubis and ischium (dorsal view, reversed); i, MNHN 1908-32-2/7; j. MNHN 1908-32-22; k, MNHN 1908-21-5, composite; l, MNHN 1925-5-41, dorsomedial view of ilium; m, MNHN 1908-32-23, reversed; n, MNHN 1925-5-32, composite; o, MNHN R146, medial view of ilium, dorsal view of pubis, reversed; p, MNHN 1908-32-45 reversed; q, MNHN 1908-32-49, reversed; r, MNHN 1908-21-6. Scale = 1 cm.

is equal to the sum of the lengths of the distal ends of the two sacral ribs, which shows that the first caudal rib did not have an osseous contact with the ilium despite its orientation.

*Pubis*

The pubis is a large, platelike bone that, judging from the vertical, well-ossified interpubic suture of MNHN 1908-21-16, must have been almost horizontal in the living animal.

In small specimens (fig. 27c), all pelvic elements were widely separated by cartilage. The immature pubis is oval in outline with the small protuberance to represent the "pectineal" tubercle and a posterolateral slit for the obturator foramen.

In contrast with the ilium the allometric growth coefficients for both length (1,2) and width (1,3) of the pubis are significantly different (table 4) from isometry. A mature pubis is wider (10,8 OLU; 2,8*x*) than long (8,6 OLU; 2,2*x*) in *Hovasaurus*. Growth in *Thadeosaurus* is isometric (Currie 1981b) and the width (9,6 OLU; 2,5*x*) is not significantly different from *Hovasaurus*. The length (6,8 OLU; 1,7*x*) is relatively smaller than in the pubis of the more aquatic *Hovasaurus*.

The proportions of the pubis show that *Hovasaurus* was broad in the pelvic region. The ratio of pubis width to anteroposterior length in the adult is 1,27 compared with 1,47 in *Thadeosaurus* and 1,22 in *Acerosodontosaurus*. In *Youngina*, the ratio is less than 1,00, but the pubis is not well ossified.

The pubis contributes only a small area (fig. 27p) to the acetabular surface.

There is a powerful "pectineal" tubercle that terminates anteroventrally in unfinished bone. It can extend as much as 0,7*x* below the main surface of the pubis. Longitudinal striations along the finished bone of the ventromedial surface of the tubercle would have served for strengthing the attachment of the ambiens and pubotibialis muscles.

The anterior margin of the pubis medial to the tubercle curves anteromedially and meets the other pubis at the midline in an acute angle. The rim is sharply offset from the shallowly concave ventral surface of the main body of the pubis.

The tubercle extends posteriorly as a ridge that decreases in height and ends a short distance anterolateral to the obturator foramen for the obturator nerve. The internal opening of the oburator foramen (fig. 27o) is lateral to the position of the external opening.

The suture with the ischium (fig. 27r) is strong and interfingering. There is no thyroid fenestra such as may have existed in *Acerosodontosaurus*. A notch in the back of the pubis of *Youngina* was attributed to incomplete ossification (Gow 1975). However, a notch as pronounced as this does not appear in the posterior margin of the pubis of *Hovasaurus* or *Thadeosaurus* at any life stage. It is possible that *Youngina* did have an incipient thyroid fenestra.

*Ischium*

The appearance of the ischium does not change much with increased size in *Hovasaurus* (fig. 27), although the curvature of the medial margin tends to be greater in juveniles. The degree of positive allometric growth ($k_{yx}' = 1,2$) in the length and width of the ischium is about the same as that of the pubis. A large specimen would have an ischium 10,9 OLU (2,8*x*) long and 8,9 OLU (2,3*x*) wide. Growth in *Thadeosaurus* is isometric, and the mature ischium is 9,7 OLU (2,5*x*) by 7,6 OLU (2,0*x*), which is significantly smaller than *Hovasaurus*.

An anterolaterally oriented facet on the ischium forms about a quarter of the area of the acetabulum. A ventral ridge borders the acetabular facet, and is scarred for attachment of joint ligaments.

The ventral surface of the ischium is flat in most specimens, and slightly concave in others. The main part of the ischium would have faced more laterally than the pubis.

*Femur*

The femur (figs. 28, 29) is a more gracile bone than the humerus. In juveniles the ossified portion is longer than the humerus. Allometric growth of the femur is positive ($k_{yx}' = 1,3$), but not as much as the humerus. When fully grown, the femur is 25,0 OLU (6,5*x*) long. The femur of *Tangasaurus* falls within the expected range of variation for *Hovasaurus*. In *Thadeosaurus*, the femur increases isometrically in length to reach 23,2 OLU (6,0*x*) at maturity, which is not significantly different from the femur of *Hovasaurus*.

The entire proximal end of the femur is unfinished bone in immature specimens, and can be concave in the smallest ones. The proximal end of one mature specimen, MNHN 1908-32-49 (fig. 29j), is well exposed. As in other eosuchians, the articular head of *Hovasaurus* turns markedly dorsally, and is well differentiated from the internal trochanter. The articulation is oval, and its longitudinal axis slopes anterodorsally about 45° when the distal condyles are horizontal. This is fundamentally the same in *Thadeosaurus*. The long axis of the articular surface is about 40 per cent longer than the greatest width of the surface measured perpendicular to the axis, and is equivalent to 1,2*x*. A cartilaginous head would have covered this slightly convex surface of unfinished bone. The acetabulum is about 40 per cent longer than the ossified head of the femur, suggesting that there was either a great deal of cartilage involved in the joint, or that the head of the femur was capable of moving a great deal in the acetabulum.

The internal trochanter for the tendinous insertion of the puboischiofemoralis externus is well-developed and makes up more than half of the dorsoventral height of the proximal head. It terminates in an oval facet with a ventromedial orientation. This is connected proximodorsally by a sharp ridge of finished bone to the proximal articulation. The femur is concave anterior to the internal trochanter with longitudinal scarring for the puboischiofemoralis internus muscle (fig. 29j), and bears a short ridge near the distal end of the trochanter.

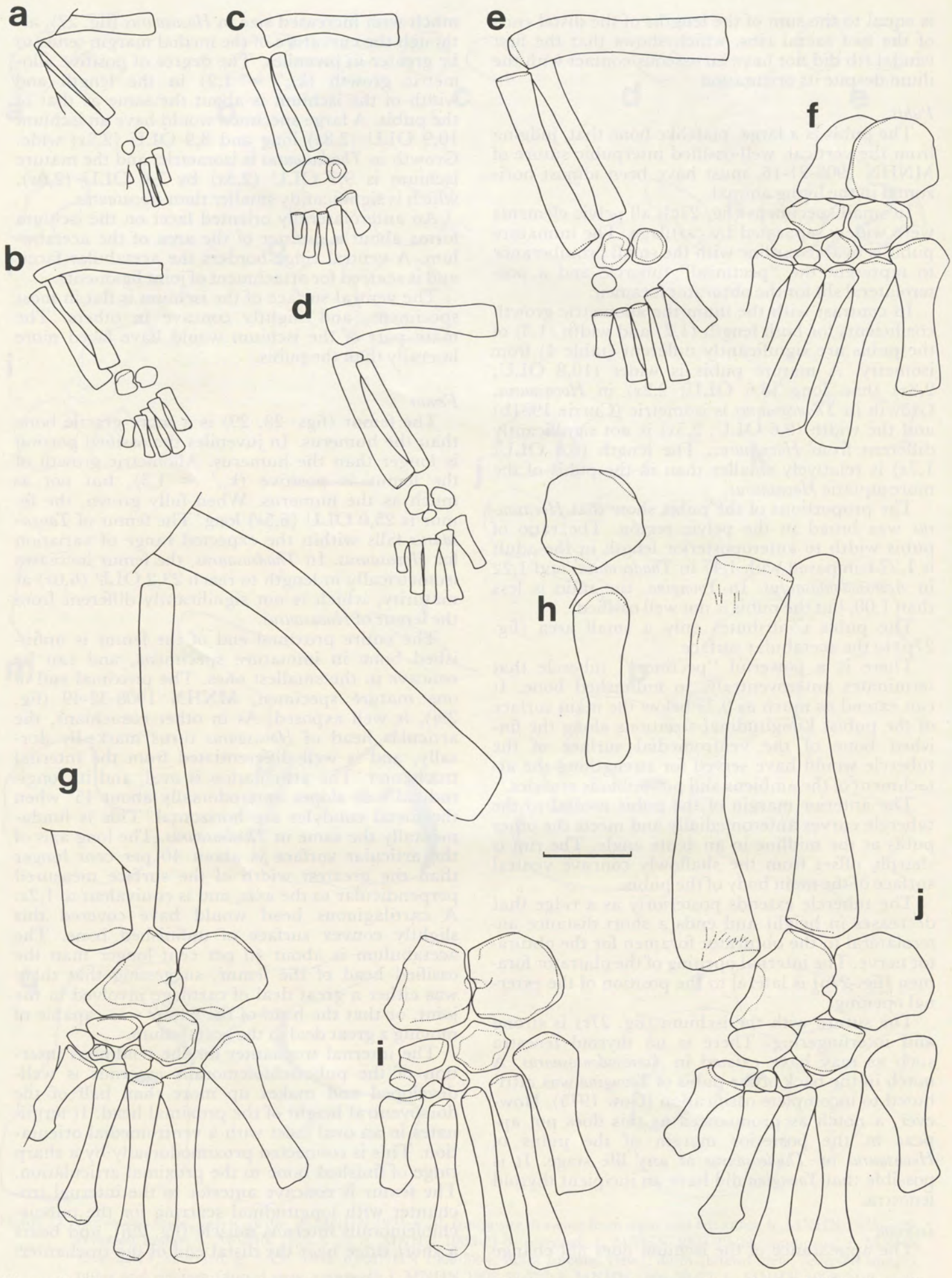



Figure 28. *Hovasaurus boulei*, femur (posterior view), tibia (posterior), fibula (anterior) and tarsus (dorsal). a, MNHN 1925-5-20, reversed image; b, MNHN 1925-5-18; c, MNHN 1908-32-21, reversed; d, MNHN 1908-21-2, reversed; e, MNHN 1925-5-41; f, MNHN 1925-8-14; g, MNHN 1908-32-24; h, MNHN 1908-21-6, calcaneum and metatarsal V, reversed; i, MNHN 1925-5-61; j, MNHN 1908-21-14, reversed. Scale = 1 cm.

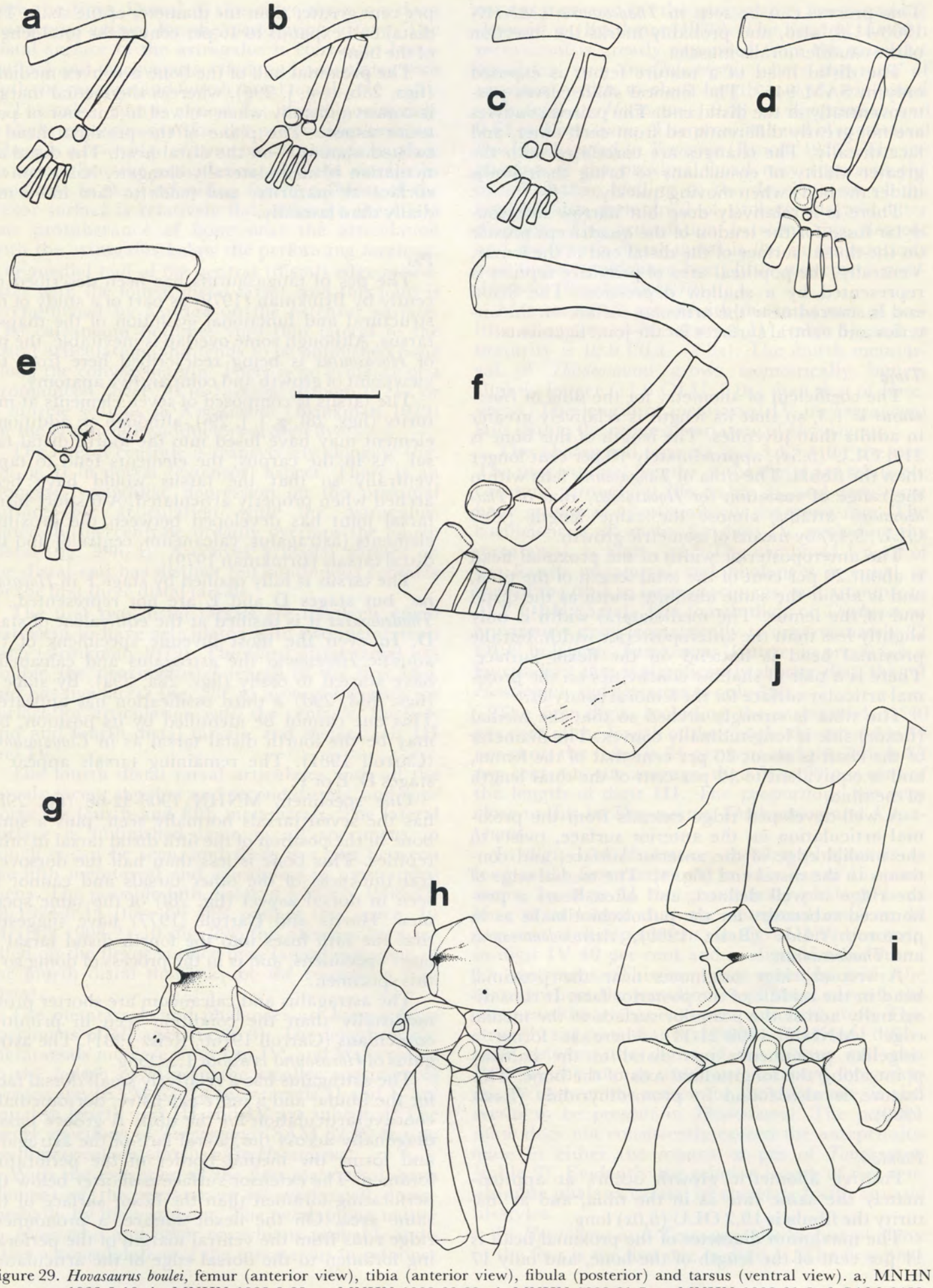



Figure 29. *Hovasaurus boulei*, femur (anterior view), tibia (anterior view), fibula (posterior) and tarsus (ventral view). a, MNHN 1925-5-10; b, MNHN 1925-5-25; c, MNHN 1908-32-29; d, MNHN 1908-21-7; e, MNHN 1908-21-5; f, SAM 9459; g, MNHN 1925-5-32; h, MNHN 1908-32-68; i, MNHN 1908-21-10, reversed; j, MNHN 1908-32-49, reversed. Scale = 1 cm.

This process can be seen in *Thadeosaurus* (MNHN 1908-11-8) also, and probably marks the insertion of the caudifemoralis muscle.

The distal head of a mature femur is exposed only in SAM 9457. The femoral shaft curves posteroventrally at the distal end. The paired condyles are not greatly differentiated from each other, and face distally. The changes are correlated with the greater ability of eosuchians to bring their limbs under the body when moving quickly.

There is a relatively deep but narrow intercondylar fossa for the tendon of the quadriceps muscle on the dorsal surface of the distal end of the femur. Ventrally, the popliteal area of primitive reptiles is represented by a shallow depression. The distal end is scarred near the articular surface on the anterior and ventral surfaces for the joint ligaments.

*Tibia*

The coefficient of allometry for the tibia of *Hovasaurus* is 1,3, so that its length is relatively greater in adults than juveniles. The length of this bone is 21,3 OLU (5,5*x*), approximately 10 per cent longer than the fibula. The tibia of *Tangasaurus* falls within the range of variation for *Hovasaurus;* that of *Thadeosaurus* attains almost the same length (20,9 OLU; 5,4*x*) by means of isometric growth.

The anteroposterior width of the proximal head is about 20 per cent of the total length of the tibia, and is about the same absolute width as the distal end of the femur. The mediolateral width is only slightly less than the anteroposterior width, but the proximal head is flattend on the flexor surface. There is a pair of shallow concavities on the proximal articular surface for the femoral condyles.

The tibia is strongly arched so that the medial (flexor) side is longitudinally convex. The diameter of the shaft is about 80 per cent that of the femur, and is equivalent to 12 per cent of the total length of the tibia.

A well-developed ridge extends from the proximal articulation on the anterior surface, twists to the medial edge of the anterior surface, and continues to the distal end (fig. 4). The medial edge of the ridge is well defined, and often bears a pronounced tuberosity for the puboischiotibialis as in protorothyridids (Reisz 1980), *Acerosodontosaurus* and *Thadeosaurus*.

A second ridge originates near the proximal head in the middle of the posterior face. It runs diagonally across the posterior surface to the medial edge (MNHN 1908-21-14) where it forms a ridgelike prominence just distal to the halfway point along the longitudinal axis of the bone. This feature is also found in protorothyridids (Reisz 1980).

*Fibula*

Positive allometric growth occurs at approximately the same rate as in the tibia, and at maturity the fibula is 19,2 OLU (5,0*x*) long.

The maximum diameter of the proximal head is 11 per cent of the length of the bone, and only 17 per cent greater than the diameter of the shaft. The distal end expands to 16 per cent of the total length of the bone.

The proximal half of the bone is convex medially (figs. 28b, c, g, j, 29g), whereas the medial margin is concave distally when viewed in anterior or posterior aspect. The plane of the proximal head is twisted about 45° on the distal head. The distal articulation is mediolaterally elongate, has a convex surface at maturity, and tends to face more medially than laterally.

*Pes*

The pes of tangasaurids has been described recently by Brinkman (1979) as part of a study of the structural and functional evolution of the diapsid tarsus. Although some overlap is inevitable, the pes of *Hovasaurus* is being redescribed here from the viewpoint of growth and comparative anatomy.

The tarsus is composed of seven elements at maturity (figs. 28f, g, i, j, 29i), although an additional element may have fused into the fourth distal tarsal. As in the carpus, the elements tend to taper ventrally so that the tarsus would have been arched when properly articulated. A distinct intratarsal joint has developed between the proximal elements (astragalus, calcaneum, centrale) and the distal tarsals (Brinkman 1979).

The tarsus is fully ossified by stage F in *Hovasaurus,* but stages D and E are not represented. In *Thadeosaurus* it is ossified at the equivalent of stage D. In even the most juvenile specimens of the aquatic *Hovasaurus* the astragalus and calcaneum have started to ossify (figs. 28a, 29a). By stage B (figs. 28d, 29d) a third ossification has appeared. This one cannot be identified by its position, but may be the fourth distal tarsal as in *Claudiosaurus* (Carroll 1981). The remaining tarsals appear in stages D, E or F.

One specimen, MNHN 1908-32-68 (fig. 29h), has the seven tarsals normally seen, plus a small bone in the position of the fifth distal tarsal in other reptiles. This bone is less than half the dorsoventral thickness of the other tarsals and cannot be seen in dorsal aspect (fig. 28f) of the same specimen. Harris and Carroll (1977) have suggested that the fifth fuses into the fourth distal tarsal in large specimens, and is in the process of doing so in this specimen.

The astragalus and calcaneum are shorter proximodistally than the condition seen in primitive eosuchians (Carroll 1976b, Reisz 1981). The astragalus of *Hovasaurus* is about 1,5*x* long.

The astragalus has a relatively small dorsal facet for the fibula, and a more extensive, dorsomedially concave articulation for the tibia. A groove passes diagonally across the lateral face of the astragalus and forms the medial border of the perforating foramen. The extensor surface is shorter below the perforating foramen than the flexor surface in the same area. On the flexor surface, a pronounced ridge runs from the ventral margin of the perforating foramen to the dorsal edge of the articulation

with the tibia. Dorsal to this ridge there is a deep transverse groove for the perforating artery. The distal surface of the astragalus is convex in longitudinal and transverse section, and articulates with both the centrale and fourth distal tarsal.

The calcaneum is almost flat medially with only a slight emargination for the perforating foramen. There is a low ridge of bone on the extensor surface to strengthen the articulation with the astragalus proximal to the perforating foramen. Most of the flexor surface is relatively flat, although there is a low protuberance of bone near the articulation with the astragalus below the perforating foramen. The medial half of the ventral (distal) edge articulates with the fourth distal tarsal, and this joint is strengthened by a ridge on the extensor surface. The calcaneum becomes very thin lateral to the distal articulation, and tends to be unfinished bone along the convex margin. There is no evidence of a pronounced "heel" as in *Youngina* (Broom 1921), or a muscle scar as in *Kenyasaurus* (Brinkman 1979) for the origin of the adductors of digit five.

The lateral centrale is transversely elongate (fig. 28f, g, j) in dorsal (extensor) aspect. There is an elongate, troughlike depression on the proximal surface for articulation with the astragalus. Laterally the centrale broadly overlaps the fourth distal (fig. 29h, i). A convex articular surface on the distal end has distinct but continuous contacts for the first three distal tarsals.

The first two distal tarsals are relatively small but seem to have articulated with two metatarsals each (Brinkman 1979). The third distal tarsal has double the proximodistal length of the first two, and has five facets (fig. 28f, g) around the extensor surface for articulation with the centrale, the second and fourth distal tarsals, and metatarsals III and IV.

The fourth distal tarsal articulates with all the tarsals except the first and second distals, and supports the fourth and fifth metatarsals. The lateral surface is unfinished bone in all specimens in which it can be seen, and there is a gap between the fifth metatarsal and calcaneum in most specimens. The possible fifth distal of MNHN 1908-32-68/1924-8-14 (fig. 29) fills part of this space. In MNHN 1908-21-10 (fig. 29i) this area has been infilled on the flexor surface by a lateral extension of the fourth distal that may be the co-ossified fifth distal.

The metatarsals and phalanges are known from specimens of all ages (table 3). The length of the metatarsals increase from I to IV, and V decreases to the length of III. In the smaller specimen of *Tangasaurus* (SAM 6231), metatarsals II and V are equal in length and III and IV are subequal. The larger specimen of *Tangasaurus* (SAM 6232) has an asymmetrical metatarsus as in *Hovasaurus*.

With the exception of the first metatarsal, each element of the metatarsus is overlapped dorsomedially by its neighbour. The overlapping nature in *Hovasaurus* and other eosuchians probably indicates a consolidation of the metatarsus in response to an increase in the propulsive force passing through it (Brinkman 1979). The head of the fifth metatarsal is greatly expanded from the primitive condition seen in *Galesphyrus* where the ratio of proximal width to shaft length is 0,33, compared with 0,53 in *Hovasaurus*, 0,53 in *Tangasaurus* and 0,63 in *Kenyasaurus*. The proximal end of metatarsal five is expanded in *Youngina* (Broom 1921). The expansion of the proximal head may represent the initial change leading to the development of the hooked fifth metatarsal of prolacertids and later diapsids. The articulation between this element and the fourth distal tarsal is flat in tangasaurids and there would have been little movement possible here (Brinkman 1979).

Metatarsal IV grows with the same rate of positive allometry as Metacarpal IV (table 4), and at maturity is 10,9 OLU (2,8*x*). The fourth metatarsal of *Thadeosaurus* grows isometrically but is slightly longer (11,6 OLU; 3,0*x*) than that of *Hovasaurus*. The length of metatarsal IV in *Tangasaurus* falls within the range of variation of *Hovasaurus*.

The phalangeal formula is 2.3.4.5.4 for the pes. The proportional lengths of the digits are relatively constant throughout life (table 3), and they must have grown at approximately the same rate. The coefficient of allometry for digit IV, excluding the metatarsal, is high (1,4). The combined length of the fourth metatarsal and phalanges is equal to that of the tibia in large specimens, and amounts to 21,2 OLU (5,5*x*). The fourth digit of *Thadeosaurus* apparently grew isometrically to approximately 22 OLU in length. *Tangasaurus* (Currie, in press) has a fourth digit that is significantly shorter than that of *Hovasaurus*, and amounts to only 4,9*x*.

The first digit, including the metatarsal, is 40 per cent of the length of the fourth, the second is 64 per cent, the third is 84 per cent and the fifth is 83 per cent. On the average, digit V is 99 per cent of the length of digit III. The proportions are very close to this in *Tangasaurus*, *Thadeosaurus* and *Kenyasaurus*.

In digit I of *Hovasaurus*, the first phalanx is as long as the first metatarsal in only one of 15 specimens. In digit II the penultimate phalanx is as long as or longer than the antepenultimate in 58 per cent of the specimens, in digit III 91 per cent, in digit IV 40 per cent and in digit V none out of 11 specimens. This contrasts strongly with the manus where the penultimate phalanx exceeds the antepenultimate bone 90 per cent of the time. This strongly suggests that there was a functional difference between the digits of the manus and pes. Possibly the manus was better adapted for grasping. Whatever the reason for the difference, it also seems to be present in *Thadeosaurus*. The penultimate does not consistently exceed the antepenultimate in either the manus or pes of *Tangasaurus* (table 3). Evidently the relative length of the penultimate phalanx cannot be correlated with aquatic lifestyles.

In *Hovasaurus* and *Tagasaurus* the largest phalanx in the foot is the first one in digit V. The first pha-

lanx in digit IV is the largest in the pes of *Kenyasaurus*. In *Thadeosaurus* (all ages), phalanges IV-1 and V-1 are subequal.

The unguals of the pes of *Hovasaurus* are similar to those of the manus, but tend to be longer in equivalent digits.

### Integument of *Hovasaurus*

Piveteau (1926: Pl. X, fig. 3) described a small specimen of skin impression that he found with the remains of *Hovasaurus* at Mt. Eliva. The scale-like impressions are small, ranging from 1 to 2 mm in diameter. The smaller ones are round, and the larger tend to be penta- or octagonal because they are more closely packed. There is no consistent arrangement, and they could be osteoderms. The presence of granules of this size and shape in the caudal region of some specimens of *Hovasaurus* indicates that this specimen (MNHN 1925-5-33) could be from the tail of this genus.

Epidermal scales can be seen in MNHN 1908-21-24 on the ventral surface between the sternum and gastralia. The scales are oval, and all are about the same size. The anteroposterior length ranges between 2,5 and 3,0 mm, and the width between 2,0 and 2,5 mm. Each scale on the right side of the specimen overlaps the anteromedial and anterolateral portions of the two sclaes posterior to it. *Saurosternon* (Carroll 1975a: fig. 6) has scales in the sternal region that are approximately the same size and configuration as those of *Hovasaurus*.

Epidermal scales are present in the anterior caudal region of *Kenyasaurus* (Harris and Carroll 1977). Dorsally they are rectangular and diverge from the midline posteriorly. On the ventral surface the scales are square and aligned parallel to the centra.

Epidermal sclaes near the tail region of *Tangasaurus* (SAM 6231) are elongate rhomboids in outline, 8 x 3 mm (Haughton 1924). Each scale has a low, longitudinal median ridge. The free posterior border of each scale overlaps the anterior edges of the two directly behind.

There is no evidence in tangasaurids of dermal ossicles along the spine as in *Youngina* (Gow 1975) and *Heleosaurus* (Carroll 1976a).

Gastralia (ventral dermal scales) underlie the abdomen between the sternum and pubes (figs. 3 and 5). They are present in the smallest specimens (MNHN 1925-5-27). Gastralia increased in size as the animal grew, and the number per individual remained constant. Approximately 40 segments can be counted along the midline of each of four specimens, which gives an average of four gastralia per vertebra. Each includes a median piece with an anteriorly oriented apex on the midline, and one or two pairs of long lateral segments. The first two have one lateral section per side (MNHN 1908-21-24), the last one has none (MNHN 1908-21-16), and four before the ultimate have one. There are two laterals on each side of every remaining median segment.

There is a rostral process on the midline of this median section (fig. 5) that is often fused to the preceding ventral scale. The bone extends posterolaterally as much as 3,5*x*, and tapers to a needle-like point. The first lateral segment is closely appressed to the anterior surface of the median element, and sometimes reaches the midline proximally. The proximodistal length of this segment can be as much as 5*x* (MNHN 1908-21-2/7), although the maximum thickness is only 0,2*x*. It does not extend far beyond the posterolateral end of the median element before it picks up the proximal end of the second lateral section on its anterior surface. The more lateral segment is the longest of the three, up to 5,5*x* (MNHN 1908-21-2/7), and is slightly thicker (0,3*x*) than the first lateral scale. The distal end does not taper as gradually as the proximal end.

Gastralia are poorly known in most eosuchians, but seem to have been universally present in the living animals. The ventral armature of *Claudiosaurus* is well preserved (Carroll 1981), and is numerically and morphologically indistinguishable from that of *Hovasaurus*. The shape and size of the gastralia in *Thadeosaurus*, *Kenyasaurus*, *Acerosodontosaurus* and *Heleosaurus* all indicate that a similar pattern of ventral armature existed in these genera.

Considering the tendencies in the ventral bones of *Hovasaurus* towards lowering the centre of gravity, it is surprising that the gastralia are not pachyostotic as in *Champsosaurus* (Russell 1956).

## DISCUSSION

*Hovasaurus* was the most highly adapted for swimming of any known tangasaurid eosuchian. The most conspicuous anatomical adaptations are in the tail, which is at least double the snout-vent length. The caudal neural spines are taller than the spines in the dorsal region. They contact along the midline above the neural canal to restrict the dorsoventral flexure of the tail. The haemal spine resembles the associated neural spine in shape and size, so the tail is dorsoventrally symmetrical. This suggests that the animal swam beneath the surface of the water. If it had swam primarily on the surface, the haemal spines probably would have been longer than the dorsals. Lateral undulations of the tail would have provided the necessary force to push the body through the water as it does in sea snakes (Hydrophiidae), semi-aquatic lizards (iguanids, agamids, varanids), crocodilians, caudate amphibians and many elongate fish.

Pachystosis of the ribs is another indication of the aquatic habits of *Hovasaurus*. Enlargement of rib shaft diameter has occurred in mesosaurs, some nothosaurs and sirenian mammals as well, and serves to increase the specific gravity of the animal.

The scapular blade is very short, as it is in *Mesosaurus*, ichthyosaurs, nothosaurs and plesiosaurs. It should be pointed out that some terrestrial animals, such as varanid lizards, also have low scapular blades. More importantly, the ventral portion of the pectoral girdle is massive to lower the centre of gravity for stability underwater, to increase the specific gravity, and for muscle attachment. As in

plesiosaurs, the scapulae of *Hovasaurus* meet at the midline to brace the girdle firmly during the power stroke.

The presence of a large mass of pebbles in the abdominal cavity is comparable with a similar mass in plesiosaurs. This would have increased the specific gravity of the animal by five to ten per cent, shifted the centre of gravity posteroventrally and stabilized the animal in the water.

Delayed ossification is a characteristic of many aquatic tetrapods. For example, the carpal and tarsal elements of nothosaurs, placodonts, marine crocodiles and mosasaurs never fully ossified. This is not the case in *Hovasaurus*. In *Thadeosaurus* and *Hovasaurus* juveniles about 16 per cent of the length of the humerus is composed of cartilage. The obturator foramen is surrounded by bone by stage B in both genera, the carpus is ossified by stage D, and the scapula and coracoid coalesce by stage E. The tarsals are all ossified in *Thadeosaurus* by stage D, but the tarsus of this life stage is not known in *Hovasaurus*. The ectepicondylar foramen is encircled by bone by stage F in *Thadeosaurus*, and not until stage G in its more aquatic relative, *Hovasaurus*. The sternal plates, which fuse into a single element by stage F in *Hovasaurus*, do not ossify until stage G in *Thadeosaurus*. Therefore, ossification is not delayed in *Hovasaurus*. At maturity this animal could have moved efficiently on land to lay eggs or extend its range.

Limb proportions are an indication of aquatic habits in *Hovasaurus*. This genus is similar to nothosaurs and plesiosauroids in that the humerus to femur ratio is less than 1,0 in juveniles, but greater than 1,0 in adults. The forearm is about half the length of the humerus in *Hovasaurus*, *Mesosaurus* and nothosaurs at maturity. The metacarpus is symmetrical, and digit IV is shorter relative to the first three digits of the manus than in *Thadeosaurus*.

Despite the presence of a powerful tail for swimming, *Hovasaurus* has powerful front limbs that, by analogy with other aquatic genera, were used when swimming. The manus, like that of *Claudiosaurus*, has become broader and more symmetrical distally than in *Thadeosaurus*. The similarity in shape of the manus to that of other aquatic genera (extinct and living) suggests that there could have been webbing between the digits. The front limb would have acted as an oar or paddle when swimming, rather than as an underwater "wing" (Robinson 1975). Like a paddle, the distal end of the front limb is broad and flattened to maximize drag. The front limb could have been used in the same manner that a duck uses its webbed feet, and it probably also behaved as a rudder for controlling direction. The front limb was not so highly adapted that it couldn't be used for walking on land or the bottom of a body of water.

The pelvic girdle and limb do not show any aquatic adaptations. The tibia is about 85 per cent of the length of the femur, a normal ratio for a terrestrial animal, compared with 50 per cent in *Askeptosaurus* (an aquatic eosuchian) and many nothosaurs. The relative lengths of the digits of the pes are not significantly different from those of *Thadeosaurus*. It would appear that the hind limb was used for walking on land or on the bottom of a body of water. On the basis of the well-developed limb with a large internal trochanter, the puboischitibialis insertion on the tibia and the perforating foramen in the tarsus, Brinkman (1979) concluded that tangasaurids were capable of terrestrial locomotion.

The coefficients of allometry were calculated for 41 common dimensions in *Thadeosaurus* and *Hovasaurus* (Currie 1981b). Differences in the coefficients between the genera are only considered significant when the coefficients of *Thadeosaurus* fall outside the 95 per cent confidence intervals of the corresponding coefficients of *Hovasaurus*. There is no significant difference in allometric growth rates for 15 dimensions, but the coefficient is significantly higher in *Hovasaurus* for 22, and lower than *Thadeosaurus* for four. These figures were calculated on the basis of the preserved, ossified portions of the bones, and do not make allowance for cartilaginous extensions. As previously indicated, gaps between the bones of the articulated skeletons of juveniles are the same relative size in *Thadeosaurus* and *Hovasaurus*. This indicates that the same percentage of the total length of the limb bones were formed of cartilage in juvenile specimens of the two genera. The percentage composition of cartilage, therefore, does not account for the higher coefficients of allometry in *Hovasaurus*. This can be confirmed by an alternate method. Even if the length of the humerus of one of the smallest specimens of *Hovasaurus* (MNHN 1908-21-8) is increased by 20 per cent (the maximum possible percentage of cartilage that would have filled the gaps between the humerus and adjacent bones in articulated specimens), the total length would have been only 12,3 mm. The expected length of the ossified portion for this element in a specimen of *Thadeosaurus* the same size is 17,4 mm, and cartilage would have increased this length. It appears that the limb elements of immature specimens of the more terrestrial *Thadeosaurus* were significantly longer than in *Hovasaurus*, even if cartilage is included, and that the differences in allometric coefficients are real.

If the limb elements of the two genera are excluded, there are 13 dimensions in the vertebrae and limb girdles in which the growth coefficients are known for both genera. Of these, there is no significant difference in seven, and the coefficients are higher in three dimensions of *Thadeosaurus* and lower in three. This is another indication that the differences in allometric growth rates are biologically significant. If the coefficient was consistently higher in *Hovasaurus* for all dimensions, it would show that differences in the coefficients of the two genera are related to negative allometric growth of the dorsal centra ($x$) in *Hovasaurus*.

It is significant that the degree of allometry is generally higher in the larger animal, *Hovasaurus*. Usually, the opposite effect is discovered in closely

related animals because allometric coefficients that differ markedly from 1,00 are strongly size-limiting (Dodson 1975b).

In juveniles, the limb bones of *Thadeosaurus* are longer than those of *Hovasaurus* (fig. 2a), and the genera are distinguishable by measurement. This is a clear indication of functional differences in the use of the limbs by juveniles of the two genera. It is possible that newly hatched *Hovasaurus* entered the water as sea turtles do, and seldom ventured onto land until mature. In adults, the higher allometric growth in *Hovasaurus* has resulted in relatively longer limb bones, and this genus could have been as mobile on land as *Thadeosaurus*. Dodson (1975b) suggests that increased relative length of limbs in *Sceloporus* adults is related to the increase in home range. Similarly, *Hovasaurus* adults could have spent more time on land for range dispersal, mating or laying eggs.

Differences in the relative lengths of the limb bones of *Thadeosaurus* and *Hovasaurus* are evident from the unit measurements based on $x$ and the OLU. The two systems correlate well, although one is a linear comparison and the other is geometric. Even though most of the bones in *Hovasaurus* grow with positive allometry, comparison of unit measurements based on the orthometric linear unit (OLU) has biological significance provided the interspecific size changes are isometric (Currie 1978). Unit measurements of 19 dimensions measured in both genera can be compared. Of these, there are no significant differences in 13 cases. Five unit measurements (length of neural spine, length of humerus, length and width of pubis, width of ischium) are greater in *Hovasaurus*, whereas the length of the fourth metacarpal is significantly less than in *Thadeosaurus*.

Unit measurements based on OLU and $x$ are not biologically significant for widths of limb bones, particularly if the comparisons are between animals of different mature sizes (Currie 1978). Bone widths are more closely related to the weight of the animal than to the function of the limb. Because *Thadeosaurus* and *Hovasaurus* have overlapping size ranges, it can be shown on scatter diagrams (fig. 2b) that differences in width measurements are insignificant.

## Relationship of the Tangasauridae to Other Primitive Diapsids

The close relationship between *Youngina* and the Tangasauridae (*Tangasaurus, Hovasaurus, Thadeosaurus, Kenyasaurus*) has been discussed elsewhere (Currie 1981a, Currie, in press). Tangasaurids are united with the Younginidae into the superfamily Younginoidea by shared, derived characters. Two subfamilies are recognized in the Tangasauridae. The Kenyasaurinae, which includes *Thadeosaurus* and *Kenyasaurus*, are essentially terrestrial animals. *Tangasaurus* and *Hovasaurus* are united as the Tangasaurinae on the basis of the specialization of the tail as a swimming appendage.

*Acerosodontosaurus* was originally considered to be a younginid (Currie 1980). A derived character in the carpus, whereby the lateral centrale has lost contact with the third distal carpal, is found in this genus, the tangasaurids, and possibly *Youngina*, but is presently not known in any other eosuchian. However, there are no accessory articulations on the neural spines such as are found in younginids and tangasaurids. It is, therefore, concluded that *Acerosodontosaurus* shared a common ancestry with *Youngina* and *Hovasaurus*, but should not be classified as either Younginidae or Tangasauridae.

In many features, coelurosauravids are the most primitive of eosuchians. There are 29 presacral vertebrae as in protorothyridids, and the atlas rib is apparently retained. Limb elements are the same relative lengths as those of protorothyridids. In other characteristics, these animals are highly specialized. The maxilla enters the orbital margin. The quadratojugal of *Weigeltisaurus* is relatively large with distinctive toothlike projections and there is some evidence to suggest that those of *Coelurosauravus* and *Daedalosaurus* (Carroll 1978) may have been the same. The ribs of *Daedalosaurus* and *Weigeltisaurus* are elongate (up to 30 times the length of a dorsal centrum) presumably to support a gliding membrane, whereas those of *Coelurosauravus* are only $3x$ in length. The ribs of tangasaurids and most other Permian eosuchians are about $7x$ long. Coelurosauravids are clearly not closely related to the Tangasauridae.

Only two partial skeletons have been identified as *Galesphyrus* (Carroll 1976b). The presence of holocephalous ribs, straight caudal ribs, a single centrale in the tarsus, and an advanced type of femur clearly indicate that this animal is an eosuchian. Carroll (1976b) assigned the genus to the Younginidae, but *Galesphyrus* is more primitive than any younginiform or prolacertiform eosuchian. The carpal and tarsal elements are as elongate as those of protorothyridids and araeoscelidians. A mesotarsal joint has not developed, and the proximal heads of the metatarsals do not overlap (Brinkman 1979). The head of metatarsal V is narrow; its width is about a third of the total length of the bone. The humerus is relatively shorter than that of *Paleothyris*, the radius and femur are the same relative lengths as those of *Paleothyris*, and the tibia is intermediate in length to those of *Paleothyris* and more advanced eosuchians. There are no derived characters known that can prove that *Galesphyrus* is not the ancestral morphotype of both younginiform and prolacertiform eosuchians.

The bladelike teeth with cutting edges along the anterior and posterior surfaces, the loss of the coronoid, the presence of a sixth cervical vertebra, and elongation of the cervicals to the same length as the dorsals are derived characters of *Heleosaurus* that are not found in younginids or tangasaurids. Carroll (1976a) has suggested that this genus is close to the ancestry of archosaurs. It does not appear to be closely related to younginids and tangasaurids.

Members of the suborder Prolacertiformes have become highly specialized in many respects. The

lower temporal bar is lost, the squamosal is tetraradiate (sickle-shaped in *Tanystropheus*), the quadrate is streptostylic with an offset pterygoid flange, there is no stapedial foramen, the teeth are implanted in sockets, the vertebrae are amphicoelous, the cervicals are longer than the dorsal vertebrae and number more than seven, and the entepicondylar foramen is lost. In at least one respect, the retention of contact between the postorbital and parietal, the prolacertiform eosuchians are less specialized than the Younginiformes. Clearly these two suborders have diverged considerably.

*Askeptosaurus* and *Thalattosaurus* are highly specialized marine reptiles that have elongate premaxillae, external nares placed far back from the anterior margin of the skull, nasals separated by premaxillae and frontals and upper temporal fenestrae that are reduced to a slit. *Askeptosaurus* has 14 cervical vertebrae and 25 dorsals. The humerus, radius and tibia are relatively shorter than in any other eosuchians. There is a large thyroid fenestra. The presence of thecodont teeth, amphicoelous vertebrae and an elongate neck, and the loss of the fifth distal carpal and the entepicondylar foramen suggest that thalattosaurs are more closely related to prolacertiform eosuchians than to tangasaurids.

Champsosaurs have many derived characters not found in other eosuchians. The posterolateral margin of the skull is greatly expanded, and the confluent external nares are located at the end of the elongate snout. The prefrontals contact each other on the midline, and the posttemporal fenestra is lost. As in tangasaurids, the ribs are pachyostotic, and the epipodials are relatively shorter than the propodials. These are characters developed in response to an aquatic life style, however, and do not indicate relationship. The postorbital-parietal contact, loss of the entepicondylar foramen, the presence of a hooked fifth metatarsal, and other features suggest that champsosaurs are more closely related to the Prolacertiformes than to tangasaurids.

Eosuchians have been considered as the ancestral stock of both archosaurs and lizards ever since the discovery of *Youngina* (Broom 1914). The origin of these and other diapsid lineages have proved to be complex problems that are not within the scope of this investigation. However, it is worth while to determine whether tangasaurids could have given rise to any other groups of reptiles.

## The Origin of Lizards

Carroll (1975a, b, 1977) has proposed that the Permo-Triassic paliguanids of South Africa are ancestral to the Lacertilia. He has provisionally placed the Paliguanidae, long considered as eosuchians, into the infraorder Eolacertilia. There are many derived characters, such as a streptostylic quadrate, shared by paliguanids and more recent lacertilians, that are not found in eosuchians. These have been discussed in detail by Carroll (1975a, 1977) and will not be reiterated here because they shed no light on the origin of the Paliguanidae.

*Palaeagama, Paliguana* and *Saurosternon* are the three known genera of paliguanids. A specimen from South Africa that was originally described as *Saurosternon* (Owen 1876) was renamed *Heleosuchus* by Broom (1913). The original specimen has been misplaced, but on the basis of a cast Carroll (1981) has suggested that this animal is a younginid. In contrast with paliguanids, the lower temporal bar is apparently complete (Carroll, pers. comm., 1981). However, the skull of this animal is broad, about 85 per cent of its length and about seven times the length of a dorsal centrum. This is very close to the estimated skull proportions (width/length = 0,85) and width (6*x*) of *Palaeagama* (Carroll 1975a). In contrast, the skulls of *Youngina, Heleosaurus, Acerosodontosaurus* and other eosuchians are more elongate and narrower (3*x*–5*x*). The neural spines are low and triangular, whereas those of younginids and tangasaurids are relatively taller and rectangular in outline. The absolute sizes and proportions of the vertebrae and limbs are very close to those of *Palaeagama*. Because of the poor preservation of the only known specimen of *Heleosuchus,* it is not possible to determine with certainty whether this genus is a paliguanid or an eosuchian. If the latter identification is correct, this animal must have been close to the ancestral stock of paliguanids.

The parietal does not contact the postorbital in paliguanids, which suggests (but does not prove) relationship with younginiform eosuchians. In contrast with prolacertiform eosuchians, the entepicondylar foramen, the fifth distal carpal and the fifth distal tarsal have been retained, and the vertebrae are notochordal. The neck is short. There are only five cervical vertebrae and all are shorter than the dorsal centra as in younginids, tangasaurids and the ancestral protorothyridids.

Paliguanids share a number of apparent synapomorphies with younginids and tangasaurids. As in *Hovasaurus,* the jaw articulation is anterior to the posterior margin of the skull. The interorbital to intertemporal width ratio (0,6) is close to that of tangasaurids, whereas most eosuchians have a higher ratio. Accessory articulating processes are found on the midline of the neural arch in *Saurosternon* (Carroll 1975a), but because the neural spine is so low in paliguanids, these processes do not resemble those of *Youngina* and the tangasaurids. The scapular blade of *Saurosternon* is very low like that of tangasaurids, but in contrast to *Youngina*. The sternum is ossified in paliguanids, and fuses into a single unit at maturity as in tangasaurids. The humerus is relatively longer than that of *Youngina* and more primitive eosuchians, but shorter than any tangasaurid humerus. The paliguanid specimens are relatively mature, but the humerus of each is at least 15 per cent shorter than the femur. The radius and tibia are more elongate than those of younginids and tangasaurids, and the femur is relatively longer than in any eosuchian. Limb propor-

tions and size suggest that paliguanids were more efficient as terrestrial animals than younginid and tangasaurid eosuchians, but do not disprove relationship.

The possible retention of two primitive characters could falsify the hypothesis that paliguanids are more closely related to the Younginoidea than to any other eosuchians. In *Palaeagama*, the lacrimal is shown as extending to the external naris. However, this region of the specimen is poorly preserved (Carroll 1975a). Because the lacrimal extends to the external naris in only the most primitive eosuchians, it is possible that this detail of the reconstruction is incorrect. As reconstructed, the lateral centrale of *Saurosternon* contacts the third distal carpal. In *Acerosodontosaurus* and the tangasaurids, these bones are separated by the medial centrale and fourth distal carpal. However, the carpus of *Saurosternon* does not show the relationship of the various elements, so it is possible that the same arrangement existed in paliguanids and tangasaurids. This hypothesis is supported by the fact that the medial centrale of *Saurosternon* is almost double the size of the lateral centrale.

It appears highly probable that the earliest known lizards, the Paliguanidae, were closely related to younginids and tangasaurids.

### The Origin of Archosaurs

In his redescription of *Heleosaurus*, Carroll (1976a) suggested that this genus may be closer to the ancestry of archosaurs than any other eosuchian known. The bladelike, finely serrated teeth are set in sockets and are not distinguishable from those of the archosaur *Euparkeria*. Other less significant similarities exist. Existing evidence suggests that *Heleosaurus* is a younginiform eosuchian. However, characteristics of the skull roof and tarsus that are used to distinguish the two major eosuchian lineages are not preserved in the only known specimen, so it is possible that *Heleosaurus* is a prolacertiform eosuchian. In either case, this animal is not closely related to tangasaurids.

There are alternative theories on the origin of archosaurs. Gow (1975), like many earlier authors, had noted the similarities between prolacertiform eosuchians and primitive archosaurs. Brinkman (1979) concluded that the tarsi in prolacertiform eosuchians, primitive rhynchosaurs and primitive archosaurs are structurally the same.

No characters are known to suggest that tangasaurids are close to the ancestry of archosaurs or rhynchosaurs.

### The Origin of Sauropterygians

Examination of the skull of the nothosaur *Anarosaurus pumilio* led Jaekel (1910) to the conclusion that sauropterygians were descendants of diapsid reptiles. Kuhn-Schnyder (1962, 1967) has also stated that diasids were the precursors of nothosaurs and plesiosaurs. For reasons discussed by Carroll (1981), most palaeontologists have looked elsewhere for the ancestry of sauropterygians.

Piveteau (1955) announced the discovery of two specimens from the Upper Permian of Madagascar representing a very primitive level of sauropterygian evolution. *Claudiosaurus* (Carroll 1981) is clearly derived from eosuchian reptiles. The sauropterygian characteristics of this genus have been described in detail (Carroll 1981). Consequently, only the eosuchian affinities will be considered here.

*Claudiosaurus*, primitive nothosaurs and plesiosaurs resemble younginiform eosuchians in the loss of contact between the parietal and postorbital. In *Claudiosaurus*, the configuration of the circumorbital bones, particularly the frontal, is similar to that in younginid and tangasaurid eosuchians. There are no accessory articulations at the base of the neural spine, and the sternum is not ossified. The humerus is shorter and more gracile than the tangasaurid humerus, but the other long limb bones are comparable in length. The primitive articulation between the lateral centrale and third distal carpal is persistent. The mesotarsal joint (Brinkman 1979) is similar to that of *Hovasaurus*, although there are some minor differences that suggest divergence since the development of the joint. The fifth metatarsal is not hooked, but has a wide proximal head as in younginids and tangasaurids. *Claudiosaurus* may be more closely related to younginiform eosuchians than to the Prolacertiformes, but is not derived from tangasaurid stock.

## CONCLUSIONS

Four genera of tangasaurid eosuchians are known from the Permo-Triassic strata of Africa and Madagascar. Specimens from Madagascar that were originally identified as *Tangasaurus* and *Datheosaurus* are now assigned to *Thadeosaurus*. *Thadeosaurus* and *Kenyasaurus* are not specialized for swimming to the degree that the other two known tangasaurids, *Tangasaurus* and *Hovasaurus*, are.

Tangasaurid specimens from Madagascar are found in the Lower Sakamena formation. Pollen, spores, macroplants, corals, bivalves, ammonites and fish fossils have been used to show that this formation is equivalent to the Dzulfian Standard Stage of the Upper Permian.

*Tangasaurus*, *Kenyasaurus* and *Thadeosaurus* are each known from a single site. *Hovasaurus* is known from at least three localities, and is the most common vertebrate in the Lower Sakamena formation.

Faunal association data suggests that there were at least four distinct palaeoenvironments. *Thadeosaurus* and *Hovasaurus* were apparently contemporaries in the same general region, but they lived in different environments.

Comparative measurements can be used to identify individual partial skeletons of *Thadeosaurus* and *Hovasaurus* that lack diagnostic characters in the preserved sections.

Two systems of relative measurement, based on the Orthometric Linear Unit (OLU) and the average length of a dorsal centrum ($x$), were found to

be useful for making comparisons between mature specimens of different genera. The two systems correlate well, although neither has biological significance for dimensions controlled by the animals' weight, such as the shaft width of limb bones. Regression analysis had to be used for comparison of immature specimens.

*Hovasaurus* is represented by hundreds of specimens, both juveniles and adults, and it therefore should be the best known Paleozoic reptile. The original description (Piveteau 1926), although well illustrated with photographic plates, was based on only seven immature specimens. This paper, the first detailed description of *Hovasaurus*, reveals that this genus is more interesting than previously suspected. It is the most highly adapted of the known tangasaurids for swimming. The skull is only partially known, but is more specialized than *Youngina* in that the jaw suspension slopes anteroventrally. The palatal teeth are long, slender and recurved distally, showing that *Hovasaurus* was carnivorous. The neck is short, and the tail is at least double the snout-vent length of the body. Accessory intervertebral articulations are present throughout the vertebral column as in *Youngina* and other tangasaurids, but are more complicated. The neural spines in the presacrum are taller than in other known eosuchians, and bear mammilary processes in the anterior dorsals. The caudal neural spines are taller than the presacral ones, and are platelike and laterally compressed. The haemal spines mimic the associated neural spines in size and shape. There is no doubt that the tail was a powerful swimming appendage. The ribs, like those of some aquatic reptiles and mammals, are pachyostotic at maturity. The dorsal portions of the pectoral girdle are reduced, and the ventral bones are relatively large and platelike. This would serve to lower the centre of gravity for increased stability in the water, and to increase the areas of attachment for muscles associated with the power stroke of the front limb. The humerus is longer than in other eosuchians, and exceeds the length of the femur. It superficially appears primitive, but analysis of the morphology and muscle insertions indicates that the front limb was mechanically more efficient than that of captorhinomorphs. The radius is almost half the length of the humerus and the manus is more symmetrical than in terrestrial eosuchians. The front limb is paddle-like in shape, and would have been used for swimming and for direction control when swimming. The hind limb is mechanically as efficient for terrestrial locomotion as in most eosuchians and it has no characters to indicate that it was used for swimming. The abdominal cavity of most specimens contains enough ingested pebbles to have raised the specific gravity of individuals by five to ten per cent. The pebble mass is positioned to shift the centre of gravity posteroventrally, possibly for greater stability when swimming.

The presence of long growth series for these genera presents a unique opportunity to study differences in growth strategies in two closely related Permian genera, one that was essentially terrestrial and the other aquatic.

The "growth rates" calculated might better be referred to as ossification rates. The amount of cartilage in the majority of endochondral bones cannot be measured, but a rough estimate of cartilaginous composition was calculated for the humerus of each genus. Humeri of immature specimens of *Thadeosaurus* and *Hovasaurus* had cartilaginous ends making up to 16 per cent of the total length of the bones. Because the amount of cartilage in the limb bones of both genera seems to be equivalent, differences in the growth rates of the ossified portions of the same bones of *Thadeosaurus* and *Hovasaurus* are regarded as biologically significant.

Unlike most aquatic genera, the replacement of cartilage with bone did not occur at a slower rate in *Hovasaurus* than in its terrestrial relative. Nevertheless, the limbs of *Hovasaurus* are relatively shorter than those of *Thadeosaurus* at birth. Allometric growth rates are similar in vertebrae and limb girdles, but are significantly higher in the limb bones of *Hovasaurus*. Usually, if there are differences in allometric growth rates in two closely related animals, the smaller form will have the higher rates because allometric coefficients that differ markedly from 1,0 are strongly size limiting. In mature specimens, the limb elements of *Hovasaurus* are relatively longer than those of *Thadeosaurus* and could have functioned as efficiently on land. It is possible that a newborn *Hovasaurus* entered the water as sea turtles do, and seldom ventured onto land until maturity. Adults may have spent more time on land for mating, laying eggs and/or range dispersal.

The improved knowledge of tangasaurids and other eosuchians makes it worth while to consider the interrelationships of the Eosuchia and related reptiles. Tangasaurids are united with the Younginidae into the superfamily Younginoidea by shared, derived characters. *Acerosodontosaurus* is neither a younginid nor a tangasaurid, but does share a common ancestry with these families. *Galesphyrus* is a primitive eosuchian close to the ancestry of all eosuchians. Despite similar adaptations for living in an aquatic environment, *Hovasaurus* is not closely related to other aquatic eosuchians (prolacertiforms, thalattosaurs, champsosaurs, *Claudiosaurus)*. It appears highly probable that the earliest known lizards, the Paliguanidae, were closely related to younginids and tangasaurids. Other eosuchians are closer to the ancestry of archosaurs and sauropterygians than tangasaurids are.

**ACKNOWLEDGEMENTS**

I am greatly indebted to Dr. Robert L. Carroll (McGill University) at whose suggestion this work was carried out. He made the majority of the casts used in this study, arranged for the loan of specimens from the Muséum National d'Histoire Naturelle, and reviewed the manuscript.

I would like to thank Dr. D. Brinkman (Museum of Comparative Zoology, Harvard), Pierre Cliquet (Directeur de l'Ex-

ploration, Coparex, Paris), Dr. P. Dodson (University of Pennsylvania), Dr. M.J. Heaton (University of Toronto) and Dr. R. Reisz (University of Toronto) who gave freely of their time for discussion of their research and provided data that had not been published before completion of this investigation.

## APPENDIX I
## Flora and Fauna of the Lower Sakamena Formation

PROTISTA
- THALLOPHYTA
  - DINOPHYCEAE dinoflagellates
    - PERIDINIALES
      - acritarchs
  - FORAMINIFERA

PLANTAE
- TRACHEOPHYTA
  - SPHENOPSIDA
    - EQUISETALES
      - SCHIZONEURACEAE
        - *Schizoneura gondwanensis*
  - CYCADOPSIDA
    - PTERIDOSPERMALES
      - *Thinnfeldia callipteroides*
      - *Taeniopteris* sp.
      - CAYTONIACEAE
        - *?Vitreisporites pallidus*
        - *?Alisporites papilio*
        - *?Pityosporites insularis*
        - *?Falcisporites enodis*
      - PELTASPERMACEAE
        - *Lepidopteris madagascarensis*
    - GLOSSOPTERIDALES
      - *Glossopteris* cf. *indica*
  - CONIFEROPSIDA
    - *Rissikia media*
    - *Voltziopsis africana*
    - *Voltziopsis wolganensis*
    - GINKGOALES
      - *Baiera* sp.
    - VOLTZIALES
      - *?Lueckisporites virrkiae*
    - CORDAITALES
      - *Dadoxylon*
    - CONIFERALES
      - *?Araucariacites australis*
      - PODOCARPACEAE
        - *?Podocarpites* cf. *elipticus*
  - GNETOPSIDA
    - GNETALES
      - *?Vittatina striata*

TRACHEOPHYTA *incertae sedis*
- *Taeniaesporites noviaulensis*
- *Protohaploxypinus pellucidus*
- *Stroter sporites panti*
- *Platysaccus* cf. *leschiki*
- *Platysaccus fuscus*
- *Platysaccus praevius*
- *Sulcatisporites prolatus*
- *Guttulapollenites hannonicus*
- *Guttulapollenites gondwanensis*
- *Inaperturopollenites* cf. *orbicularis*

ANAMALIA
- COELENTERATA
  - STROMATOPOROIDEA
    - STROMATOPORIDEA
      - ACTINOSTROMIDAE
  - ANTHOZOA
    - TABULATA
      - AULOPORIDAE
        - *Syringopora* sp.
        - *Cladochonus* sp.

MOLLUSCA
- BIVALVIA
  - PTERIOIDA
    - BAKEVELUIDAE
      - *Gervillia elianae*
    - POSIDONIIDAE
      - *Posidonia* cf. *becheri*
  - MODIOMORPHOIDA
    - MODIOMORPHIDAE
      - *Modiolopsis stockleyi*
  - PHOLADOMYOIDA
    - EDMONDIIDAE
      - *Edmondia* cf *amabilis*
- CEPHALOPODA
  - GONIATITIDA
    - POPANOCERATIDAE
      - *Popanoceras* sp.
    - CYCLOLOBIDAE
      - *Cyclolobus walkeri*
  - PROLECANITIDA
    - MEDLICOTTIIDAE
      - *Propinacoceras* sp.
    - EPISAGECERATIDAE
      - *Episagecerus* sp.
  - CERTATITIDA
    - XENODISCIDAE
      - *Xenaspis* sp.

ARTHROPODA
- CRUSTACEA
  - CONCHOSTRACA
    - ?ASMUSSIIDAE
      - *Estheria minuta*
    - ESTHERIELLIDAE
      - *Esteriella* sp.

CHORDATA
- OSTEICHTHYES
  - CHONDROSTEI
  - PALAEONISCIFORMES
    - *Atherstonia colcanapi*
- AMPHIBIA
  - TEMNOSPONDYLI
    - RHINESUCHIDAE
      - cf. *Rhinesuchus* sp.
- REPTILIA
  - COTYLOSAURIA
    - PROCOLOPHONIA
      - PROCOLOPHONIDAE
        - *Barasaurus besairei*
  - EOSUCHIA
    - YOUNGINIFORMES
      - YOUNGINOIDEA
        - *Acerosodontosaurus piveteaui*
      - TANGASAURIDAE
        - KENYASAURINAE
          - *Thadeosaurus colcanapi*
        - TANGASAURINAE
          - *Hovasaurus boulei*
  - EOSUCHIA *incertae sedis*
    - COELUROSAURAVIDAE
      - *Coelurosauravus elivensis*
      - *Daedalosaurus madagascariensis*
  - SAUROPTERYGIA
    - CLAUDIOSAURIDAE
      - *Claudiosaurus germaini*
  - THERAPSIDA
    - DICYNODONTIA *incertae sedis*
    - THERIODONTIA *incertae sedis*

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