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*Full paper presented at PSSA First Conference, July 1979

PALAEONTOLOGICAL SOCIETY OF SOUTHERN AFRICA
FIRST CONFERENCE: NATIONAL MUSEUM, BLOEMFONTEIN
2nd–5th JULY 1979

Programme

MONDAY 2nd JULY
Opening by Prof. R. van Pletzen, Chairman, Council of the National Museum.

TUESDAY 3rd JULY
Welcome by the President, Dr. C.K. Brain.
J.J. OBERHOLZER: Bloemfontein — its museums and environment.
C.K. BRAIN: Presidential Address — Taphonomy as an aid to African palaeontology.
CHAIR: Prof. J.A. Hopson
M.A. RAATH: A system for the registration and documentation of research projects at the Bernard Price Institute (Palaeontology).
A.W. KEYSER: A biostratigraphic subdivision of the Beaufort Group in the western part of the Karoo basin.
ELISABETH S. VRBA: Some aspects of the relationship between time, morphological change and the environment.
J.A. HOPSON: Tooth function and replacement in heterodontosaurid ornithischians of the Stormberg series — implications for aestivation.
B.W. OELOFSEN: The fossil record of the Chondrichthyes in southern Africa.

WEDNESDAY 4th JULY
CHAIR: Prof. M.A. Raath
C.E. GOW: Pachygenelus, Diarthrognathus and the double jaw articulation.
B.W. OELOFSEN and J.C. LOOCK: A first record of a fossil cephalochordate.
J.A. VAN DEN HEEVER: Aspects of therocephalian classification and function.
J.W. KITCHING: A cluster of six dinosaurian eggs from the Upper Triassic Elliot Formation (Red Beds) of the Orange Free State.
C.S. MACRAE: Fossil spores and pollens from a borehole in the Soutpansberg coalfield.
A.S. BRINK: An illustrated bibliographical catalogue of the Synapsida: progress report.
J.A. HOPSON: Traversodontid cynodonts (Reptilia: Therapsida) of the Upper Triassic of southern Africa and Nova Scotia.
CHAIR: Dr. E.S. Vrba
R.D.F. OOSTHUIZEN: An attempt to determine the provenance of the southern Dwyka from palaeontological evidence.
F.E. GRINE: New evidence pertaining to the taxonomy and palaeobiology of *Diademodon* (Reptilia: Therapsida).
H.C. KLINGER: Transgressive events in the Cretaceous sediments of southern Africa.
ÉVA KOVÁCS-ENDRÖDY: The deceptive effect of broad sense specific circumscriptions.
J.A. VAN HEERDEN: The classification of the Saurischia (Reptilia).

THURSDAY 5th JULY
CHAIR: Dr. J.W. Kitching
F.E. GRINE: Quantitative and qualitative aspects of ontogeny and sexual dimorphism in the Permian anomodont *Aulacephalodon.*
MARCELLE LEVINSON and C.E. GOW: The use of wax in controlled acid preparation.
D.E. VAN DIJK: A study of the type locality of *Lidgettonia africana* Thomas 1958.
B.R. TURNER: The occurrence, origin and stratigraphic significance of bone-bearing mudstone pellet conglomerates from the Beaufort Group in the Jansenville District, Cape Province, South Africa.

Palaeont. afr., **24** (1981)

PRESIDENTIAL ADDRESS: TAPHONOMY AS AN AID TO AFRICAN PALAEONTOLOGY*

by

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SUMMARY

Palaeontology has its roots in both the earth and life sciences. Its usefulness to geology comes from the light which the understanding of fossils may throw on the stratigraphic relationships of sediments, or the presence of economic deposits such as coal or oil. In biology, the study of fossils has the same objectives as does the study of living animals or plants and such objectives are generally reached in a series of steps which may be set out as follows:

STEP 1. *Discovering what forms of life are, or were, to be found in a particular place at a particular time.*
Each form is allocated a name and is fitted into a system of classification. These contributions are made by the taxonomist or the systematist.

STEP 2. *Gaining a fuller understanding of each described taxon as a living entity.*
Here the input is from the anatomist, developmental biologist, geneticist, physiologist or ethologist and the information gained is likely to modify earlier decisions taken on the systematic position of the forms involved.

STEP 3. *Understanding the position of each form in the living community or ecosystem.*
This step is usually taken by a population biologist or ecologist.

Hopefully, any competent neo- or palaeobiologist (I use the latter term deliberately in this context in preference to "palaeontologist") should be able to contribute to more than one of the steps outlined above. Although the taxonomic and systematic steps have traditionally been taken in museums or related institutions, it is encouraging to see that some of the steps subsequent to these very basic classificatory ones are now also being taken by museum biologists. The trend is a desirable one as it will ensure the continued viability of museums as research institutions in the mainstream of biological progress.

As I have mentioned, I believe that the aims of palaeobiologists should be similar to those of their neobiological colleagues. The two kinds of biologists should centre their aims on the complete understanding of living things, both as individual expressions of life's processes, and as integrated parts of communities and ecosystems. It is an obvious fact that palaeobiologists have to interpret traces of past life while neobiologists can study living things in the very act of living. The burden on the former group of scientists is an obvious one and it is not difficult to understand why the progress in palaeo-studies should have been so much slower than it has been in neobiology. Despite its problems and frustrations, the reconstruction of past life is an enthralling occupation, the fascination of which must surely have been experienced by all palaeontologists. I have frequently pondered on the psychological basis of palaeontological fascination — perhaps it is similar to that of detective work in which the attention of the investigator is held as each new scrap of evidence is uncovered and slots into place. Such work has the elements of a strip-tease performance which would doubtless be boring if all were to be laid bare at once. Fortunately for palaeontology (and strip-tease performances for that matter), the picture emerges but slowly and the work invoived becomes pure fun, as all productive research ought to be. My friends in the field of animal behaviour tell me that the motivation for research has its origins in ritualised hunting — that excitement mounts as the time for the kill, or the major discovery, approaches. Maybe they are right, but their conclusion need not detract from the intense pleasure to be had from the pursuit of palaeontology.

The obvious point I wish to make is that fossils are the dead relics of once-living things — it is necessary to reconstruct them and, in our imagination, to bring them back to life, if we are to make any biological sense of them as individual once-living things, or as parts of once-living communities. It is in this reconstructive process that taphonomy has its usefulness, some aspects of which I hope to bring to your attention.

What is taphonomy?

It would be misleading to suggest that taphonomy is a new branch of science, as I am sure that geologists and palaeontologists have been thinking about those processes now regarded as taphonomic ones for a century or more. It would be true to say though that only recently has the study crystallised into what might be regarded as a discipline. The crystallisation process began when, in 1940, Prof. I.A. Efremov, a Russian geologist and palaeontologist, defined and

*Full paper presented at PSSA First Conference, July 1979

described the term "Taphonomy" to mean, literally, the laws of burial. As Everett Olson has pointed out, taphonomy "concerns all aspects of the passage of organisms from the biosphere to the lithosphere" and, since Efremov's original definition was formulated, Olson has been prominent in his application of taphonomic concepts to his study of Triassic vertebrates in the United States. By the early 1970s, enough people were actively working on taphonomic problems to allow the planning of an international symposium on the subject. The symposium was hosted by the Wenner-Gren Foundation for Anthropological Research and took place in Austria during July 1976. Its theme was "Taphonomy and vertebrate palaeoecology with special reference to the late Cenozoic in sub-Saharan Africa" and it was jointly organised by Andrew Hill, Kay Behrensmeyer, Alan Walker and myself. Its proceedings are currently being published as a book entitled "Fossils in the Making" by the University of Chicago Press.

The aspects of taphonomy are many and varied but, from the palaeobiological point of view, I believe the central issue to be this: *fossils are relics of once-living things which have suffered a series of losses since they were last alive. It is in understanding these losses, and compensating for them, that taphonomy may serve as an aid to palaeontology.*

In the comments which follow, I will be referring almost entirely to the taphonomy of terrestrial, Caenozoic vertebrates simply because this is the field in which I have had practical experience. Hopefully, some wider principles are involved here so that extrapolation to other palaeontological fields will not be difficult.

Taphonomic reconstruction of individual animals

Upon death, an animal (or plant for that matter) gives up the fight to maintain the integrity of its body and the inevitable process of subtraction begins. Here it must be remembered that no animal, not even an amoeba, can be regarded as a homogeneous blob of protoplasm which will disintegrate and disappear in a uniform manner. It is inevitable that some parts of any body will be more susceptible to the processes of decay or predator action than others and that those particular parts will be more effective in their resistance to disintegration. The effect of fossilisation is to stop the progress of disintegration at a particular stage in the process and to maintain the *status quo* of that stage for as long as the enclosing sediment remains intact.

In the case of a vertebrate, various components of its body will vary considerably in their ability to resist destruction. At one end of this scale of destructability will lie the blood and similar soft connective tissues, while, at the other, are the heavily mineralised parts of the skeleton. Regrettably, it is only some of the skeletal parts that can survive the destructive forces operating on them before fossilisation inhibits further degradation. It is possible, in the case of any vertebrate skeleton, to predict with confidence which parts of that skeleton will resist destruction most effectively and, I suspect, this kind of prediction will become a routine procedure in taphonomy.

I have had personal experience of how a taphonomic investigation can throw light on a problematic situation in palaeontology. When Prof. R.A. Dart published the results of his pioneering analysis of a large fossil sample from Makapansgat in 1955, he found that parts of the skeletons represented there occurred in very unnatural proportions. Primates and carnivores were largely represented by their skulls while, in the case of antelopes, certain skeletal parts were found to the partial or complete exclusion of others. Distal humeri for instance proved to be ten times as common as proximal ones, while parts such as caudal vertebrae could not be found at all. Never having encountered such a situation before, Prof. Dart assumed that such disproportions must surely have resulted from artificial selection by hominids. He postulated that those bones found in abundance were ones brought to the cave because of their suitability for tools. Those that were missing had simply not been brought back at all. On the basis of this and similar evidence, Prof. Dart built up his theory of the "osteodontokeratic culture" of *Australopithecus*.

In the hope of elucidating the situation, I made a study during the 1960s of goat bones discarded by Hottentots and subsequently gnawed by dogs in Namib desert villages. The skeletal parts remaining were those which had been able to survive the combined feeding action of the Hottentot/dog combination. To my surprise at the time, it was impossible to find the intact proximal humerus of a single goat, while distal humeri were extremely abundant. On the basis of the whole goat-bone assemblage, it was possible to work out percentage survival figures for each skeletal part and the correspondence between these figures and those for the Makapansgat fossil assemblage was certainly remarkable. Both samples were found to contain resistant skeletal elements to the complete or partial exclusion of delicate ones. The need to postulate artificial selection in the case of the Makapansgat bones fell away and other agents of accumulation could then be investigated.

The Hottentot study showed that any bone's ability to resist destruction could be correlated with some of its inherent characteristics. Foremost of these is compactness of the bone which may be expressed as specific gravity. Linked to this is the ratio of a bone's surface area to its volume. Consider the case of a thin flat bone such as a scapula. Although composed of compact bone, its surface area relative to its volume is so great that a scapula blade is a delicate structure, readily destroyed and thus frequently absent from fossil assemblages.

A bone's characteristics of compactness and shape are naturally of significance when that bone is transported in water before reaching its fossilisation site. The point about this is sim-

ply that a transported bone assemblage will consist of those skeletal elements which ended up where they did for good hydraulic reasons. Taphonomists such as Kay Behrensmeyer and Noel Boaz have studied bones as sedimentary particles in fluviatile environments and their results should be of interest to any palaeontologist having to deal with a fossil assemblage which had undergone water transport.

Taphonomic reconstruction of communities

In attempting to reconstruct individual animals on the basis of their relics, a taphonomist will try to assess and interpret the losses which the bodies of each of these animals have suffered. When attention is turned to the reconstruction of communities, however, the preoccupation is with a preserved *assemblage* derived from that original community. During its transformation into an assemblage, a community has obviously lost a good deal of its substance, but the chances are good that this loss has not been uniformly suffered by all parts of the community. Those parts to have suffered more loss will obviously be less well represented in the assemblage, with the resultant appearance of a *bias*. The nature of biases will vary from one fossil assemblage to another and generalisations are probably pointless. However, I would like to mention two common predator-induced biases as examples of the kind of thing to be taken into account.

In the first case it should be remembered that a predator typically selects prey within a certain preferred size-range. Potentially edible animals whose size falls above or below this range are generally ignored with the result that, if an assemblage is built up by this particular predator, that assemblage will be seriously biased in favour of the carnivore's feeding preference.

Secondly, the time at which hunting takes place will determine what prey spectrum is taken. Most owls, for instance, restrict their hunting to the evening or night, resulting in a bias towards the remains of crepuscular or nocturnal prey species in the owl-accumulated assemblage.

When using an assemblage as an indicator of a community's original composition, it is important to consider the death rates of the various animals in that community. Consider the case of an area of land capable of supporting ten elephants and ten shrews at any one time. Each elephant lives for 50 years but each shrew for only one year. If remains of all these animals found their way into an assemblage, shrews would be over-represented in that assemblage by a factor of 50, simply because they die 50 times as frequently as elephants do. In reconstructing the composition of the community, as it was at any given moment in time, correction would have to be made for the death-rate bias.

I have said enough to make it clear that the major task of the taphonomist in reconstructing a community from an assemblage lies in the recognition of biases which affected the assemblage's composition, and in correcting for such biases. If the taphonomist does his work well, the assemblage can be used as a high-fidelity reproduction of the community which it represents. This is one of the ways whereby taphonomy may serve as an aid to palaeontology.

Some suggestions for further reading

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BIOZONATION OF THE BEAUFORT GROUP WITH SPECIAL REFERENCE TO THE WESTERN KAROO BASIN*

by

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ABSTRACT

The lithostratigraphic subdivision of the Beaufort Group is discussed in its historical perspective. The Adelaide Subgroup (lower Beaufort) is now divided into two formations, as the lithostratigraphic subdivision used in the Eastern Cape is not applicable in the western part of the Karoo Basin. The Ecca–Beaufort transition is discussed.

The *Abrahamskraal Formation* lies conformably on the Waterford Formation of the Ecca Group and is distinguished from the overlying Teekloof Formation by the presence of numerous continuous "chert bands", the higher percentage of sandstone and the paucity of red mudrock. Continuous "chert bands" do not occur in the Teekloof Formation.

The existing biostratigraphic subdivision of the Beaufort Group is examined.

The lower three-quarters of the existing *Tapinocephalus* zone is referred to as the *Dinocephalian Assemblage Zone*. The lowest "chert band" associated with the arenaceous Poortjie horizon coincides with the last occurrence of dinocephalian remains. The strata between this point and the first occurrence of *Tropidostoma* are referred to a *Pristerognathus-Diictodon Assemblage Zone*. This assemblage zone is now considered to be part of the Teekloof Formation.

The *Tropidostoma-Endothiodon Assemblage Zone* is associated with the Hoedemaker Member of the Teekloof Formation which contains very few sandstones. This is overlain by the *Aulacephalodon-Cistecephalus Assemblage Zone* which is mainly associated with the Oudekloof Member of the Teekloof Formation which contains numerous prominent channel sandstones. *Oudenodon baini* also occurs in this sequence. This zone is followed by the *Dicynodon lacerticeps-Whaitsia Assemblage Zone*. These three zones are restricted to the Teekloof Formation in the western part of the basin.

The *Lystrosaurus-Thrinaxodon Assemblage Zone* is mainly associated with the Katberg Formation of the Tarkastad Subgroup (upper part of the Beaufort strata). The *genus Lystrosaurus* does, however, occur both above and below the Katberg Formation. The *Kannemeyeria-Diademodon Assemblage Zone* occurs in the upper two-thirds of the Burgersdorp Formation.

It is concluded that most of the larger uranium discoveries have been made in strata assigned to the *Pristerognathus-Diictodon* and *Tropidostoma-Endothiodon Assemblage zones* within a stratigraphic thickness of about 300 m.

It is expected that a more detailed biostratigraphic subdivision will become possible when taxonomic revisions of the genus *Diictodon* and the smaller endothiodonts are effected.

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It was also presented at the 18th Congress of the Geological Society of South Africa in 1979.

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SOME ASPECTS OF THE RELATIONSHIP BETWEEN TIME, MORPHOLOGICAL CHANGE AND THE ENVIRONMENT*

by

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ABSTRACT

What is the relationship between morphological change (along a lineage) and speciation? Must the environment always change in order to produce morphological change and/or speciation; or could the passage of time alone be responsible for producing morphochange in the form of increasingly better adaptation to the *same* environment? What is the distribution of rates of change along lineages? How many "modes" of evolution are there, and which one predominates? These questions are the essence of the hotly fought current debate on how evolution progresses. The majority of biologists either explicitly or implicitly believe, as did Darwin, that gradual, inexorable change predominates, with no increase in evolutionary rate with lineage splitting (phyletic gradualism). Some think that change is by no means gradual or inexorable; but that equilibrium is the rule while change/speciation is rare (punctuated equilibrium). These two models can be tested in a variety of ways, and particularly effectively by palaeontological data. This contribution contains a review of some tests suggested by others, as well as some new ideas on the subject.

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TOOTH FUNCTION AND REPLACEMENT IN HETERODONTOSAURID ORNITHISCHIANS OF THE STORMBERG SERIES — IMPLICATIONS FOR AESTIVATION*

by

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ABSTRACT

Thulborn (1978) suggests that ornithischian dinosaurs of the upper Stormberg Series (Late Triassic–Early Jurassic) of southern Africa underwent aestivation during an annual dry season. His argument, based on an interpretation of tooth function and replacement in heterodontosaurids, is: (1) unequivocal evidence of tooth replacement is not seen, and (2) piecemeal replacement of the dentition would be incompatible with maintenance of a fore-aft grinding function of the teeth; therefore, the entire dentition must have been rapidly replaced as a unit during periods of non-feeding, i.e. during aestivation. However, study of tooth wear patterns in *Lanasaurus*, *Lycorhinus*, and *Heterodontosaurus* show that jaw movements during mastication were orthal (open-and-close) and lateral to medial, *not* forwards and backwards. Differences in degree of tooth wear would not interfere with masticatory movements. Patterns of differential wear indicate that tooth replacement was not periodic but continuous, as in other reptiles. *Zahnreihen*, with a Z-spacing of about 3,0, are recognizable. Replacement ceased in mature individuals. The dentition shows adaptations for prolonging its effective life despite heavy wear. Differential tooth wear is incompatible with the idea of replacement of the entire dentition *as a unit* during an hypothesized period of aestivation.

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THE FOSSIL RECORD OF THE CLASS CHONDRICHTHYES IN SOUTHERN AFRICA

by

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ABSTRACT

The fossil record of the class Chondrichthyes in southern Africa is reviewed and some important new fossil finds are announced.

INTRODUCTION

The fossil record of the Chondrichthyes is incomplete and usually restricted to material such as detached teeth and spines because the cartilaginous parts of the skeleton fossilise only under extremely favourable conditions. For this reason only a few three-dimensionally preserved specimens of chondrichthyan neurocrania are known and all of these come from Europe and North America.

Described fossils of this class from the Gondwana continents are virtually non-existent but for a few isolated teeth and spines mostly from Brazil (Silva Santos 1946, Pinto 1965, Silva Santos and Sardenberg 1970, Figueiredo 1972, Ragonha 1978).

FOSSIL RECORD

Record to Date

Only a single shark species has been described from the Palaeozoic and Mesozoic of southern Africa. The holotype is an almost complete fish in the South African Museum (SAM-1082). It is a small hybodont shark *Hybodus africanus* Broom from the lower *Cynognathus* zone of the Beaufort. It comes from Bekkerskraal near Rouxville, Orange Free State. Romer (1966) lists *Lissodus* from the lower Triassic of southern Africa but does not mention *Hybodus africanus* Broom. *Lissodus,* however, is not mentioned by Jubb and Gardiner (1975) in a review of the identifiable fossil fish material from southern Africa.

The only other indication of the possible presence of chondrichthyans is spiral coprolites from the shales above the Dwyka tillite from near Douglas, Cape Province (McLachlan and Anderson 1973).

In contrast to the limited record from the Palaeozoic and Mesozoic, detached elasmobranch teeth from South African Cenozoic deposits are plentiful and represent three families, six genera and 11 species of sharks (Jubb and Gardiner 1975).

New Material

New discoveries of chondrichthyan material were recently made in South Africa of which one specimen in particular is of great importance.

1. The oldest chondrichthyan material now known from South Africa comes from the third Bokkeveld shale and was found by Mr. A. de Vries on his farm between Barrydale and Ladismith, Cape Province. Impressions of pleuracanth (ctenacanth)-type teeth occur together with placoderm fragments in a brown mudstone. The teeth have two large lateral cusps and a much reduced central cusp, on a button-like base. The middle to upper Devonian age of the upper Bokkeveld is equal to the oldest records for pleuracanths.

2. The tentative identification of spiral coprolites from nodules in a marine horizon in the Prince Albert formation near Douglas, Cape Province (McLachlan and Anderson 1973) is supported by the discovery of a shark neurocranium associated with spiral coprolites from the same stratigraphic horizon by R. Oosthuizen in the Prince Albert district. This marine horizon in the Prince Albert formation has yielded a fauna which includes osteichthyans and cephalopods from Douglas and, amongst other marine forms, a goniatite from near Mariental in Namibia (South West Africa) (Martin and Wilczhewski 1970). From Uruguay a stratigraphically similar nodular marine horizon at the top of the Itararé formation has yielded a similar fossil fauna of goniatites, Radiolaria (Closs 1967) and osteichthyans (Beltan 1978). To date, however, no chondrichthyan material has been reported from the Uruguayan nodules. The South American Irati Formation (Paraná basin) on the other hand has yielded an abundance of fossil shark teeth and spines (Ragonha 1978) whilst none are known from the equivalent Whitehill Formation of the South African Karoo basins (Oelofsen 1981).

The neurocranium mentioned above was preserved in a nodule of radiolarian tests. The cartilage of the skull disappeared after burial in the radiolarian ooze and the greater part of the cartilage is represented in the nodule as cavities, the walls of which are lined with the impressions of calcite crystals from the superficial layer of calcified cartilage. The radiolarian ooze flowed into the skull through apertures such as the nasal openings, foramen magnum and the foramina of the parietal fossa. In this way, internal structures such as the ampullae, sacculus, utriculus and lagena of the inner ear as well as the meninges were extensively preserved.

The cranial anatomy of this shark indicates a

close relationship to forms such as *Danaea* and *Cobelodus* and it is at the level of organisation which Shaeffer (1967) regards as clododont and which Zangerl (1973) calls the anacanthous design. A description of the neurocranium is in preparation and will be published elsewhere.

Apart from the fact that this is the first important record of chondrichthyans from the Palaeozoic of southern Africa or any other Gondwana country (Zangerl, pers. comm.) this braincase, as far as can be assessed from the literature (Romer 1964, Zangerl and Case 1967), seems to be the most complete and best preserved chondrichthyan braincase of Palaeozoic age known to date.

3. A nodule from the upper Witteberg shales collected by Mr. Oosthuizen in the Prince Albert district, Cape Province, contains a spine, numerous placoid scales and impressions of calcite crystals from the calcified layer of cartilage. That this nodule contains the remains of a shark is certain, but a study of the material has not yet been attempted, so a more specific identification is not yet possible.

4. From the Cretaceous deposits at Swartkops and Knysna (Brenton) Cape Province, Mr. Oosthuizen has retrieved three shark teeth. One of the teeth from the marine beds at Swartkops was lodged in a fossilised *Pinna* and it is therefore certain that it did not come from the overlying Alexandria beds. The one from Brenton was found with fossils of Cretaceous age. The other Swartkops specimen shows a strong resemblance to the teeth of *Charcharias taurus* Rafinesque which has a range from the upper Cretaceous to the present. Further collection and study will, however, be necessary to confirm this identification.

SUMMARY

In summary it can be said that although the fossil record of the chondrichthyans is still very incomplete, the new material has made an important contribution in filling in some of the gaps (see table 1).

ACKNOWLEDGEMENTS

I am indebted to Mr. Roy Oosthuizen for information and access to his specimens.

TABLE 1
The fossil record of the Class Chondrichthyes in Southern Africa

Rock Units	*Age*	*Fossil material*
Gravel member Varswater formation Langebaan	Latest Miocene–Early Pliocene	Detached shark teeth. Hendey (1976) Table 3 lists 11 families and 18 genera.
Uloa and Sapolwana Beds, Zululand	Miocene	3 families, 6 genera with 11 species (Jubb and Gardiner 1975).
Alexandria beds	Eo- to Miocene	Haughton (1925) described teeth referred to *Isurus hastalis* and *I. silimani*.
Bogenfels, Namibia	Eocene	Detached teeth.
Umzamba beds, Pondoland	Upper Cretaceous (Senonian)	Detached shark teeth (Du Toit 1954).
Sundays River beds, Swartkops		2 teeth from the Sundays River beds, Swartkops; 1 possibly of *Charcharias taurus*?
Knysna: Brenton Cretaceous beds	Upper Cretaceous	One tooth from Brenton beds. In the collection of R. Oosthuizen.
Beaufort	Upper Permian to Triassic	*Cynognathus* zone *Hybodus africanus* Broom; various specimens from Bekkerskraal, Rouxville. *Lissodus*? mentioned by Romer (1966).
Prince Albert formation (Lower Ecca)	Upper Carboniferous to lower Permian	Spiral coprolites, upper Dwyka shales, Douglas (McLachlan and Anderson 1973). 3-dimensionally preserved neurocranium and spiral coprolites, Prince Albert district. Collection of R. Oosthuizen.
Lake Mentz formation, Witteberg Group	Lower Carboniferous	Placoid scales, spine and impressions of calcified cartilage from a nodule, Prince Albert district. Collection of R. Oosthuizen.
Bokkeveld Group	Upper Middle Devonian	Impressions of pleuracanth (ctenacanth)-type teeth in a dark-brown mudstone. Collected by A. de Vries, Barrydale.

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PACHYGENELUS, DIARTHROGNATHUS AND THE DOUBLE JAW ARTICULATION

by

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The ictidosaur, *Diarthrognathus*, from the Clarens Formation (Cave Sandstone) (Crompton 1958) is generally held to exhibit the expected morphological grade intermediate between advanced cynodonts and mammals; more specifically, it is thought to have both reptilian and mammalian jaw joints. However, several of Crompton's interpretations of the morphology of the lower jaw and its articulation with the skull were wrong; some, but not all, of these he has conceded in print (Crompton 1972).

It is possible that there are only two species of ictidosaur in the Red Beds. The first specimen described was *Tritheledon* (Broom 1912), which comprises a pair of maxillae having mesiodistally compressed teeth of distinctive crown morphology. *Pachygenelus* (Watson 1913), a partial lower jaw with some teeth, is an apparently valid second genus but the position is complicated by the fact that upper and lower teeth are now known to be strikingly dissimilar in ictidosaurs. Hopson and Kitching (1972) have synonymised *Diarthrognathus* under *Pachygenelus*.

Re-study (now in progress) of the types of all three genera in conjunction with new materials discovered since will probably clarify the taxonomy. This is important, for, if it can be shown that most of the ictidosaur material is referable to a single species, the problem of understanding the jaw joint is considerably simplified.

Most of the confusion surrounding the nature of the jaw articulation of *Diarthrognathus* arises from Crompton's (1958) misidentification of the quadrate as the articular. Parts of the squamosal he thought to be quadrate and part of the articular. It was therefore possible for Crompton to conclude that: "The double articulation was possible because a single glenoid cavity was formed by both the quadrate and the squamosal." However, once the quadrate is correctly positioned such a glenoid configuration is no longer tenable. Crompton (1972) conceded this, although still maintaining that *Diarthrognathus* (but perhaps not *Pachygenelus)* had a dentary condyle.

On present evidence the author is disinclined to accept a dentary-squamosal jaw hinge in *Diarthrognathus*. It may be some time before clarity is obtained on this issue but it is useful at this stage to throw the whole question wide open.

The teeth of *Diarthrognathus* have now been prepared and described, and compared with those of *Pachygenelus* (Gow 1980).

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A FIRST RECORD OF A FOSSIL CEPHALOCHORDATE*

by

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ABSTRACT

An imprint from the White Band shales, interpreted as a fossil cephalochordate, is the first record of a fossil of this subphylum.

The anatomy of the specimen as well as the palaeosedimentary environment are suggestive of a pelagic mode of life in contrast to that of modern burrowing forms. This poses the question as to whether the burrowing habit of modern forms really is as primitive as generally believed.

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ASPECTS OF THEROCEPHALIAN CLASSIFICATION AND FUNCTION*

by

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ABSTRACT

The so-called primitive or early Therocephalia of the Upper Permian of South Africa, typified by the Pristerognathidae, have up to the present largely eluded attempts at devising a satisfactory classification for them. The task has been generally complicated by the poor state of preservation, an intractable matrix, relatively few complete skulls and a paucity of postcranial material. Consequently external cranial features have predominated in past classifications with the emphasis on the number and type of teeth. This method is unsatisfactory since lost or replacing teeth may directly influence even the familial status of specimens. This is demonstrated by the Lycosuchidae where the second canine in each maxilla, which was considered to typify the family, turned out to be a replacement tooth. Additional preparation of selected material appears to show that certain differences which exist in the literature might not be valid, e.g. the postfrontal of *Lycosuchus vanderrieti*, and that the group might be more uniform than previous classifications indicate.

A programme involving the use of photoelasticity to determine possible jaw function in the early therocephalians has been initiated with the Department of Engineering at the University of Stellenbosch and preliminary investigations appear to indicate that a scavenging mode of life may have prevailed.

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PRELIMINARY REPORT ON A CLUTCH OF SIX DINOSAURIAN EGGS FROM THE UPPER TRIASSIC ELLIOT FORMATION, NORTHERN ORANGE FREE STATE*

by

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ABSTRACT

Up to the present time, dinosaurian egg remains have been described from the Upper Jurassic sediments of Spain and from the Tendaguru Formation of Tanzania, while the majority of known specimens came from the Cretaceous sediments of Mongolia, China, France and North and South America.

The discovery of a cluster of six dinosaurian eggs containing foetal skeletons, from the upper horizons of the Elliot Formation (Red Bed Stage) of the Orange Free State, seems to be the first record of fossil eggs of Upper Triassic age.

The specimens are embedded in a block of hard reddish-brown sandy mudstone blasted from a road-cutting locally known as Rooidraai (Red Bend) in the Golden Gate Highlands National Park, some 17 km east of Clarens, Orange Free State.

Prior to this discovery and the description of two small ornithischian dinosaurs, *Clarencea gracilis* Brink, the present author had on a number of occasions noted the occurrence of isolated long bones of the prosauropod *Massospondylus* weathering out of the face of the now much widened road-cutting; a partial skeleton is still embedded in the face.

From the remains of two partial eggs exposed on one side of the block of sandy mudstone, housed in the Bernard Price Institute, it seems evident that there were originally more than only six eggs in the cluster. Of the six eggs present, three contain foetal remains in an advanced stage of development while one juvenile seems to have hatched prior to the fossilisation of the others, leaving in the matrix a shapeless egg "shell".

The "wrinkled" and to a certain degree flattened state of the eggs seems to indicate that they were leathery as in the eggs of some modern-day reptiles. As preserved they have a long axis of 65 mm and a short axis of approximately 55 mm with an estimated thickness of the egg-shell of 0,5 mm. Microscopically the outer surface or upper prismatic zone shows a very finely roughened surface with minute, well-spaced respiratory pores.

Dinosaurian features that can at present be distinguished on the partially exposed embryonic skull include the very short parietal region, the position of the postorbital, the parietal/supraoccipital suture, and the position and shape of the lachrymal which forms the posterior border of the antorbital fenestra.

This skull is reasonably well preserved and measures 10 mm across the squamosals and 7 mm from the anterior border of the orbit to the supraoccipital. It is in the process of being prepared, but because of the hardness of the matrix and frail state of the bone this will be a long and tedious task, complicated by the fact that parts of the skeleton overlie the anterior portion of the skull.

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AN ILLUSTRATED BIBLIOGRAPHICAL CATALOGUE OF THE SYNAPSIDA

by

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At the Karoo Symposium held at the Bernard Price Institute in 1977 I briefly announced my intention of producing a loose-leaf illustrated bibliographical catalogue of the Synapsida. Each loose leaf deals with a separate species (Appendix A, B). The front page contains the text, which consists of a genus-species-author-date title and material is handled in a standard sequence under six headings: Synonyms, Bibliography, Holotype, Referred material, Generic diagnosis, and Specific diagnosis. The reverse side contains, as far as possible, four views of the skull: lateral, dorsal, ventral and posterior, to standard scale and style.

Any palaeontologist will be welcome to submit entries, each being treated as a separate contribution with the author's name and address.

The catalogue is at present confined to the Synapsida but the possibility of expanding it to other reptile groups and even the whole spectrum of vertebrates has been borne in mind. A major problem has been the numbering of separate entries in such a way that they could be arranged in taxonomic rather than alphabetical order. The solution was to devise a filing code embodying the taxonomy of every individual genus and species. The code extends from class to family and within each family the genera and species are arranged in alphabetical order. When families are arranged in numerical order, they will automatically sort into taxonomic order. This code appears at the top left hand corner of every page. For a typical entry the code would be:

J213C211B *Diademodon tetragonus*

where J refers to the Class

J2	Subclass
J21	Infraclass
J213	Superorder
J213C	Order
J213C2	Suborder
J213C211	Infraorder
J213C211B	Family

Two important matters emerge immediately:

Firstly, if only for the sake of convenience and uniformity in terms of the codal system, the Subphylum Vertebrata is regarded as if it comprises 12 Classes and would-be "Classes": the Agnatha, Placoderma, Chondrichthya, Osteichthya, Amphibia, "Anapsida", "Parapsida", "Euryapsida", "Diapsida", "Synapsida", Avea, and Mammalia.

The 12 Classes and would-be "Classes" of the Vertebrata will resort under 5 Superclasses:

Superclass Pisc*es*
- A Class Agnath*a*
- B Class Placoderm*a*
- C Class Chondrichthy*a*
- D Class Osteichthy*a*

Superclass Tetrapod*es*
- E Class Amphibi*a*

"Superclass Reptil*es*
- F "Class" Anapsid*a*
- G "Class" Parapsid*a*
- H "Class" Euryapsid*a*
- I "Class" Diapsid*a*
- J "Class" Synapsid*a*

"Superclass Av*es*"
- K Class Ave*a*

Superclass Ther*es*
- L Class Mammali*a*

Secondly, across the spectrum of vertebrate taxonomy there are many instances where a need is not felt for providing names for all ranks. In the codal system proposed for pagination and classification of entries it is imperative that every rank is properly designated to avoid the use of zero for any of the digits in the code. I have tentatively derived names from lower and higher levels, whichever alternative I have regarded as most appropriate.

In the process of adjusting vertebrate taxonomy in areas where there is no consensus of opinion, or in areas thusfar left blank, it is felt that taxonomists in general will welcome any endeavour to standardise the terminations of ranks higher than that of Superfamily. There can be no doubt regarding the convenience of using ranks ending in *-oidea*, *-idae* and *-inae* without qualifying them additionally as Superfamily, Family or Subfamily respectively. Similarly it will be equally convenient to regard ranks terminating in *-ica*, *-ida* and *-ina* as those of Superorder, Order and Suborder respectively so that these can also be used without the rank qualifications.

Unfortunately at ranks above Superfamily one is confronted with some difficulties preventing perfect standardisation. A wide variety of terminations (*-ta, -da, -a, -es, -ii, -ini, -morpha, -formes*) — used rather haphazardly at present — are subject to gender, declension, the last letter(s) of the root, or otherwise mere custom or tradition.

Easton (1960) proposed that the following terminations be used consistently (while dealing with the Invertebrata):

Superorder	*-ica*	Superfamily	*-icae*
Order	*-ida*	Family	*-idae*
Suborder	*-ina*	Subfamily	*-inae*

While the termination *-icae* corresponds with *-ica* and could therefore pass for being more logical, it is suggested that its use be confined to the Invertebrata, while in the Vertebrata we adhere to the more traditional *-oidea*. In the botanical field there are other terminations at various levels which may remain customary for that field.

I should like to expand Easton's proposal to cover the full range as follows:

Phylum	*-ta*
Subphylum	*-ta*

Superclass	*-es*	Superorder	*-ica*	Superfamily	*-oidea*
Class	*-a*	Order	*-ida*	Family	*-idae*
Subclass	*-ia*	Suborder	*-ina*	Subfamily	*-inae*
Infraclass	*-ii*	Infraorder	*-ini*		

This proposal will sound less frightening if one bears in mind that these terminations are not supposed to be fixtures; that they are required to change with promotions and demotions — comparable to declensions of nouns in Latin. When a Family is promoted to Superfamily it will automatically, by existing custom, change its termination from *-idae* to *-oidea*.

From the following scale it can be seen that the matter is not problematical at all. The synapsid taxon "Anomodontia" is used here as if it could feature at any level from Phylum to Subfamily:

Phylum	Anomodon-*ta* (*t* part of termination)
Superclass	Anomodont-*es*
Class	Anomodont-*a* (*t* part of root)
Subclass	Anomodont-*ia*
Infraclass	Anomodont-*ii*
Superorder	Anomodont-*ica*
Order	Anomodont-*ida*
Suborder	Anomodont-*ina*
Infraorder	Anomodont-*ini*
Superfamily	Anomodont-*oidea*
Family	Anomodont-*idae*
Subfamily	Anomodont-*inae*

The classification used is by no means a final classification; the idea is that every contributor may submit his own recommendations for any adjustments. It is hoped that a final version will gradually evolve, embodying the consensus of opinion of the vast majority of vertebrate palaeontologists. Should this materialise, also for other vertebrate classes, the consequences could have immense value; to mention only one very useful repercussion: a standard universal codal system would become available for computer processing of museum collections. It is particularly with a view to computer processing that the standardisation of terminations is advocated — as standard "computer language".

The break-down is so designed that it remains unaffected upwards and downwards when a rank is added or subtracted, promoted or demoted, or transferred. This is achieved by the use of a combination of letters and digits. In computer programming digits within digital series should preferably not exceed nine. Fortunately across the entire vertebrate spectrum one rarely finds that super-, sub- or infra-ranks for any substantial taxon approach nine in number. Substantial ranks (Class, Order, Family) do tend to exceed nine in number, but they never exceed 26 — the alphabetic potential. The code can thus cope with more than nine Classes and the numerous osteichthyan and avian Orders approaching 26 in number within a single Superorder.

No doubt the eye will soon grow accustomed to this codal system where at a glance it can be seen that letters of the alphabet represent the three substantial ranks: Class, Order and Family. A digit in front of a letter indicates a super-rank and a digit following a letter indicates a sub-rank. The third digit in-between indicates an infra-rank.

APPENDIX A

J213B321B *Herpetogale marsupialis*

HERPETOGALE MARSUPIALIS KEYSER AND BRINK, 1979

SYNONYMS

Herpetogale saccatus (in errore) See Keyser and Brink 1979.

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1979 Keyser, A.W. and A.S. Brink, *Ann.geol.Surv.S.Afr.*, **12**: 91-105; p.91; fig.1.
Idem *(Herpetogale saccatus)*, p.103, table 5.1 (in errore).

HOLOTYPE

R337 GSO Good skull with lower jaw from Etjo mountain, Rhenosterfontein, Kalkfeld, Namibia - Anisian Omingonde Formation, M.Trias. See Keyser 1973; Keyser and Brink 1979.

REFERRED MATERIAL

Nil.

GENERIC DIAGNOSIS *Herpetogale* Keyser and Brink, 1979.

Bauriid therapsid with complete postorbital arches; short snout; short, wide intertemporal region; definite pineal foramen between postorbital bars, well in front of short, narrow intertemporal crest; snout tapering, nasals reaching far forward, rendering external nares barely visible in dorsal view; premaxillaries not penetrating between nasals; palatines situated far back, not reaching folds of soft secondary palate; hard secondary palate formed posteriorly by maxillaries only; posterior margins at internal choanae at level between second and third post-canines; small suborbital vacuities; interpterygoid vacuity a long, narrow slit reaching back to parashpenoid; pterygoid extensions to quadrates wide apart with straight outer margins; opisthotics massive; occipital condyle distinctly double; dentaries short and robust with distinct chin, and pronounced coronoid and angular processes; extensive fossae massetericae over lateral surfaces; dentition reduced to I4 : C1 : Pc5 upper and I3 : C1 : Pc5 lower; first lower incisors very large and inclined forward; lower canines tend to occlude on outside of upper alveolar margin; upper incisors and canines (worn ?) blunt at tips; all postcanines molariform; upper incisors incline outward and increase in size from first to fourth; upper post-canine series extend far medially relative to the far laterally placed canines; cheek pockets thus formed, well defined dorsally by extensive crista faciales and ventrally by pronounced shelves on the dentaries.

SPECIFIC DIAGNOSIS

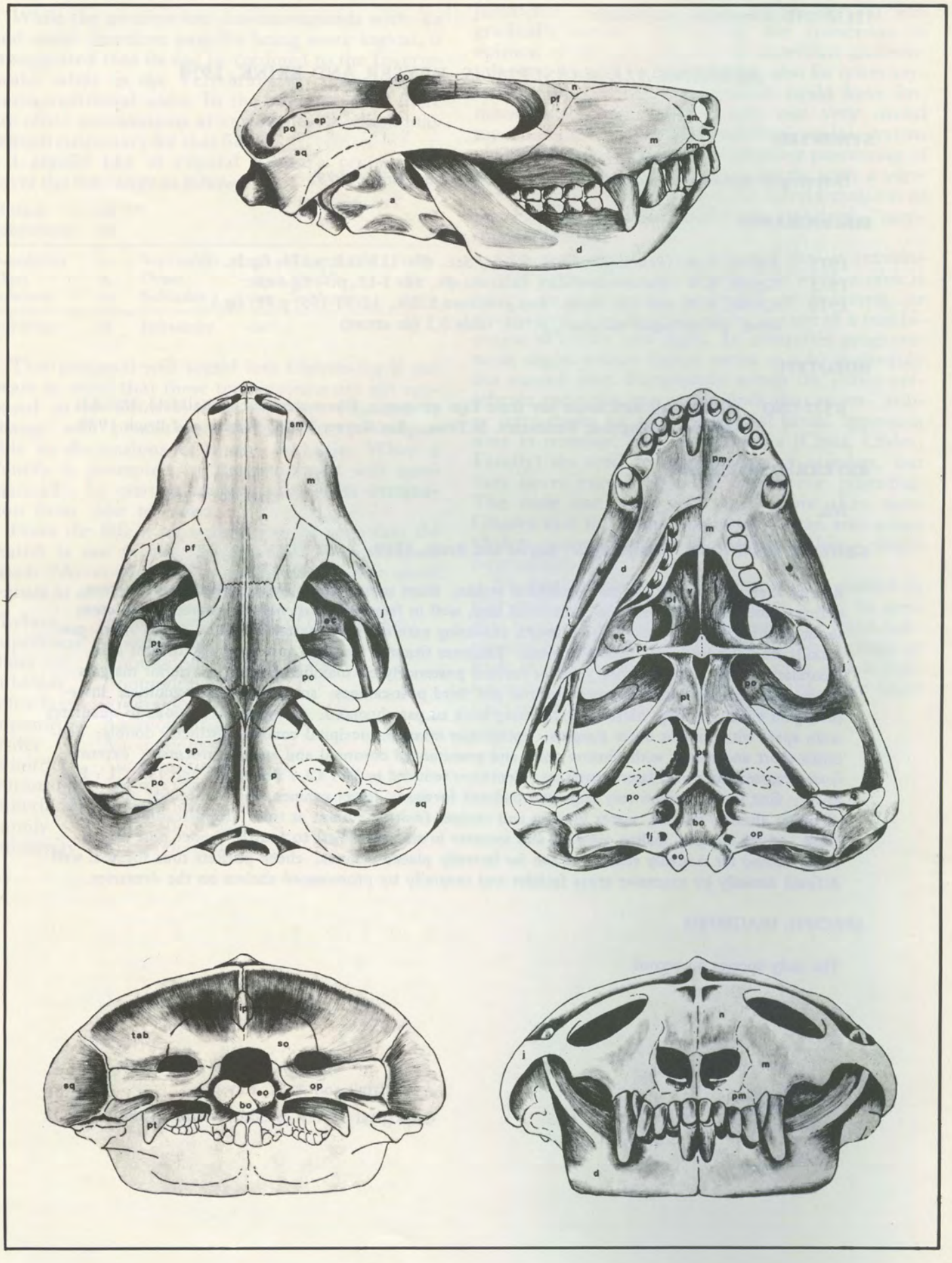
The only species on record.

A. S. Brink and A. W. Keyser,
Geological Survey of South Africa, 1980,

J213B321B

APPENDIX B

HERPETOGALE MARSUPIALIS R337 GSO X 1



Palaeont. afr., **24** (1981)

AN ATTEMPT TO DETERMINE THE PROVENANCE OF THE SOUTHERN DWYKA FROM PALAEONTOLOGICAL EVIDENCE

by

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ABSTRACT

Conflicting evidence regarding the palaeo-iceflow direction of the Dwyka is discussed. A study by Debrenne of archaeocyathid-bearing erratics in Dwyka tillite is reviewed, and new material, associated fossils and their localities documented. The need for more intensive study is stressed to decide whether the Nama group could be the source of the fossiliferous erratics.

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INTRODUCTION

Since the recognition during the latter part of the last century of the Dwyka tillite as glacial in origin, there has been much speculation as to the provenance of these deposits in the extreme southern part of the Karoo basin. Du Toit (1954: 277, fig. 41) postulated a northern provenance for most of the tillite, including the outcrop belt from Laingsburg through Prince Albert to Willowmore, the area under discussion in this paper. Striated pavements, on which Du Toit partly based his conclusions, do not occur in the southern part of the Karoo basin. Du Toit also made use of comparisons of erratic rock-types with outcrops to the north. Stratten (1970: 483, fig. 1), through study of tillite fabric and erratic types, envisages a general iceflow direction from the west, while Theron and Blignaut (1975: 352, fig. 24.3), by analyses of structures associated with east–west striae (mostly relating to the western side of the basin), state that the palaeo-iceflow was in the opposite direction, i.e. from the east, with the ice sheet spreading-centre near the east coast of South Africa. Recently Visser (1979: 73, fig. 3) postulated a provenance to the south-east, based on striated pavements, fabric analyses and archaeocyathid-bearing erratics. It is, therefore, clear that to date no general agreement has been reached on the provenance of the glacial deposits in the south.

PALAEONTOLOGICAL EVIDENCE

The abovementioned archaeocyathid-bearing erratics were first discovered by the author in 1965 on the farm Zwartskraal in the Prince Albert district. One large, light-grey limestone erratic (*c.* 15 cm in diameter) was sent to F. Debrenne of the Palaeontological Department of the National Museum of Natural History, Paris. She found 18 species of archaeocyathids, a new family (Pseudosyringocnemididae), two new genera (*Flexanulus* and *Statanulocyathus)* and three new species (*Flexanulus oosthuizeni*, *Statanulocyathus oosthuizeni* and *Andalusicyathus cooperi)* in the erratic (Debrenne 1975). Trilobite fragments were also present (Debrenne, pers. comm.). Debrenne compared the archaeocyathids from the erratics with archaeocyathids known from other parts of the world (see Debrenne 1975, table 1) and found that of the four species occurring most commonly, three are known only from Antarctica — *Erugatocyathus scutatus* (Hill), *Pseudosyringocnema* cf. *gracilis* (Gordon) and *P.* cf. *uniserialis* (Hill) — while the fourth, *Thalamocyathus tectus* (Debrenne), is known also from Australia. Species of the genus *Protopharetra* are cosmopolitan and of little value in this study. The rest are known only from Antarctica, and/or Australia. Another point of interest is the presence of equatorial forms with pectinate (comb-like) tabulae, e.g. *Thalamopectinus*, which occurred only in shallow equatorial seas in the early Cambrian (Debrenne 1973: 33, fig. 4). This could restrict the likely provenance of the fossils to a large extent, as it seems improbable that two widely separated lower Cambrian Gondwana areas (e.g. Antarctica and South West Africa, the two most likely sources) could both have been aligned on or near the equator and they would be difficult to fit into Zhuraveleva's Australo-Antarctic equatorial region (Hill 1972: E42, fig. 28). However, this would depend on the actual position of the Gondwana continent in relation to the equator in the Cambrian. Unfortunately, very little is known of this era.

A subsequent thorough search by the author of the tillite outcrops on the farms adjoining Zwartskraal has produced scores of archaeocyathid-bearing limestone erratics. A number of these archaeo-

cyathid-bearing erratics were found *in situ*, embedded in the tillite matrix. These limestone erratics, though extremely rare, occur from the base of the tillite right to the very top, which would imply that during the deposition of the entire southern Dwyka at least some of the material was derived from an archaeocyathid-bearing source. The fossil-bearing limestone erratics vary in colour from medium-grey to off-white, the latter being predominant. The matrix is very fine-grained and fairly uniform. The fossil-bearing erratics were traced by the author over 70 km in an east–west direction, and over *c.* 10 km in a north–south direction. They have also recently been reported by J.C. Loock from Leeuwkloof (Willowmore district) and north of Gamka Poort dam (Loock, pers. comm.).

As the study of archaeocyathids is highly specialized (involving thin sectioning, differential solution, etc.), it is not yet possible to say with any certainty if new species were recovered, but at least a few large single-walled specimens were found which were not present in the material examined in the first study. A number of trilobite fragments, mostly sections of segments, one small complete pygidium and a librigena? (free-cheek) were also encountered. One large erratic contains numerous possible hyolithids which appear to belong to the genus *Quadrotheca*, a Cambrian form. Onkolites and stromatolites (both algal) were found. They all occur in the same type of limestone and all these forms are normally associated with archaeocyathids in biohermal strata (Hill 1972: E27).

The only other fossils from the tillite (obviously of a much later age), are of plant origin. One black carbonaceous boulder found *in situ* near the base of the tillite is packed with flattened plant stems. A striated reddish sandstone cobble with stem impressions was also found higher up in the tillite. Phosphatic erratics within tillite nodules from near the top of the succession contain possible radiolarians.

CONCLUSIONS

Although Debrenne's evidence points to an Australo-Antarctic provenance for the southern Dwyka tillite (see also Cooper and Oosthuizen 1974), in which case Visser's palaeo-iceflow direction is acceptable, one cannot completely discount the possibility of a northerly provenance. If one ignores the slight possibility that all the fossil-bearing lower Cambrian material that may have existed somewhere to the north was completely denuded by the Dwyka ice, then the Nama Group in South West Africa and the north-western Cape seem to be the only other possible sources. The Kuibis subgroup is generally accepted to be of Precambrian age because of its "Ediacara-type" fossil assemblage. The latest dating of the Schwarzrand is based on Precambrian age (Vendian) acritarchs from this subgroup (Germs, pers. comm.). The limestones of this subgroup are moreover almost exclusively dark in colour. This seems to leave only the Fish River subgroup as a possible source. Germs suggests that a thorough search for subtidal carbonates in the Fish River subgroup in the Niewoudtville area of the north-western Cape could possibly produce a source for the archaeocyathids. Intertidal marine sandstones and shales have already been recognised in South West Africa (Germs, pers. comm.), so if subtidal carbonates do exist here they will probably be covered by the Kalahari sands to the east. Unfortunately the alleged archaeocyathids described from the Nama Group in South West Africa (Haughton 1960, Germs 1972, Kaever and Richter 1976) are not archaeocyathids at all, but trace fossils (Häntzschel 1975: W37), serpulids, or structures of mineral origin (Debrenne and Lafuste 1979: 143–144). Moreover, some of these fossils occur in sandstone, which excludes these rocks as a source for the archaeocyathids in the erratics (Hill 1972: E27).

The object of this paper is, therefore, to stress the necessity of: (a) widespread search of the Dwyka tillite for erratics containing achaeocyathids and associated fossils to establish their total distribution; and (b) a more intensive search of the calcareous members of the upper Nama Group in the north-western Cape Province and South West Africa for these fossils. If glacial material containing archaeocyathids was derived from both the north and the south, the distribution of different species may help to determine their respective depositional limits more accurately. (Incidentally, it should be stressed that the phylum Archaeocyatha — which occurs almost exclusively in limestone — could be an excellent age indicator if found in the Nama Group, as this phylum is known only from the Lower Cambrian to the base of the Middle Cambrian.) Because of the absence of striated pavements in the southern Cape and the controversies regarding the provenance of the tillite, it seems logical to make the best use of all evidence in solving this elusive problem.

ACKNOWLEDGEMENTS

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NEW EVIDENCE PERTAINING TO THE TAXONOMY AND PALAEOBIOLOGY OF *DIADEMODON* (REPTILIA; THERAPSIDA)*

by

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ABSTRACT

Bivariate (allometric) and multivariate analyses of diademodontine crania from South Africa and Zambia have shown that these specimens conform to a biometrically homogeneous ontogenetic growth series. The specimens, which include fossils attributed previously to several different genera and species, display a remarkable degree of morphometric similitude. It appears that only a single species, *Diademodon tetragonus*, is represented by the South African and Zambian material. The implications of this growth series are examined. It is postulated that whilst younger individuals were more insectivorous, the adults were more selectively herbivorous. Also, it is concluded that *Diademodon* exhibited polyphyodont, posteriorly directed sequential tooth replacement. The dentitions of numerous specimens representing various ontogenetic ages seem to support these statements. Furthermore, the enamel of the postcanine teeth is relatively thin and prismless, and it was worn away rapidly. *Diademodon* skulls exhibit rostral depressions; the most parsimonious interpretation of these cavities is that they housed salt glands. The evidence for prolonged ontogenetic growth, polyphyodont tooth replacement, prismless enamel and the probable possession of salt glands indicates that *Diademodon tetragenus* was more reptilian than mammalian in its general physiological organization.

* Full paper presented at PSSA First Conference, July 1979.

Palaeont. afr., **24** (1981)

TRANSGRESSIVE EVENTS IN THE CRETACEOUS SEDIMENTS OF SOUTHERN AFRICA*

by

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ABSTRACT

There are three major transgressive events in the Cretaceous sediments of southern Africa: upper Lower Albian, Lower Coniacian and Middle Santonian. The faunal assemblages occurring in each of these transgressive sequences are well documented. Each of these transgressive sequences is characterized by a high proportion of endemic faunas, rapid rate of evolution, and extreme intraspecific variation.

The implications of these faunal features on our current concepts of evolutionary theory and stratigraphic principles are briefly discussed.

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"BROAD SENSE INTERPRETATION" OF *GLOSSOPTERIS* LEAVES: A CRITIQUE

by

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ABSTRACT

According to Arber (1905), palaeobotanists attempting to identify *Glossopteris* leaves must choose between the methods of "grouping broadly" or "distinguishing in detail". The taxonomic treatment of *Glossopteris* according to these two alternatives is briefly reviewed. It is concluded that if palaeobotanists are allowed to choose between different interpretations of specific names, disparity and taxonomic confusion are unavoidable. A plea is made for a return to traditional methods of identification based on objective criteria.

INTRODUCTION

Palaeobotany is considered by some researchers to be an empirical science. However, even the initial examination of a specimen usually implies more than mere observation alone. The application of a bionomial name when a specimen is identified presupposes some conception of the term "species", especially in respect of the particular species to which the specimen is assigned. This cognitive aspect of the study is theoretically based and the species, as a concept, cannot be perceived empirically.

Different schools of philosophy, of evolutionary theories and of applied methodology affect the process of identification at all stages from the examination of characters to the designation of the specimen as belonging to a certain taxon. Debates ranging over a wide field, from the problems of nomenclature to those of the nature of evolution, have resulted in many published articles recently. The number of papers, and their often agitated tone (e.g. the recent debate about the use of cladistics at the British Museum of Natural History), testify to the importance of the whole complex problem. If knowledge was attainable on empirical grounds alone, the present theoretical controversy in systematics would not occur.

In the case of fossils, the problems of species-concept and of the evaluation of characters are more complicated by the time factor and by the fragmentary nature of specimens than is the case in identification of living plants and animals. Specific names must be used, but their meanings depend on the evaluation of the characters in the specimens studied. Irrespective of the aim of any study in this field, whether it deals with systematics or biostratigraphy, the first concern must be the accurate determination of specific characters.

This paper concentrates on aspects of specific identification of glossopterids; these aspects are not connected directly with evolutionary theories although the author is aware that the concept of species, and thus the evaluation of the specific significance of characters, cannot be separated from the concept of evolution. If evolution takes place through imperceptible gradual changes of characters through time, then there can be no discrete species and consequently no "specific characters". Classification in such a case is bound to be artificial and the separation of species arbitrary. Species are, however, objective entities with constant essential characters if speciation events take place in a comparatively short time relative to the lifespan of species. The individual differences may then be evaluated as variations of constant specific characters.

The arbitrary separation of *Glossopteris* leaves in the 20th century has not resulted from acceptance of a "gradualist" model of evolution. There has indeed been very little theoretical explanation behind the introduction of "broad sense interpretations" of *Glossopteris* leaves; it was originally intended to be a practical means of naming leaf-impressions which were believed to be mutually indistinguishable. This so-called "broad sense interpretation of leaves" has replaced the species as an objective entity. Some of the consequences of this approach are reviewed below.

THE HISTORY OF "BROAD SENSE INTERPRETATIONS" AS APPLIED TO *GLOSSOPTERIS* LEAVES

Seward (1897) was the first palaeobotanist to discuss in general "the extreme difficulty of drawing satisfactory distinctions between such forms as are included under *G. browniana*, *G. indica* and *G. angustifolia* . . . these three names cannot be maintained as standing for three well-marked species of *Glossopteris*" (p. 317). The three species mentioned were the first ones described by Brongniart in 1830 and as such they formed the basis for comparison when other species were described later. Seward also found that the "very large number of leaves of this genus (i.e. *Glossopteris)* described by Feistmantel from *different horizons* in the Gondwana series of India have in several instances formed the types

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of new species founded on quite inadequate grounds . . . It is difficult, or indeed impossible, to admit the existence of adequate grounds for some of Bunbury's species . . ." (p. 316) (emphasis mine). In his descriptions of the specimens Seward (1897) repeatedly called attention to the lack of distinguishing specific characters in leaves: e.g. "This fragment is of interest as illustrating the difficulty of drawing any sharp line between *G. browniana* and *G. indica* . . . It is also identical, as regards both size and venation, with some of the large fronds described by Bunbury from Nagpur as *G. browniana* var. *indica, G. stricta,* Bunb., and other species . . ." (pp. 320—322).

These comments of Seward (1897) represented a new sceptical tone in *Glossopteris* studies. Seward maintained this attitude and consistently dealt with *Glossopteris* in this manner. He came to the conclusion that the "accurate identification or diagnosis of *Glossopteris* fronds, and their separation into specific types, is, I believe, a hopeless task . . ." (Seward 1903: 80). "The arbitrary separation of sterile leaves, which differ by small degrees from one another in form and in the details of venation, by the application of specific names is a thankless task necessitated by custom and convenience; it is, however, idle to ignore the artificial basis of such separation" (Seward 1910: 507). When it is recalled that Seward was at the time a professor at Cambridge and was therefore a recognised authority, and that megaplant fossils are generally impressions of sterile leaves, then the serious impact of Seward's scepticism can be appreciated.

Seward made no attempt to establish a method for the identification of indistinguishable leaves. It was Arber who put Seward's intentions into practice. In his Catalogue, Arber (1905) gave an identification key and re-defined, by "grouping broadly" (p. 46), the *Glossopteris* species already described. In doing so, he influenced the study more profoundly than Seward, his professor. His catalogue is an often-used and much quoted source of information to this day. Arber, too, was convinced that "It is a most difficult and thankless task to attempt a general revision of these specific determinations, for it is almost impossible to obtain any definite aggregrate of characters to serve as a standard in dealing with details confined to the shape of the sterile frond and its nervation; the characters on which any classification must at present be based" (Arber 1905: 45).

Arber's first justification for creating an artificial classification was that "there has been considerable difference of opinion already on this subject." The second cause of his discouragement was "a considerable variation in the form and shape of the leaf of *Glossopteris*, and in the details of the nervation" (Arber 1905: 45); "Indeed, a detailed examination shows that there are hardly any characters which may be regarded as constant in fronds of the same species" (p. 46). Here the question arises: how did he know, then, which were the "fronds of the same species"? What did he regard as a species? If he had formed a concept of species in general and of certain species in particular, then surely he should be able to evaluate the "considerable differences" of opinion; they could be "right" or "wrong" as compared with the diagnosis by the author of the species. In the same way, he should have been able to find those characters that were constant among the "considerable variations" of shapes and venation patterns of leaves.

Arber (1905) came to the conclusion that "since an artificial classification is without alternative, and seeing that the value of such a classification depends largely on its convenience, it would seem more convenient . . . to maintain comparatively few species, and to group together those fronds which, though they may differ in one or more details from the typical form, are not sufficiently dissimilar in the aggregate of their characters to warrant separate specific rank. . . . In this manner, it has been possible to reduce the number of specific determinations to thirteen" (pp. 46–47). It is left to the reader to decide which "one or more details" might "differ from the typical form" and thus which leaves are "not sufficiently dissimilar", to warrant separate specific rank. It is also not made clear what is to be regarded as the "typical form" in this method.

Consider, as an example in Arber's sense, the first described "species" of *Glossopteris, G. browniana* Brongniart: The shape of *G. browniana* was defined by Brongniart (1830) as "subspathulatis obtusis"; by Arber (1905) as "spathulate, oval-linear, suboval, or almost oblong" (p. 50). Arber (1905) synonymized many species under the name *G. browniana* (pp. 48–50), irrespective of the horizons of the localities of type specimens. The synonymized species are dissimilar to *G. browniana* either in the shape of leaf, or in the characters of venation. Indeed, *G. wilkinsoni* does not share any character with *G. browniana*. Arber had to adjust the description to embrace all these species. Despite the fact that Arber's definition of *G. browniana* is very general, some of the species he assigned to it still disagree with it in one or more characters. If it is permissible for a fossil at hand to "differ in one or more details" even from Arber's broad interpretation of *G. browniana*, then the name can be applied to *any Glossopteris* leaf. Thus the "differences of opinion" about the aggregate of specific characters have turned into confusion over the years since publication of Arber's Catalogue.

Arber doubted the specific value of characters of leaves, but he could not replace them with anything else in his circumscriptions of species. Not only did he broaden the specific circumscriptions, but he also changed them, as illustrated in the following examples from his key compared with the original definitions:

Original definition	*Arber's (1905) definition*
Glossopteris indica Schimper: "areolis secum rachim positis abbreviatis, latiusculis"	"meshes . . . not as a rule markedly broader on the borders of the midrib"

G. stricta Bunbury: "frond narrow, strap-shaped, with nearly parallel edges."	"lanceolate"
G. divergens Feistmantel: "meshes being short close to the midrib, and becoming oblong towards the margin"	"Meshes . . . of nearly equal size through the lamina and very elongate"

Seward (1910) commented: "Mr Arber recently published, in his valuable *Glossopteris* Flora, an analytical key which serves to facilitate the description and determination of different types of frond." Maheshwari (1966: 39) called Arber's interpretation "broad-based specific circumscription" and found it "unsatisfactory".

Lambrecht *et al.* (1972) proposed a new scheme of "broad sense interpretation" of glossopterid leaves; this differs from Arber's, and is even broader.

THE CONSEQUENCES OF "BROAD SENSE INTERPRETATION" OF *GLOSSOPTERIS* LEAVES

By changing the specific characters, Arber (1905) changed the concepts of the specific names, too. He created artificial categories which could not be recognised in fossil leaves without accepting that "one or more details" could differ. Great freedom was given to personal opinion in deciding which characters could differ from Arber's already flexible and vague definitions, and to what extent they could differ. Thus the "broad sense interpretation" is not one kind of comprehension, but many. The "broad sense" attribute means that it is not restricted by principles or standards. The broad-based specific circumscription itself has such a broad meaning that it allows different interpretations of similar fossils, or the use of the same name for different leaves.

Some palaeobotanists lost confidence in the taxonomic value of external characters of *Glossopteris* leaves and tried instead to identify the species according to epidermal characters. However, the external characters could not be completely ignored, because even the epiderms are attached to leaves. Furthermore, as Maithy (1965: 249) comments: "In recent years the evidences of the cuticular studies of Glossopteridalean remains have exhibited that leaves with a similar external morphology, may have different types of epidermal structures . . . , leaves with different morphological characters, may possess cuticles with similar epidermal structures". Which, then, are the more reliable characters — the external, or the epidermal? Similar difficulties arise because different parts of fossil plants are classified separately: for example, even if a fructification is found in direct organic connection with *Glossopteris* leaves, the two are given separate names; in the hypothetical case of a leaf with an attached fructification, with seed in the fructification and with pollen in the pollen chamber, each part would be classified separately.

Biostratigraphy and intercontinental correlations are largely based on specific names summarised from the literature. Consequently, any geological conclusions drawn will be comparably as precise or as broad-based as the identifications of the fossils in the layers. If the separation of *Glossopteris* leaves into specific types is a "hopeless task", then so is any stratigraphic analysis based on them. If the characters of *Glossopteris* leaves are unreliable and they cannot be identified, then any conclusion based on them would have to be regarded as unreliable, too. The author, however, does not share this pessimistic view.

ALTERNATIVES TO "BROAD SENSE INTERPRETATION" OF *GLOSSOPTERIS* LEAVES

More than 80 years have elapsed since Seward's first sceptical comments on the taxonomic value of morphological characters of sterile leaves. However, as has been pointed out, the great majority of megaplant fossils are sterile leaves without preserved cuticles. Comparisons either for systematic or for stratigraphic purposes cannot be based on rarely preserved characters such as cuticles or fructifications. Leaf-impressions of *Glossopteris* are abundant in many fossiliferous layers; they represent the most readily available material for research. According to Arber, in their study "the choice lies between grouping broadly, and distinguishing in detail" (Arber 1905: 46). Grouping them broadly had led to confusion. Distinguishing in detail thus seems to be the better alternative. It means turning back to the traditional means of identification, i.e. to the exact evaluation and comparison of characters in the type specimens and in the studied fossil leaves.

There is only one kind of comprehension of species in the sense of traditonal identification: the fossil at hand has to share the characters of the original diagnosis and type-specimen of the species. The fossil is misidentified if the researcher overlooks or misinterprets an essential character. All scientists make such mistakes, which is only human. Errors can be corrected by comparing against the reliable characters of objective entities, i.e. of species. In an artificial classification a species is a mental construction and the criterion for its size and definition is its usefulness. This criterion depends on personal inclination and, in consequence, so does the definition of the species. Artificial taxa that are useful to one researcher may be useless to another. The definition can be changed to such an extent that it can become the diametric opposite of the original description. For example, Bunbury (1861) distinguished *Glossopteris leptoneura* from *G. angustifolia* as follows: "In *G. angustifolia*, the veins appear to be coarse and rather distant", in *G. leptoneura* "they are very fine and close" (Bunbury 1861: 330) — hence the descriptive specific name of the latter. On the other hand, Lacey *et al.* (1975: 361) perceived *G. angustifolia* "with closely set . . .

veins" and *G. leptoneura* "distinguished by the secondary veins producing wide meshes". In this definition the leaves have been "interpreted in a broad sense" (Lacey *et al.* 1975: 360). The limits of the broad sense interpretation are not set, not defined; thus the definition cannot be regarded as being "right" or "wrong". Errors can be corrected and by corrections science advances, but names with multiple meanings cannot be subjected to correction. The type-specimen or first diagnosis becomes meaningless for comparison, because the species is not comprehended as an objective entity; the meanings of specific names are formed and reformed by successive authors, and confusion reigns.

A species is an objective entity, a unit, which in neontology is represented by an interbreeding population, or a number of potentially interbreeding populations. The same gene-pool which determines the ability to interbreed is also responsible for all specific morphological characters in individuals. There is no reason to believe that the gene-pool which determines the characters of epiderms and fructifications acts differently with respect to the venation pattern of leaves. The genes also assure stability of species in time and provide the constancy in specific characters. In palaeontology similar fossils in a bedding plane, or within stratigraphically related horizons, represent a number of potentially interbreeding populations, or in other words, a species.

There are always certain characters in the diagnoses and type specimens of *Glossopteris* species which together constitute a set of characters typical of the species. Seward (1897) stated that he could not distinguish between *Glossopteris browniana* and *G. indica*, but Schimper (1868: 645–646) clearly separated the two species on size, shape of leaf, shape of apex, and in characters of the venation. Seward (1897) also stated that it is impossible to distinguish between Feistmantel's and Bunbury's species. Such a serious allegation should be substantiated with a study of random transitions of characters illustrated by specimens. However, no such study has been offered thus far. The alleged taxonomic unreliability of external characters of *Glossopteris* leaves is not proved.

Seward and Arber proposed the method of "grouping broadly" because they could not find definite aggregates of characters which could be considered as specific. Even if their scepticism was justified, their broad sense interpretation has aggravated the difficulty. The reliability of characters was doubted and therefore artificial categories were created; these categories have been formulated in different ways by subsequent authors and consequently no definite aggregates of reliable characters have emerged from the different perceptions. Thus *Glossopteris* studies move in a vicious circle. One way to break out of the vicious circle and to check on the reliability of specific characters is to return to traditional methods of identification. The alternative to broad grouping is exact identification.

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QUANTITATIVE AND QUALITATIVE ASPECTS OF ONTOGENY AND SEXUAL DIMORPHISM IN THE PERMIAN ANOMODONT *AULACEPHALODON**

by

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ABSTRACT

A biometrical (allometric) analysis of a number of *Aulacephalodon* crania, several of which have been assigned to different species, was undertaken. The results suggest that this material represents a morphometrically homogeneous ontogenetic growth series. Features ultilized previously in the diagnosis of *Aulacephalodon* species can be accounted for by the phenomenon of allometric growth. A quantitative assessment of sexual dimorphism was, for the most part, inconclusive. However, the results of a qualitative investigation of nasal boss and temporal arch morphologies suggest that these features are related to sexual dimorphism. It is proposed that adult females possessed somewhat flattened nasal bosses, whilst males showed bulbous nasal bosses and, with advanced size (age), thickened lateral borders of the temporal arches. Sexual dimorphism appears to have been expressed in individuals with a basal cranial length of between 190 mm and 245 mm. Locality and stratigraphic data were examined, and these data appear to support the hypothesis that we are dealing with a single species, *Aulacephalodon baini*, which showed sexual dimorphism.

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THE USE OF WAX IN CONTROLLED ACID PREPARATION

by

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For preparing blocks of cave breccia rich in microfaunal remains, some method was needed to confine acid action to the upper surface of the blocks and thus prevent delicate bones on the lower surface from being crushed by the weight of the rock as they become exposed, and generally to make the whole procedure more manageable. Conventional methods are either time consuming (latex) or expensive (silicone rubber). The method described here is quick and effective and the cost is negligible.

Blocks are first treated in 3 per cent formic acid, washed and dried. All exposed bone is coated with a solution of "Glyptal" G1276 cement diluted with lacquer thinners. This treatment cleans and roughens the surface providing a good surface key for the wax. A string cradle is made to hold the block, which is then dipped in paraffin wax heated in a double boiler. Six to eight dippings are usually adequate. The first skin of wax chills immediately on contact with the breccia. Surplus string is then cut away and the block is ready for further acid preparation, using concentrations of 5 per cent to 10 per cent formic acid. The wax forms a perfect seal against acid penetration and it can be easily removed as preparation progresses. Wax can be written on using a felt pen; it can be cleaned and re-used.

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A STUDY OF THE TYPE LOCALITY OF *LIDGETTONIA AFRICANA* THOMAS 1958

by

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ABSTRACT

The circumstances of the discovery of the type locality of *Lidgettonia africana* Thomas 1958 and of Thomas's description of this fructification are placed on record and the fossils mentioned by him are listed. The horizon, depositional environment and modes of fossilization are discussed, and the present known flora and fauna are outlined, compared with Thomas's list and with those of other sites, and illustrated with particular regard to the variety of fossils and modes of fossilization. The presence of several species of *Glossopteris* and three fructification taxa show Thomas's associations of leaf taxa with *Lidgettonia* and *Eretmonia* to be arbitrary. On the basis of the present known flora and fauna the type locality of *Lidgettonia* is provisionally considered to be, like the Mooi River site, lower Beaufort.

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INTRODUCTION — HISTORY OF RESEARCH AT THE LIDGETTONIA SITE

Interest in *Lidgettonia africana* Thomas 1958 has recently been stimulated by the discovery at a different site (Mooi River) of numerous specimens of this important pteridosperm fructification (Lacey *et al.* 1975). Arising out of consequent interest in the type locality and the fortuitous finding of a portion of the wing of an homopteran plantbug, the site has been the subject of recent study; unusual preservation of the fossils at the site has been the subject of two reports (Van Dijk *et al.* 1975, 1978). Gordon-Gray *et al.* (1976) did a preliminary study of the equisetalean fossils, Riek (1976a) included two insects from the site in a description of new Permian fossil insects, and Van Dijk, Hobday and Tankard (1978) referred to the site as an example of one type of bay-fill facies. Apart from the paper in which *Lidgettonia* was described, these appear to be the only papers in which there is anything more than a mention of the site and its fossils. The present paper attempts to record something of the history of the discovery of the site, to assess the significance of the site, to list and illustrate its present known palaeoflora and -fauna and to elucidate the palaeoenvironmental setting.

An enquiring letter was sent to Dr. A.O.D. Mogg, the discoverer of the site, on 27th April 1976 (his 90th birthday). He described the discovery as follows:

> "The Thompsons farm fossils I discovered June or July 1917 when I was working on Styfsiekte for Division of Veterinary Services, Dept. Agriculture.
>
> I found some Ecca shale flakes in the stream with clearly defined *Glossopteris* Fossils & photographed them, my native driver holding one in his hand.
>
> Working back a foot I came across doorsteps 3–6″ thick & removed about half a dozen approx. 15″ × 10″ × 3–5″.
>
> These I sent to:
> a/ Hamshaw Thomas, Cambridge, Eng.
> b/Director Geological Survey, Pretoria
> c/ Director Veterinary Services, Pretoria
> d/ Curator Natal Museum, Durban,
> & I *believe* to National Herbarium, Botany Dept., Pretoria."

Thomas (1958: 180) states of the site and material: "This plant bed was originally discovered by Mr. A.D.O. Mogg, he kindly sent two large blocks to the author, who visited the locality in 1929 and made a collection of specimens, which have only recently been studied." That the original material collected, and that collected by Dr. Thomas in 1929, was not entirely forgotten between 1929 and 1958 is known from a request made by Dr. Thomas in 1950 to Mr. M.P. Rilett while he was a student at Cambridge, for the col-

lection of more material when he returned to South Africa (M.P. Rilett, pers. comm.). Thomas does not refer to a second visit which he made to the site — in 1956, according to the present owner of Bella Vista, Mr. A.S. Thompson (pers. comm.). The publication of descriptions of *Glossopteris* fructifications by Dr. Edna Plumstead (1952, 1956) appears to have been the stimulus for Dr. Thomas to revisit the site and to publish a description of the site and of the new fructification, *Lidgettonia africana*.

Subsequent to the publication of Thomas's paper, visits were made to the site by Dr. Plumstead with Dr. Mogg and with students, and by Miss A.K. Benecke (now Dr. Malleson). Plumstead (1969) refers to material collected by Malleson: "On Pl. XVII, fig. 3 is a figure which I feel may add one more link in the chain of evidence. The specimen was collected by Miss Benecke from the same area as that described by Thomas (1958) and given to me to illustrate *Lidgettonia*. The photograph reveals an elongated 'scale' leaf with Lidgettonia 'flowers' on small pedicels and apparently, a small convex scale leaf attached to the top of the elongated scale leaf. Both *Arberiella* (top right) and small seeds can be seen in the vicinity. There is also a larger isolated scale leaf on the right hand side. The specimen suggests that much of the evidence of previous authors may be combined in this lucky specimen." (pp. 50–51). (The association of seeds with the cupules of *Lidgettonia* was suggested by Thomas (1958: 84) "A well preserved seed is seen lying in contact with one of the cupules, but its position may have been accidental".)

In 1974, Dr. W.S. Lacey visited South Africa to work on material from the Mooi River site discovered by the present author and Mr. B. Schaller, and he was taken to the Lidgetton site for comparative topotypical material. There the author collected a small slab of material from a point in the stream bed which Mr. A.S. Thompson (pers. comm.) later identified as precisely that on which Thomas concentrated in 1956. The slab contained, in addition to all the types of plants mentioned by Thomas, the distal half of an homopteran insect wing (cf. fig. 57). This was the first insect fossil from the site. The site was later visited by the present author with senior Botany students, and Mr. John Oliver discovered a plecopteran (stonefly) wing (fig. 56). In the latter half of the year the site was the subject of a third year Geology exercise by Mr. Owen R. Dix at the suggestion, and with the guidance, of the author. Mr. Dix found a beautiful homopteran wing (of the same species as the original fragment (fig. 57), a nymphal insect specimen (fig. 55), two *Glossopteris* specimens which were very distinctly different from those described by Thomas (figs. 7, 10), and a small slab which showed trackways (figs. 2, 3). The homopteran and plecopteran wings have already been studied (Riek, 1976a). Further work by the author has yielded many more specimens (e.g. figs. 54, 58–76). Table 1 compares the present collection with that described by Thomas (1958).

METHODS

Besides unsystematic collecting of material, the orientation of which could not be retained during collection, systematic collection of slabs was attempted. Dips were recorded. Removal of coherent slabs was then attempted. So far this has rarely been successful through a succession of layers. The intactness of fossiliferous layers could rarely be retained when the slabs were split, because of the coherence and uniformity of texture of the sediments and the paucity of bedding planes. Appropriate material was clipped off, or sawn off with a dry saw, and embedded in polystyrene-polyester resin (Natal Chemicals Syndicate 7036); this material could then be sectioned with a water-cooled diamond saw to expose a surface without this disintegrating; after lapping and polishing with pumice suspension the surface could then be etched for examination under the scanning electron microscope (figs. 48–50), or for acetate peels using Schwann-Stabilo OHP-Transparent-Foils 0,08 mm (figs. 43–46). Acetate peels and replicas of the fossils, as exposed, were also made for optical microscope observation (figs. 40–42). Profiles of a few of the ripple-surfaced layers above the main fossiliferous layer were prepared by sawing, lapping, polishing on glass and coating with "dope" (fig. 1). Hydrofluoric Acid digests (concentrated, i.e. approx. 50 per cent, overnight) were made of portions of the most carbonaceous layer, which did not show clear fossils macroscopically and may have been overlooked by Thomas (fig. 47).

LOCATION, HORIZON AND NATURE OF THE EXPOSURE

The site is located at 29°25′55″S; 30°07′08″E at an altitude of approximately 1 180 m; the location is ringed in the map (fig. 80) and indicated by a white arrow in the aerial photograph (fig. 81), in which landmarks are shown to the east (pylon), south (spring) and north (fence).

Through the kindness of Dr. J.W. du Preez of the Geological Survey in Pietermaritzburg it was possible to include in the map information from geological mapping at present in progress for the Geological Map 2930A; beds which are lithologically Beaufort are shown hatched horizontally (towards the north-west and south-west), while the rest of the map area is lithologically Ecca or dolerite or alluvium. Plumstead (1969, caption Plate XVII, fig. 3) placed the Lidgetton site in the Upper Ecca without comment, while Thomas (1958: 180) comments: "*Age of the specimens.* The organic remains in the bed furnish no clear indications of its age, and there is a heavy cover of soil and vegetation in the area. According to the latest map published by the Geological Survey of South Africa the outcrop is of Ecca age in the Karroo System. The boundary between the Ecca and the Beaufort series is not far distant, and it is thus possible that the material is of Upper Ecca age.

TABLE 1

* **Thomas 1958**
N.B. including only one species of *Glossopteris*, compared by Thomas to three taxa.
** **Present Collection** including specimens collected by D.E. van Dijk[1], O.R. Dix[2], J. Oliver[3], G.H. Hickman[4], Jacques van Dijk[5], David Stuckenberg[6], Miss J.R. John[7], A.B. Cunningham[8]; identifications by D.E. van Dijk[1], K.D. Gordon-Gray[9], E.P. Riek[10].

	*	**
PLANTAE		
Thallophyta		
Eumycophyta		? Hyphae, on *Glossopteris*
Embryophyta		
Bryophyta		*Buthelezia mooiensis* Lacey, Van Dijk and Gordon-Gray (Bryophyte), including acetate peels and replicas
Tracheophyta		
Sphenopsida	cf. *Neocalamites carreri* Zeiller stems, pith-casts, branches, leaves	+ + + + diaphragms[1; ident. 9] (some *in situ*) histological detail from acetate peels and replicas cytological detail from pyritized material by SEM and peels and replicas of etched sections
Pteropsida		*Sphenopteris* leaf fragments in HF digests
Cycadopsida		
Pteridospermales	*Glossopteris* sp. leaves (cf. *indica* Schimper, *communis* Feistmantel, *arberi* Srivastava)	+ histological and cytological detail as above *Glossopteris* cf. *browniana* Brongniart[3, 1; ident. 1] } See criteria, Table 1, *Glossopteris* cf. conspicua Feistmantel[3, 1; ident. 1] } Lacey *et al.* 1975 *Glossopteris* sp. unidentified
	Scale leaves	+ *Vertebraria indica* Royle[1, 3; ident. 1]
	Lidgettonia africana Thomas (gen. et sp. nov.)	+
	Samaropsis cf. *S. seixasi* (White) Sew. seeds	+ *Plumsteadia* sp. 1 very good specimen *Eretmonia natalensis* Du Toit
	microsporangia cf. sporangia of *Eretmonia natalensis* Du Toit (microsporangia now known as *Arberiella* Pant and Nautiyal)	+
Coniferopsida		
Cordaitales		Pyritized wood, cytological detail by HF digests
Incertae sedis	Winged spores of various sizes	Winged spores of various sizes ? Spore similar to type known from Mooi River and Mt. West
ANIMALIA		
? **Annelida**		? Burrows (difficult to distinguish from post-depositional roots) Worm tracks
? **Mollusca**		Tracks, ? molluscan
Arthropoda		
Crustacea		Crustacean tracks Conchostracan shells, 14 specimens Type A, 13 specimens (7 with pyrites surface replication) Type B (cf. *Leaia*)[6], 1 specimen, with pyrites surface replication
Insecta		120+ specimens, half of which fragmentary, mainly in the case of what are apparently exuviae of nymphs, of which there are 56 specimens Plecopteran *Euxenoperla* Riek[4; ident. 1] sp. nov.[ident. 10] 1 specimen ? Plecopteran nymphal exuviae[1,3], ? of *Euxenoperla*, numerous specimens[ident. 1], rather small to be nymphs of *Euxenoperla*[(1, 10)] Paraplecopteran *Mioloptera* Riek[5, 1; ident. 1] cf. *stuckenbergi*[ident. 10] Homopterans[1, 3, 8] at least 20 specimens, including 1 very complete specimen 4 or more types[ident. 1], including Prosbolids[ident. 10] Aleyrodid hemipteran *Aleuronympha* Riek 1 specimen, apparently late nymphal instar (cf. Riek 1974) 6 specimens of a smaller scale insect, ? earlier instar Scale insect[5], possibly related to *Aleuronympha* Coleopteran[ident. 1] (cf. *Molenocupes* Riek[ident. 10]) 1 specimen Unclassified wings, body fragments[1-9], legs
Chordata		
Osteichthyes		Fish scales (impressions) 6 specimens

But there is little lithological difference between the rocks of the Ecca and those of the Beaufort series, as is stated by du Toit, and it is also possible that the forms described are of Beaufort age." In a later publication than those referred to by Thomas, Du Toit (edited Haughton 1954) commented on the upper limit of the Upper Ecca having been undefined "since no clear line of demarcation from the overlying reptilian-bearing strata, styled the Beaufort Beds, was apparent" (p. 280). Haughton (1969: 352), discussing the problem of distinguishing Upper Ecca and Lower Beaufort, writes of characteristic Beaufort beds in the northern Karoo as follows: "The coloration of these argillaceous members tends to disappear in a north-easterly direction and, in the absence of vertebrate remains differentiation between the Upper Ecca and the Lower Beaufort in this region is partly a subjective exercise." The significance of vertebrate fossils follows immediately (new paragraph): "The advent of continental reptilian life within the main basin appears not to have preceded Beaufort times; but there are stretches of country near the presumed Ecca–Beaufort boundary in which reptilian fossils have not as yet been found and over these the boundary line is to a certain extent doubtfully placed." Barry (1970: 653) reported on the "recent discovery of vertebrate fossils in Ecca defined beds . . ." and discussed the Ecca–Beaufort boundary.

Two important sites lie close to the (lower) margin of the Beaufort, namely Bulwer and, north of Lidgetton, Mount West, while the rest of the main Beaufort sites are situated higher in the Beaufort — at an altitude of approximately 1 390 m in the case of the Mooi River site, i.e. 210 m higher than the Lidgetton site (see the map, fig. 1, p. 351 in Lacey *et al.* 1975). Figure 80 shows that the base of the Beaufort, on lithological criteria, lies between 1 200 m and somewhat more than 1 300 m in the south-west, while it lies at about 1 350 m in the north-west of the map area. If the beds at the level of the Lidgetton site have a similar regional dip, then they might be expected above 1 200 m (light shading) north of the Lions River valley and progressively further below 1 180 m southwards in the south-east of the map area (unshaded). New exposures are being sought; completion of the Geological map of this area, which will give details of the dips, will greatly aid the search. It should be mentioned that the immediate vicinity of the fossil site is influenced by dolerite intrusions, the dip of the beds being quite different at a point about 20 m south of the site.

Thomas (1958) refers to fine dark shales in which the fossils are carbonaceous compactions, to coarser grey shales, and to fine pale buff material in which the plant substance has disappeared or is represented by ferruginous material. The material in this study is in the dark shales; as mentioned above the material is from precisely the same point as that studied by Thomas. At this point the exposure is partially to wholly submerged in a stream. According to Mr. Thompson (pers. comm.), Dr. Mogg stated, when visiting the site, that he had collected upstream from this point, but could not find further material upstream, while Dr. Plumstead collected material downstream from this point. The site studied lay immediately upstream of the roots of a large living wattle tree which had toppled downstream on the eastern edge of the stream before Thomas's 1956 visit. Recently this tree was removed to permit a systematic study of the site. Fortunately the beds dip at about 5° and 7° in the north-westerly direction and therefore emerge from the stream on its eastern edge. Excavations towards the eastern bank were begun in order to produce a vertical transect, and these excavations at the same time provided samples of the main fossiliferous layer and the layers immediately above. An accurate, detailed, transect is not yet possible.

DEPOSITIONAL ENVIRONMENT, FOSSILIZATION AND FOSSILS

A detailed study of the depositional environment at the Lidgetton site is intended in the future when further information is available about the lateral extent of the various layers. The beds studied lie at the bottom of an upwards-coarsening sequence which ranges from dark carbonaceous shales to lighter, less reducing, or oxidizing, conditions above. The upwards-coarsening sequence suggests a deltaic environment and the still reducing conditions suggest a backswamp environment in a delta. The northerly direction of the ripples in the upper layers (fig. 1) accord with observations elsewhere in the Beaufort.

The main fossiliferous unit, which is about 6–8 cm thick, contains most of the *Glossopteris* leaves and associated fructifications near the bottom, followed by slender sphenopsid stems with leaves, and then the larger sphenopsid stems, while the top of the unit is coarser and contains, in addition to *Glossopteris* leaves and small sphenopsids, rhizomes (*Vertebraria,* fig. 16) and evidence of superficial bioturbation. It is possible that the sequence of fossils represents in part a sorting phenomenon rather than a purely chronological sequence, since the larger sphenopsid stems may have settled more slowly because of contained air. In the sediments of this unit there is apparently a range from strongly reducing anaerobic at the bottom to aerobic at the top. A detailed analysis of this unit is intended concomitantly with study of the lateral extent of all the beds, somewhat in the manner so admirably pioneered in South Africa by Dr. Heidi Anderson for the various sites which she has studied (Anderson 1975). It is important to note that a statement of Thomas (1958: 180) gives the erroneous impression that the *Glossopteris* leaves and associated fructifications and sporangia are mainly found above the sphenopsids, when he states of the former: "With these, towards the bottom of the bed, are parts of equisetalean plants, stems, pith-casts, branches and leaves."

A few tentative comments are possible at this

stage on the fossils and their mode of fossilization Firstly there is replication of the surfaces of *Glossopteris* leaves (figs. 24, 25, 28–30) and conchostracan shells (figs. 77, 78) by pyrites deposition, suggesting contemporaneous precipitation through the action of hydrogen sulphide from the rotting organisms with iron salts in solution in the pools or the connate water (see figs. 31–39, 78). The fact that pyrites is also found to be preferentially deposited on wound surfaces of some leaves, and other parts, such as *Lidgettonia* cupules and attached seeds, which may be presumed to have been actively growing at the time of detachment, is also strongly suggestive of contemporaneous deposition. Secondly, subsequent pyritization (by which is meant infilling and not substitution — *vide* Schopf 1971) appears to have occurred in hollow parts particularly, for instance the conducting tissue of sphenopsids, and to have occurred while much structure still remained (see figs. 31–39). Schopf (1971) discusses the process of silicification and much of what he says is, *mutatis mutandis,* relevant to pyritization. Preservation of so much cellular detail in the Permian Gondwana deposits has apparently very rarely been discovered: Plumstead (1962: 82) reported the absence of cellular detail in pyritized stems from the Triassic of Antarctica. Thirdly, there is evidence of a biocoenosis nearby with conchostracans, the whole bodies of which were deposited (figs. 77, 78), with fishes (or a fish, if all the scales are on precisely the same layer) which disintegrated in, or close to, the deposits (fig. 79), and with numerous aquatic nymphs the exuviae of which are preserved in the deposits, in some cases at least as HF-resistant body fossils (fig. 55 inset). In the most carbonaceous layer are fairly complete specimens of *Buthelezia* (figs. 17, 42), which provides evidence that the plants described (from Mooi River, Lacey *et al.* 1975), which are of similar size and appearance, were fully grown, while the presence of rhizoids or root-hairs on one of the described specimens, and the completeness of the specimens in the Lidgetton deposits, suggests that *Buthelezia* grew in swamps. Another moss-like plant is also present (fig. 18), while there is evidence of penetration of mud-covered leaves by roots and/or burrows (fig. 21), as well as evidence of fungal attack, probably during decay (fig. 20).

Of the insects so far obtained most are related to modern plant-piercing sap-sucking types (figs. 57–65, 69–74) and their wings appear to show the same kind of plant-dwelling camouflage as in present-day insects such as jassids (cf. fig. 71). Phytophagous (biting) types may be represented by the beetle (figs. 67, 75), while the plecopteran (fig. 56) probably lived near water as do living stone-flies. Several sporophylls of *Lidgettonia* with holes in them suggest that they may have been attractive to insects, as young shoots are today, and this might have facilitated pollination, or perhaps favoured out-breeding. The shapes of the *Lidgettonia* sporophylls (figs. 11, 12) suggest that they may have been aggregated into a cone-like structure, but otherwise there is no evidence as to their relationship to other structures. It should be noted that inferences from associations are very risky, and in particular that Thomas's inclusion of the commonest type of sterile leaf in the diagnosis of *Lidgettonia* is particularly risky, as there appear to be at least three types of *Glossopteris* (figs. 5, 6, 7, 10), whatever they prove to be, as well as three fructifications — *Lidgettonia, Eretmonia* and *Plumsteadia* (figs. 11–13, 15, and 14 respectively). Any of the leaf taxa, or others not noted, could have been associated with any of the fructifications. (On the basis of his failure to find *Eretmonia,* Thomas 1958: 187, states: "It seems very probable that *Eretmonia* was a fertile structure from another plant with *Glossopteris* leaves, possibly *G. cordata* Feist. If this is so, *Lidgettonia* and *Eretmonia* may well be related, though they could scarcely be regarded as species of the same genus.") Leaves attributable to *G. cordata* had not been found at Lidgetton, thus providing some evidence against relationship between *G. cordata* and *Eretmonia.*

Thomas (1958: 181), in attributing all the *Glossopteris* leaves to one species in his diagnosis of *Lidgettonia africana,* remarks: "They vary considerably in size, their venation is uniform, but differs somewhat in appearance on the two sides of the leaf, and there is no reason to suppose that more than one species is represented." The types of difference between the leaves illustrated in Figures 5 and 6 (and together in fig. 4) would not be expected on the two sides of the same leaf, but Thomas's observation of differences (? between axial and abaxial surfaces) does emphasize the inadvisability of detailed descriptions of venations based on single, or even a few, specimens.

The absence, so far, of *Sphenophyllum* and glossopterid leaves with an open reticulation (of the *G. retifera* type), including *Belemnopteris* (*sensu* Lacey *et al.* 1974, 1975) is interesting, since these occur at Mooi River, Bulwer and Mt. West (see table 2 and van Dijk *et al.* 1977). Common to Lidgetton and Mt. West is the presence of apparently aquatic nymphs (fig. 55), and to these sites and Mooi River, and possibly (different species?) also Bulwer, are *Mioloptera* wings (fig. 54). *Aleuronympha* (figs. 64, 74) and *Euxenoperla* (fig. 56) occur at Lidgetton and Mooi River. A similar age (in the Upper Permian) of the Lidgetton site to that of Mooi River is suggested; when the fossils now available have been fully studied the advisability of placing the sites in a common zone can be considered. As noted above, the absence of tetrapod fossils can no longer be regarded as diagnostic of Ecca deposits, as is very strongly suggested by the work of Barry (1970).

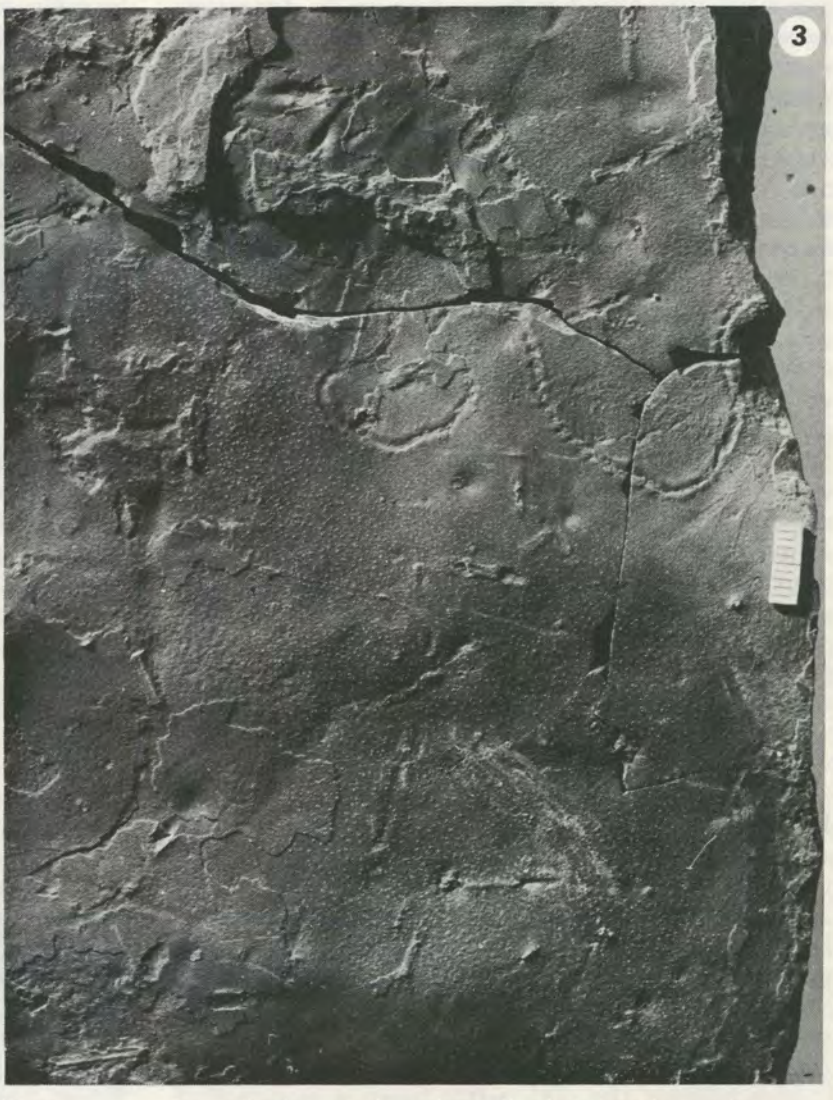
DISCUSSION

Productivity of the site

The present account is based on a study of material collected during six excursions to the site, in addition to the basically geological study of Mr. O.R. Dix. Every full day of searching through the







1. Layer of shale about 15 cm above the fossiliferous layer, in vertical section NNW–SSE, x 1; showing rippled surface (current direction NNW, to left) and buried ripples, apparently with a similar wavelength and direction.
2. Surface of a layer immediately below the one in Figure 1, x 1; showing trackway of small arthropod and short tracks which are probably feeding grooves. Collected by Mr. O.R. Dix.
3. Same as Figure 2, x 2.

material has yielded at least one valuable insect fossil per searcher (the author or Jacques van Dijk); layers known to be productive yielded about four insect fragments per worker-hour, in the case of an experienced worker.

Significance of the site

The fossil site on the farm Bella Vista, near Lidgetton, will remain important as the type locality of a female fructification, *Lidgettonia africana*, which, like the male fructification, *Eretmonia natalensis*, is now known in considerable detail, differing in this respect from the several other fructifications to which megaspores or microspores have not yet been found attached. In addition the site is already a fossil insect type locality (Riek 1976a: 769 and 779), and further fossil insect genera and species will be described from the site, the importance of which in this respect can be evaluated by considering the other Gondwana, and particularly African Palaeozoic, fossil insect sites.

Plumstead (1963) illustrated and discussed insect damage on fossil leaves, and discussed possible biotic interactions, particularly between insects and *Glossopteris* plants. She commented: "Winged insects of this age have not up to now been re-

Captions to Figures

Figure *Page 50*

4. *Glossopteris spp.*, x 1.
5. *Glossopteris* sp. from Figure 4 left, x 2,4 *(G. indica/ communis)*.
6. *Glossopteris* sp. from Figure 4 right, x 2,4.
7. *Glossopteris* sp., x 10; cf. *G. browniana*.
8. *Glossopteris* sp., x 1; bract-like, viewed from concave side.
9. Same as Figure 8, x 2.
10. *Glossopteris* sp., x 10; cf. *G. conspicua*.

Figure *Page 51*

11. *Lidgettonia africana*, x 1.
12. *Lidgettonia africana*, x 1.
13. Cupule of *Lidgettonia africana*, x 10.
14. *Plumsteadia* sp., x 5, and counterpart x 10 (inset).
15. *Eretmonia natalensis*, x 1.
16. *Vertebraria indica*, x 1.
17. *Buthelezia mooiensis*, x 5.
18. Bryophyte? (Hepaticae), x 5.
19. Spore?, x 10 and 25.
20. Hypha of fungus?, x 250; scanning electron micrograph of *Glossopteris* leaf.
21. Leaf with chewed margins and penetrated by ? root, x 1.
22. Leaf with chewed margins (right side and top right), x 1.
23. Leaf with lesion, x 5; ? insect damage.

Figure *Page 52*

24. *Glossopteris* leaf with pyritization, x 5; pyrites superficially covering carbonaceous cellular material.
25. Same as Figure 24, x 10.
26. *Glossopteris* leaf without cuticle, x 14, showing epithelial cells.
27. *Glossopteris* leaf with pyrites infilling, x 5.
28. Pyrites replica of *Glossopteris* cuticle (cf. figs. 24, 25), x *circa* 150; scanning electron micrograph, uncoated.
29. As Figure 28, x *circa* 150; epidermal cells at bottom left.
30. As Figures 28, 29, x *circa* 40; pyrites replica of cuticle viewed from within, and epidermal cells.

Figure *Page 53*

31. Small sphenopsid stem infilled with pyrites, x 40.
32. Small specimen as Figure 31, x 40, scanning electron micrograph, uncoated.
33. Same as Figures 31, 32, x 80, scanning electron micrograph, uncoated.
34. Sphenopsid stem, acetate peel, x *circa* 40; scanning electron micrograph of surface opposite to the acetate film, coated.
35. Same as Figure 34, x *circa* 360; showing bordered pits.
36. Same as Figure 34, x *circa* 360; showing scalariform thickening, probably tracheids.
37. Same as Figure 34, x *circa* 360; showing bordered pits.
38. Same as Figure 34, x *circa* 360; showing wall with numerous pits.
39. Same as Figure 38, x *circa* 600.

Figure *Page 54*

40. Sphenopsid stem, acetate peel, x 55; showing the different modes which reveal the cells, the cell walls appearing clear in the upper internode and dark in the lower internode, while the large cells of the node are not visible in a mounted peel, except under phase contrast.
41. Sphenopsid stem, acetate peel, x 55; showing cells revealed by diffraction from the unmounted replica on acetate film, with narrower cells on the right near the ridges of conducting tissue.
42. *Buthelezia mooiensis*, acetate peel, x 100; showing thicker middle of the leaf and cells on one side.
43. Sphenopsid stem, acetate peel of etched face of a transverse section, x 55; showing effect of deep etching.
44. As Figure 43, different specimen, x 55; showing effect of light etching.
45. *Glossopteris* leaf, acetate peel of etched face of transverse section of pyritized region, x 55.
46. Same as Figure 45, different specimen, x 55.
47. Spore from hydrofluoric acid digest, x 600.

Figure *Page 55*

48. Sphenopsid stem, etched face of a transverse section, x *circa* 40; scanning electron micrograph, coated (note supporting plastic on the right).
49. Same as Figures 48, x *circa* 400.
50. *Glossopteris* leaf, pyritized midrib, cracked and etched; scanning electron micrograph, x *circa* 250.
51. Coniferopsid stem, pyritized, broken open longitudinally, x 20.
52. Same as Figure 51, etched face, x *circa* 100; scanning electron micrograph
53. Same as Figure 51, different field, x *circa* 300.

Figure *Page 56*

54. Paraplecopteran wing (cf. *Mioloptera stuckenbergi* Riek), x 5; collected by Dr. G.H. Hickman.
55. ? Plecopteran nymph (exuvia), x 5; collected by Mr. O. Dix. Inset: fragment of same taxon? from HF digest.
56. Plecopteran wing *(Euxenoperla* Riek), x 5; collected by Mr. J. Oliver.
57. Homopteran (prosbolid) wing, x 5; collected by Mr. O. Dix.
58. Homopteran (? prosbolid) wing, x 5; collected by Miss J. Johns.
59–62. ? Homopteran wings, x 5; see also enlargements, Figures 70, 71.
63. Homopteran insect, x 4,5.
64. Hemipteran (Aleyrodid) cf. *Aleuronympha* Riek, x 5; see also enlargement Figures 73, 74.
65. Hemipteran ("Scale insect"), x 5; collected by Jacques van Dijk.
66–68. Insects represented by more than just a single wing, x 5; Figure 67. Coleopteran (cf. *Moltenocupes* Riek), see also enlargement, Figure 76 — this is the first known Permian beetle in Africa.

Figure *Page 57*

69. Same as Figure 63, x *circa* 9; showing stylet (passing behind a microsporangium), the characteristic, transversely ridged postclypeus, and legs with two rows of spines.
70. Same as Figure 61. (counterpart), x 10.
71. Same as Figure 60, x 10.
72. Same as Figure 65, x 10.
73. Same as Figure 64, x 10.
74. ? Aleyrodid hemipteran, ? earlier stage of the aleyrodid in Figure 73, x 10.
75. Same as Figure 67, x 10.
76. Unidentified arthropod fragment, c, x 10.
77. Conchostracan shell (cf. *Leaia)*, x 10; collected by David Stuckenberg.
78. Conchostracan shell, type B, x 5.
79. Fish scale, x 10.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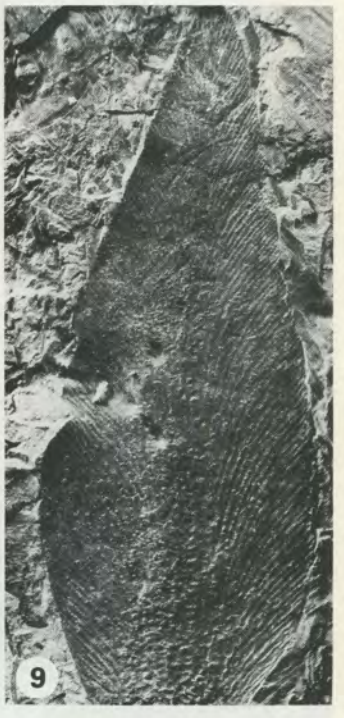
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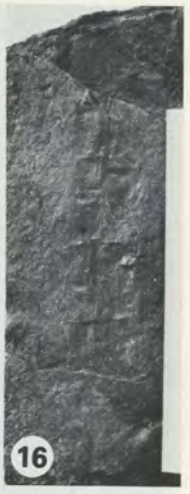
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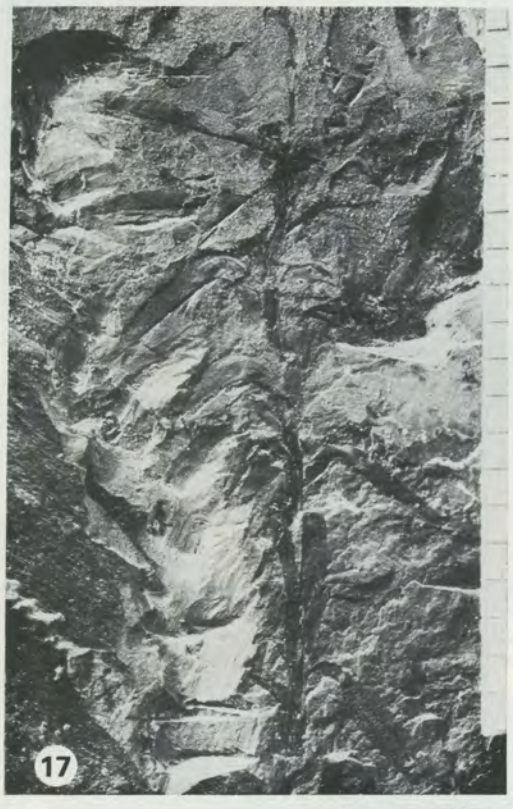
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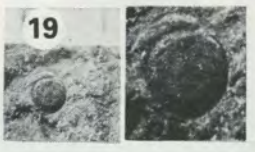
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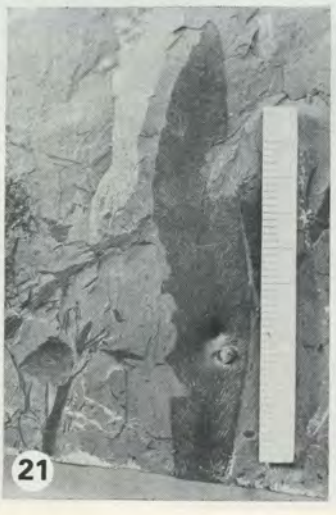
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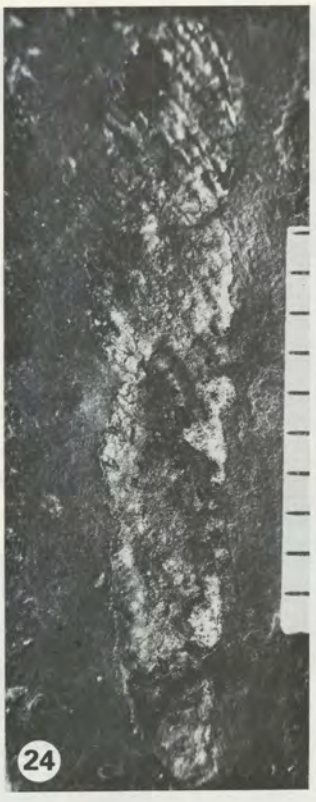
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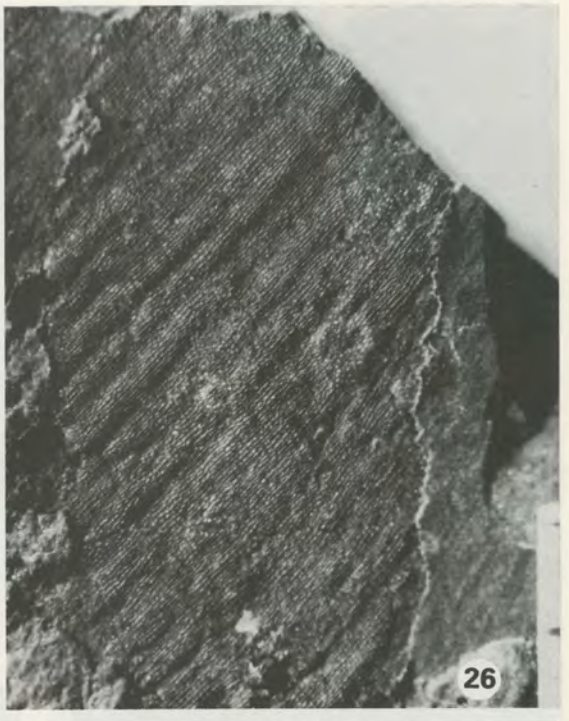
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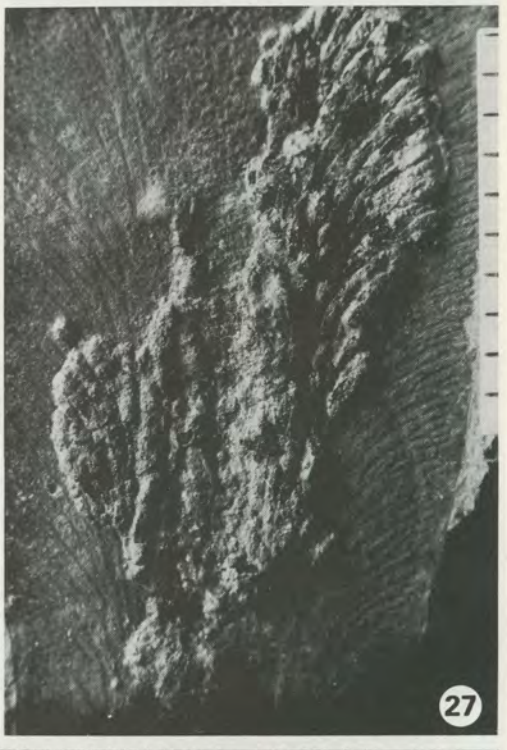
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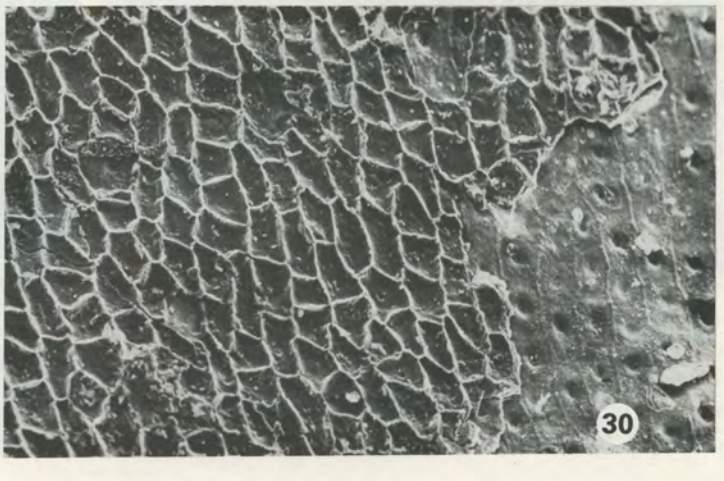
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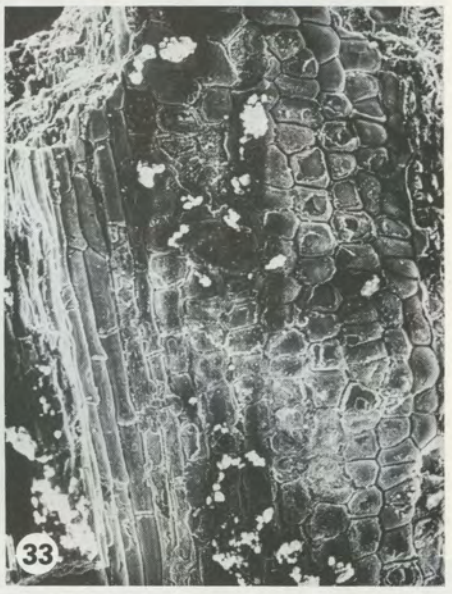
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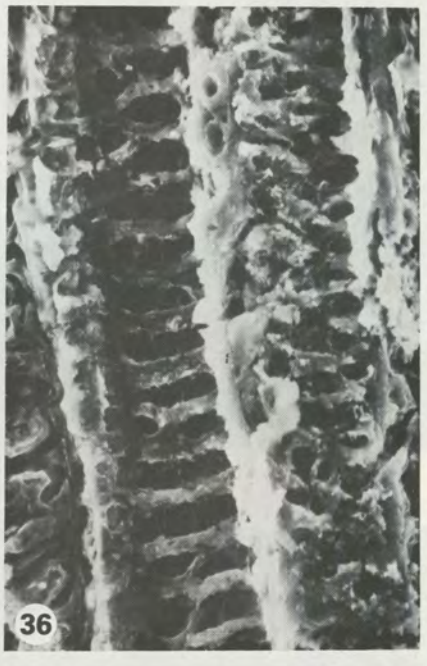
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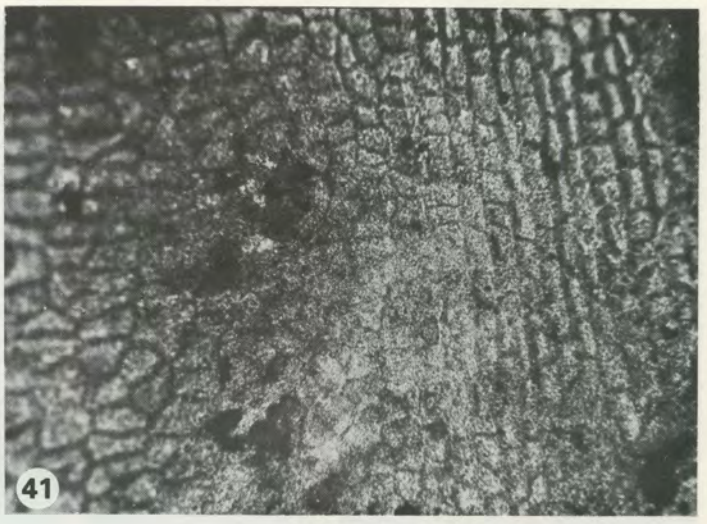
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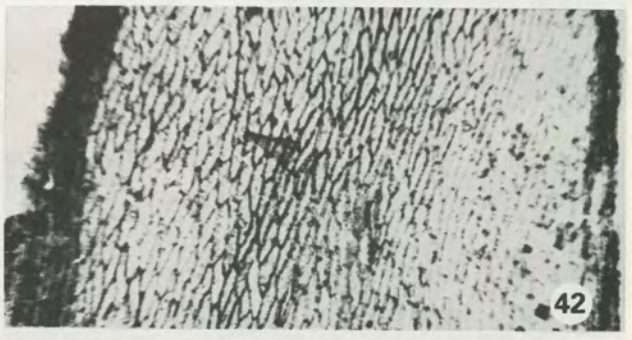
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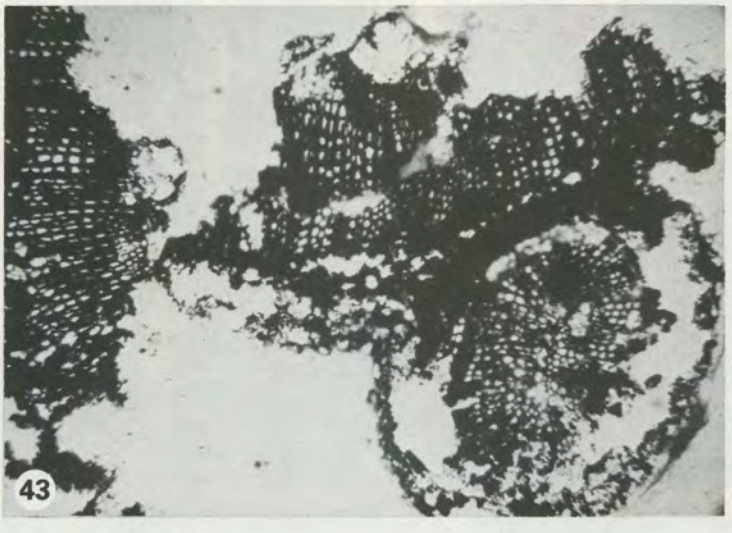
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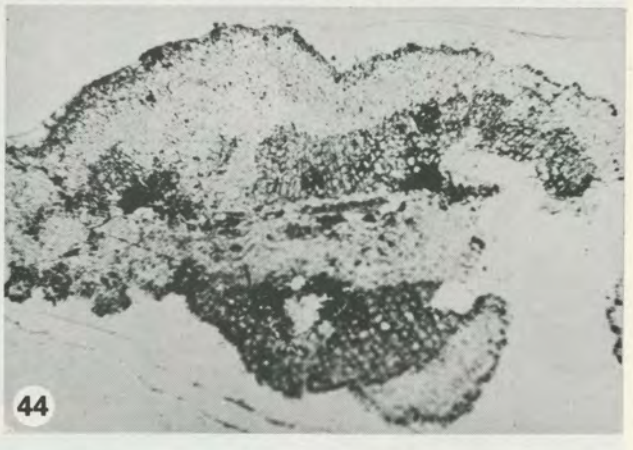
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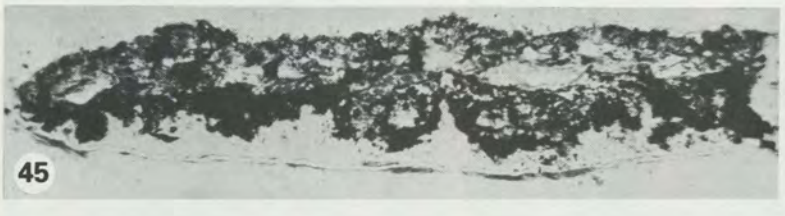
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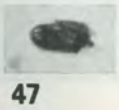
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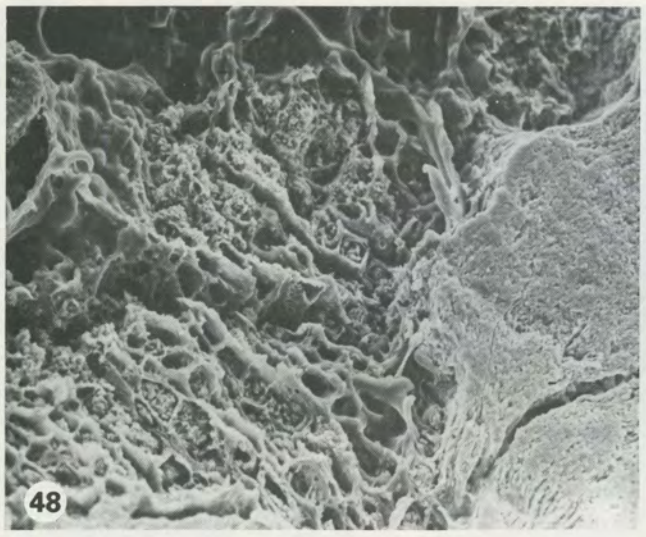
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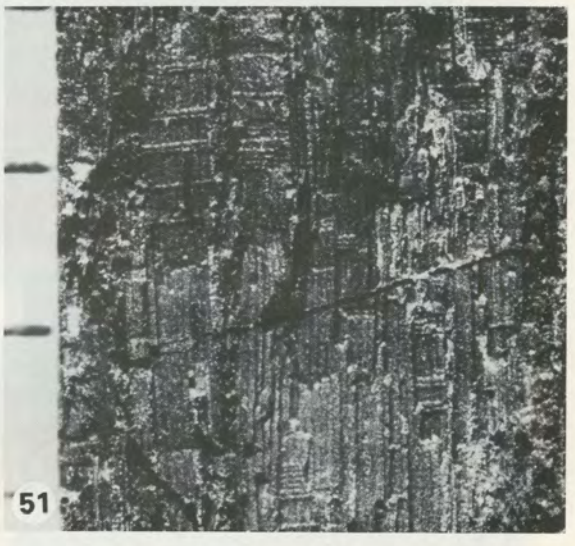
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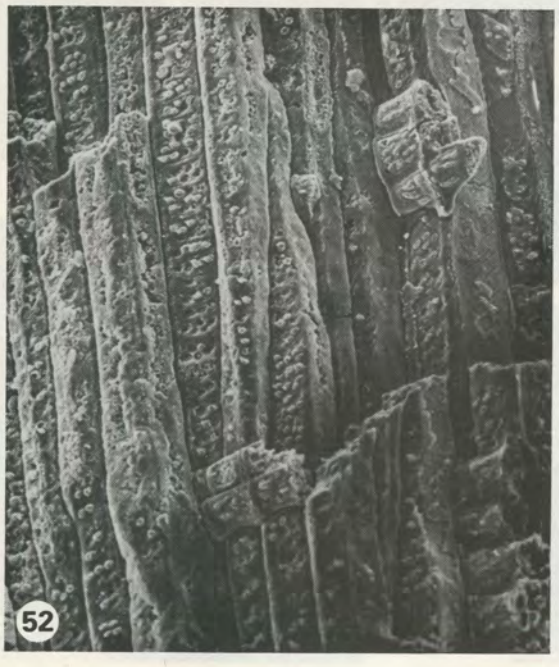
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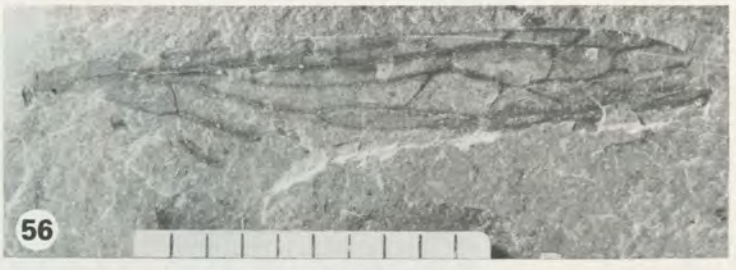
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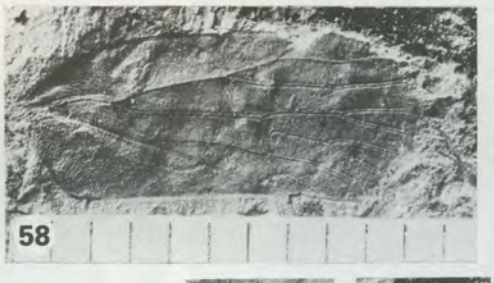
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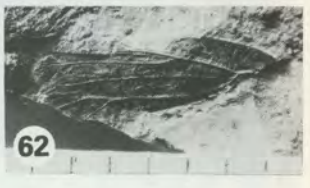
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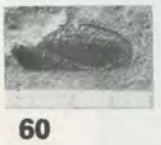
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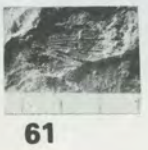
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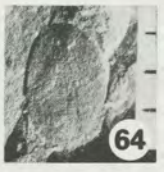
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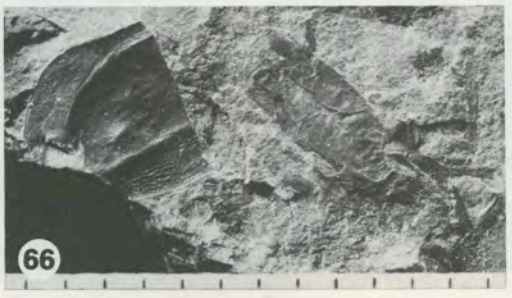
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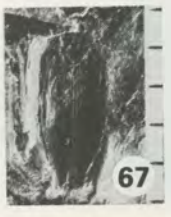
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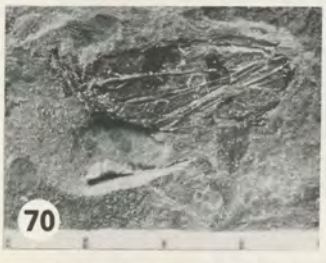
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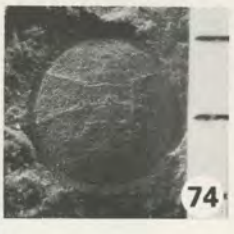
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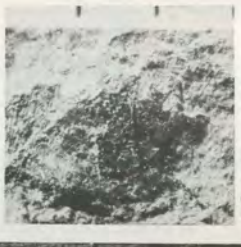
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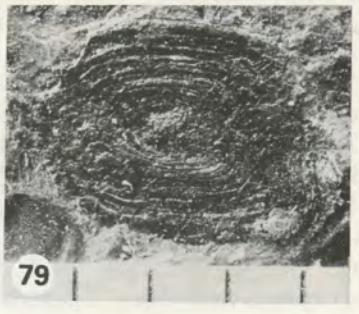
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TABLE 2

Comparison of the fossils at the Lidgetton Site with the fossils of possible stratigraphic significance at three sites in the Lower Beaufort

Lithostrata	Beaufort	Sites			
	Ecca	Lidgetton	Mt. West	Bulwer	Mooi River
Taxa					
Plantae					
Bryophyta					
Buthelezia (mooiensis)		+	—	—	+
Tracheophyta					
Sphenopsida					
cf. *Equisetites* (cf. *Neocalamites carreri)*		+	+	+	+
Sphenophyllum (speciosum)		—	+	+	+
Pteropsida					
Sphenopteris (alata)		+(fragments)	+ (? sp.)	+	+
Cycadopsida					
Pteridospermales					
Glossopteris indica		+	+	+	+
G. communis					
G. browniana		+ (cf.)*			+
G. conspicua		+ (cf.)*			+
G. sp.		+			— or few
Belemnopteris (elongata)		—	+	+	+
Lidgettonia (africana)		+	+		+
Plumsteadia sp.		+	+	?+ (1 specimen)	+
Eretomonia (natalensis)		+		+	+
Coniferopsida		+(pyritized)			+(silicified)
Cordaitales					?+(carbonized)
Animalia					
Arthropoda					
Crustacea					
A and B (cf. *Leaia)*		A B	A B	A	A B
Insecta					
Paraplecoptera (Liomopteridae)					
Mioloptera (stuckenbergi)		+	+	? Mioloptera	+
Plecoptera					
Euxenoperla (spp.)		+	? (fragment)		+
? Plecoptera					
Nymphs		+	+	?+	
Homoptera					
Aleuronympha (bibulla)		+ (? sp.)			+
Arthropoda (unclassified)					
C		C† (fig. 76)			

*For criteria see Lacey *et al.* 1975, Table 1

†Present at new locality at Balgowan.

corded from S. Africa. The difficulty in distinguishing a wing tracery from the reticulate venation of underlying and overlying leaves probably accounts for the paucity of the record and more detailed and determined hunting in the future should prove rewarding. That such insects existed contemporaneously with early Glossopteridae is proved by fossil impressions of wings found in formations of the same age in the Congo (Pruvost 1934), Falkland Islands (Halle 1912) and in Antarctica (Plumstead 1962)" (Plumstead 1963: 148–149). To the above could have been added Rhodesia (now Zimbabwe) (Zeuner 1955), Kashmir (Handlirsch 1906–1908), Brazil (Woodworth 1912, quoting Olivieri in litt. 1908, Carpenter 1930, Olivieri 1930, Petri 1945, Mezzalira 1948, this last not seen in the original — see Carpenter 1930 and Pinto 1972 for bibliography) and New South Wales (Tillyard 1917, 1921 and numerous other papers on the fossil insects of sites such as Belmont — see Riek 1976a for bibliography). Since 1963, 16 further African Palaeozoic insect sites have been discovered, of which eight, like Pruvost's Congo site and Zeuner's Rhodesian site, are represented by one specimen each — Loskop, Wagondrift, and Rondedraai, near Estcourt (Riek 1973), Emakwezini, near Empangeni (Riek 1976a), Matabola Flats, in Zimbabwe (Riek 1975b), Modderdrift and Krantz Poort in the southern Cape (McLachlan and Anderson 1977), and Kilburn dam-site, near Oliviershoek, where the author collected a wing fragment. The Matabola Flats is of Dwyka age with "apparently the oldest recorded insect in the Southern Hemisphere"; Modderdrift and Krantz Poort are Upper Dwyka; Hammanskraal, in Transvaal, with a collembolan and three insect

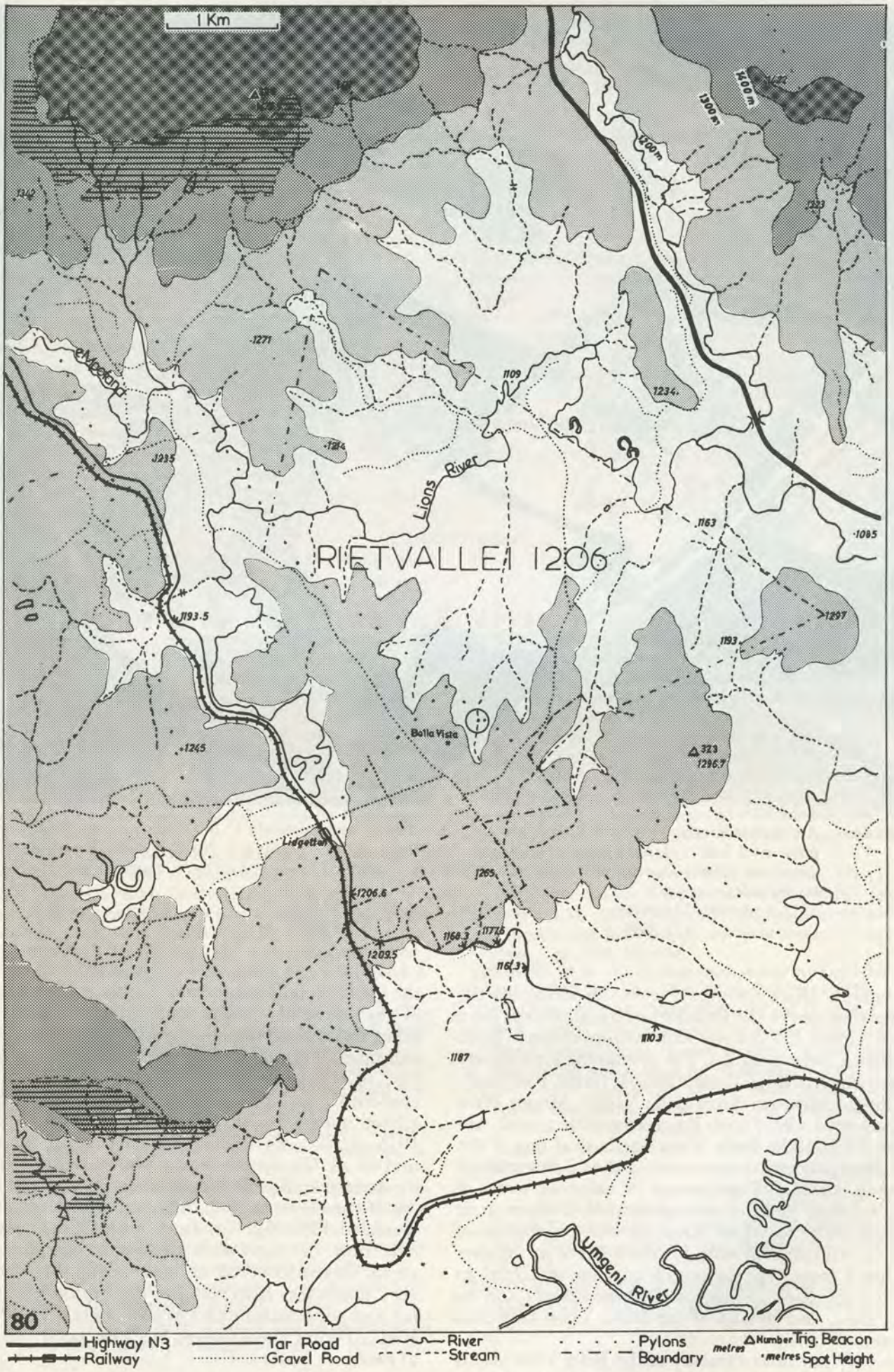

Figure 80. Map of Lidgetton region, 1 : 50 000; from Topographical Map 1 : 50 000 Series, 2930 AC Howick, with Beaufort strata from Geological Map 1 : 125 000 Series 2930 A (in preparation) indicated by horizontal hatching. The type locality of *Lidgettonia africana* Thomas 1958 is ringed.

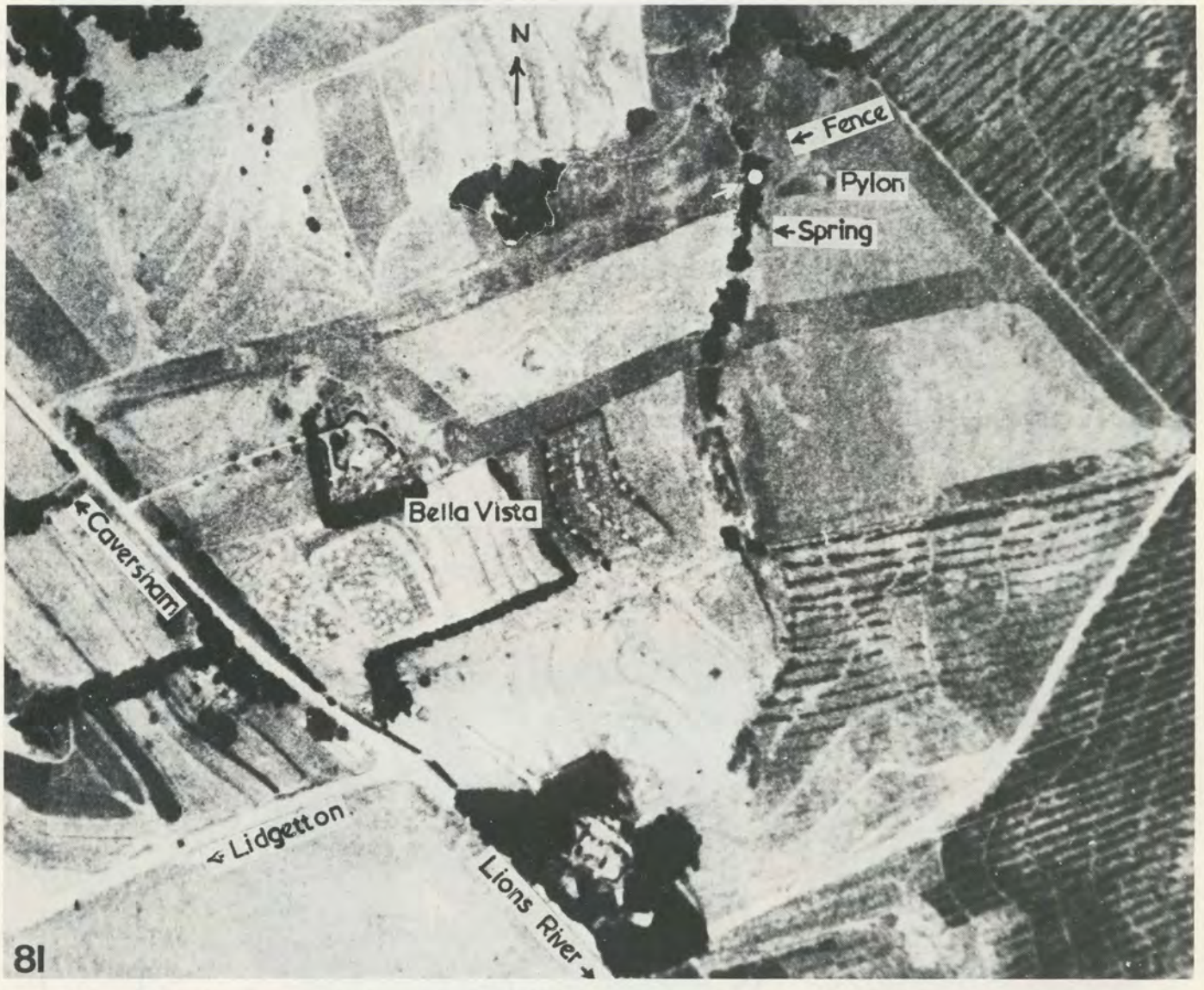

Figure 81. Aerial photograph of the farm Bella Vista, Lidgetton district, approximately 1 : 8 000; rephotographed from Trigonometrical Survey Aerial Photograph 1973, 1 : 50 000 Series, Job 717, Strip 6, Number 2680. The type locality of *Lidgettonia africana* Thomas 1958 is shown as a white spot indicated by a white arrow. For stereoscopic study the following pairs were used:

1973, 1 : 50 000 717 6 2680; 1963, 1 : 36 000 471 4 6800
717 6 2694; 471 4 6801

specimens (Riek 1976b,c), is in the Ecca; all the other sites are in the Beaufort of Natal, except for a Cape Upper Dwyka site with two specimens (B.W. Oelofsen, pers. comm.). The remaining six sites are Mooi River, Mooi River Quarry (farm Far End), Bulwer, Lidgetton (farm Bella Vista), Mount West (discovered 1975) and Balgowan (discovered August, 1976). The Bella Vista site is thus one of the six most productive sites among the 17 insect fossil sites in Africa of Permian age or older. In terms of the number of species represented, Lidgetton is second only to Mooi River in the Palaeozoic of Africa, and second only to Mooi River in number of fossil insect specimens of any age collected in Africa (cf. Riek 1975b, on Triassic insects and insect sites, and details of the Bella Vista collection presented here).

A very important feature of the Bella Vista site is the exceptionally good state of preservation of some of the material in comparison with that of most other Palaeozoic Gondwana sites, particularly African ones. This applies to the detail of some replicas, to the presence of cellular layers, including epidermis, and, particularly, to the presence of pyritized material with cellular detail (Van Dijk *et al.* 1975, 1978). Pyritized vascular tissue from the midrib of *Glossopteris* leaves shows detail such as the presence of well-preserved scalariform thickening of the elements (fig. 50; Van Dijk, Hobday and Tankard 1978, fig. 8j). In August 1976 similar pyritization of *Glossopteris* leaves and sphenopsid stems was discovered at Wagondrift, but there is very much less material and preservation of cellular and subcellular detail is not as good as at Bella Vista. Poorer pyritization has also been observed at Estcourt (since 1979).

CONCLUSIONS

1. The fossil site discovered at Bella Vista in 1917, near Lidgetton, besides its importance as type locality of *Lidgettonia africana* Thomas 1958, has a considerable flora and extensive fauna, largely insect and largely new, as revealed by studies since 1974 by the present author and associates.
2. Some of the Bella Vista fossils, particularly pyritized material, is exceptionally well preserved when compared to other Gondwana Palaeozoic fossils, and warrants detailed study.
3. Studies of the Bella Vista site, and of a number of new Lower Beaufort sites in Natal, have provided a basis for biostratigraphic and palaeoecological comparisons; there is a clear need for early study and publication of the fossil floras and faunas of individual sites in the Karoo deposits, as well as compilations from many sites such as Anderson's (1975) — thus far only Indian Gondwana sites appear to have received much detailed attention. Studies of this kind are intended for sites readily accessible from Pietermaritzburg, where material will be housed in the Natal Museum.

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THE OCCURRENCE, ORIGIN AND STRATIGRAPHIC SIGNIFICANCE OF BONE-BEARING MUDSTONE PELLET CONGLOMERATES FROM THE BEAUFORT GROUP IN THE JANSENVILLE DISTRICT, CAPE PROVINCE, SOUTH AFRICA

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ABSTRACT

The lack of useful lithostratigraphic markers in the Beaufort Group in the southern Karoo Basin has focused attention on the biostratigraphy of the sediments. As a result a more refined scheme of biostratigraphic classification is now possible which may prove useful in fixing the stratigraphic position of the uranium mineralized horizons. The most important mineralized horizon in the Beaufort West area (contains about 90 per cent of all known uranium occurrences) is associated with the *Pristerognathus/Diictodon* assemblage zone, but the way in which this relates to the important uranium occurrences farther east, between Graaff-Reinet and Jansenville, is uncertain because of the lack of biostratigraphic control.

Vertebrate remains have recently been found in mudstone pellet conglomerates in Beaufort channel sandstones along the Bullrivier in the Jansenville District, in an area that is extensively mineralized. The sandstones were deposited as point bar sands within a meandering river system flowing towards the north-east. The rivers drained a dry, arid to semi-arid alluvial plain and were characterized by fluctuating discharge and periods of low or negligible flow. These conditions promoted flood scour and fill activity and the deposition of internal mudstone pellet conglomerates. Hydrodynamic considerations suggest that estimates of bone transport velocity from their hydrodynamically equivalent quartz sphere is of limited value and can seldom, if ever, be applied to fossil bone accumulations.

Identification of the bones from the conglomerates indicates that they belong to the Dinocephalia biozone and not the overlying *Pristerognathus/Diictodon* zone. This suggests that the lower part of the Beaufort succession (formerly the *Tapinocephalus* zone) extends farther east than previously thought, and that the main mineralized horizon in this area occurs lower down in the succession than that around Beaufort West.

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INTRODUCTION

Uranium exploration in the upper Permian sediments of the Beaufort Group in the southern part of the Karoo Basin (west of longitude 25°E) has been handicapped by the lack of regional stratigraphic guides. The relationship between mineralized areas in different parts of the basin is a major problem: do they occur at a similar stratigraphic level or at different stratigraphic levels? The lack of useful stratigraphic markers has focused attention on the biostratigraphy of the sediments with the result that a more refined scheme of biostratigraphic subdivision is now possible for the *Tapinocephalus* and *Cistecephalus* zones (Keyser and Smith 1978). These are the two lowermost zones in the Beaufort succession and the most important from the point of view of uranium mineralization. Although the scheme has only been applied to the

area between Sutherland, Beaufort West and Aberdeen, reconnaissance studies indicate that it may be possible to extend it farther east.

Dinocephalians have always been regarded as diagnostic of the lower and middle part of the *Tapinocephalus* zone (Kitching 1977); a fact that has been incorporated into the new biostratigraphic scheme which recognises the following biozones from the base upwards: (1) Dinocephalia; (2) *Pristerognathus/Diictodon;* (3) *Tropidostoma;* (4) *Aulacephalodon;* and (5) *Daptocephalus* (about to be changed to the *Dicynodon lacerticeps* zone). These zones may prove useful in fixing the stratigraphic position of mineralized horizons, especially as they appear to correspond with broad lithological divisions defined essentially on the changing ratio of sandstone to mudstone. For example, the most important mineralized horizon in the Sutherland, Beaufort West and Aberdeen areas coincides with the *Pristerognathus/Diictodon* zone and this in turn fixes the position of a thick (up to 150 m) sandy horizon, known as the Paalhuis Member of the Abrahamskraal Formation (Turner 1979). The base of this sandy horizon, which includes the Poortjie sandstone (Rossouw and De Villiers 1953), the Rietkuil sandstone and possibly the Rystkuil sandstone, contains something like 90 per cent of all known uranium occurrences. However, the way in which this mineralized horizon relates to the important uranium occurrences farther east, between Graaff-Reinet and Jansenville, is uncertain because of the lack of adequate biostratigraphic control.

Vertebrate fossil remains have recently been discovered in Beaufort sandstones along the Bullrivier in the Jansenville District (fig. 1) in an area that is extensively mineralized. Identification of the fossil material indicates that the lower part of the Beaufort succession (formerly the *Tapinocephalus* zone) extends much farther east than previosuly thought (Kitching 1973), and that the main mineralized horizon in this area occurs lower down in the succession than that around Beaufort West. Regional studies suggest that this part of the Beaufort succession was deposited mainly by high sinuosity meandering rivers (Turner 1978). The sandstones along the Bullrivier fit this regional pattern, and on the basis of their sedimentary properties and comparison with modern depositional environments, provide a means of interpreting the conditions under which they and the bone-bearing mudstone pellet conglomerates were deposited.

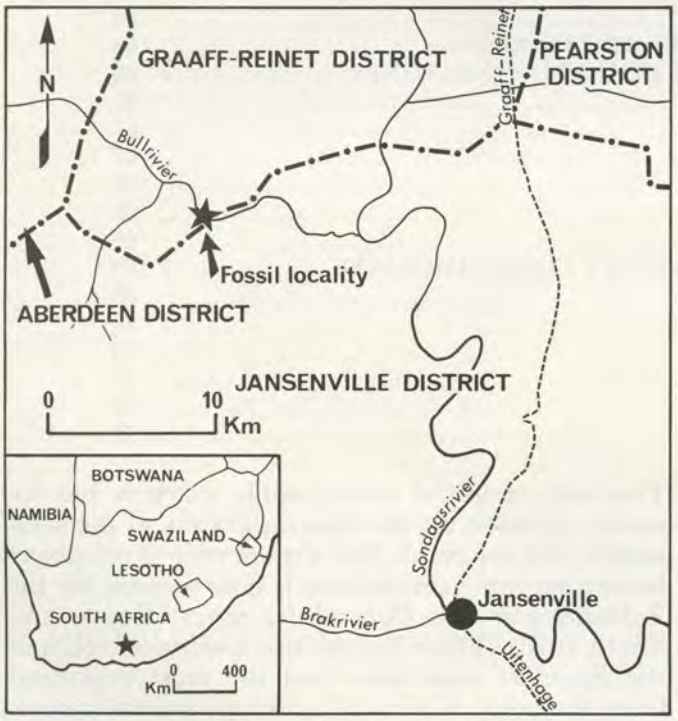

Figure 1. Map showing location of fossil site.

SEDIMENTOLOGICAL SETTING

Beaufort Group sediments in the southern part of the Karoo Basin cover an area of about 25 000 km^2, attain a maximum thickness of 2 700 m and consist mainly of sandstones and mudstones. A systematic upward decrease in the ratio of these two lithologies, together with changes in their sedimentary properties and comparison with modern depositional environments, enables the succession to be divided into low sinuosity channel, high sinuosity channel and floodbasin facies associations (Turner 1978). The facies associations are believed to represent the proximal, intermediate and distal components of an extensive fluvial depositional system which built out from a distant source to the south and west.

Uranium mineralization is only significantly developed in the upper part of the high sinuosity channel facies association where the ratio of mudstone to sandstone is about 4 to 1. The facies association is characterised by fining-upward sequences consisting of a basal scoured surface of low relief generally incised into mudstone, overlain by intraformational conglomerate, sandstone, siltstone and mudstone. In places mudstone is missing and the sequence is terminated by siltstone. The intraformational conglomerate consists predominantly of mudstone clasts, although siltstone clasts, reworked calcareous concretions, bone fragments and plant material are present locally. The sandstones are fine-grained, lenticular, and range from 1 to 24 m in thickness. Internally they are structured by horizontal lamination, cross-bedding (both trough and planar types with foresets directed to the north and east) and ripple cross-lamination. No preferred arrangement of these structures is discernible in the sandstones, although ripple cross-lamination tends to be most common in the finer-grained sandstone and siltstone higher in the sequence, and may include ripple drift cross-lamination. Current-rippled surfaces are common and confirm bimodal currents flowing to the north and east. The mudstones are maroon and bluish-grey, and contain calcareous concretions, red and green mottled horizons, thin sandstones and silstones, which are commonly ripple cross-laminated, and desiccation cracks.

The fining-upward textures and sedimentary

structures resemble the high sinuosity meandering stream model of Allen (1965, 1970) and Visher (1972). Thus the intraformational conglomerate overlying the scoured surface at the base of the sequence is interpreted as a channel lag derived from scouring of the floor and cutbank of the channel. The sandstone records deposition on the sloping surface of a point bar — the sequence from horizontally laminated and cross-bedded sandstone lower down to ripple cross-laminated sandstones higher up corresponds closely with point bar development in meandering streams in response to

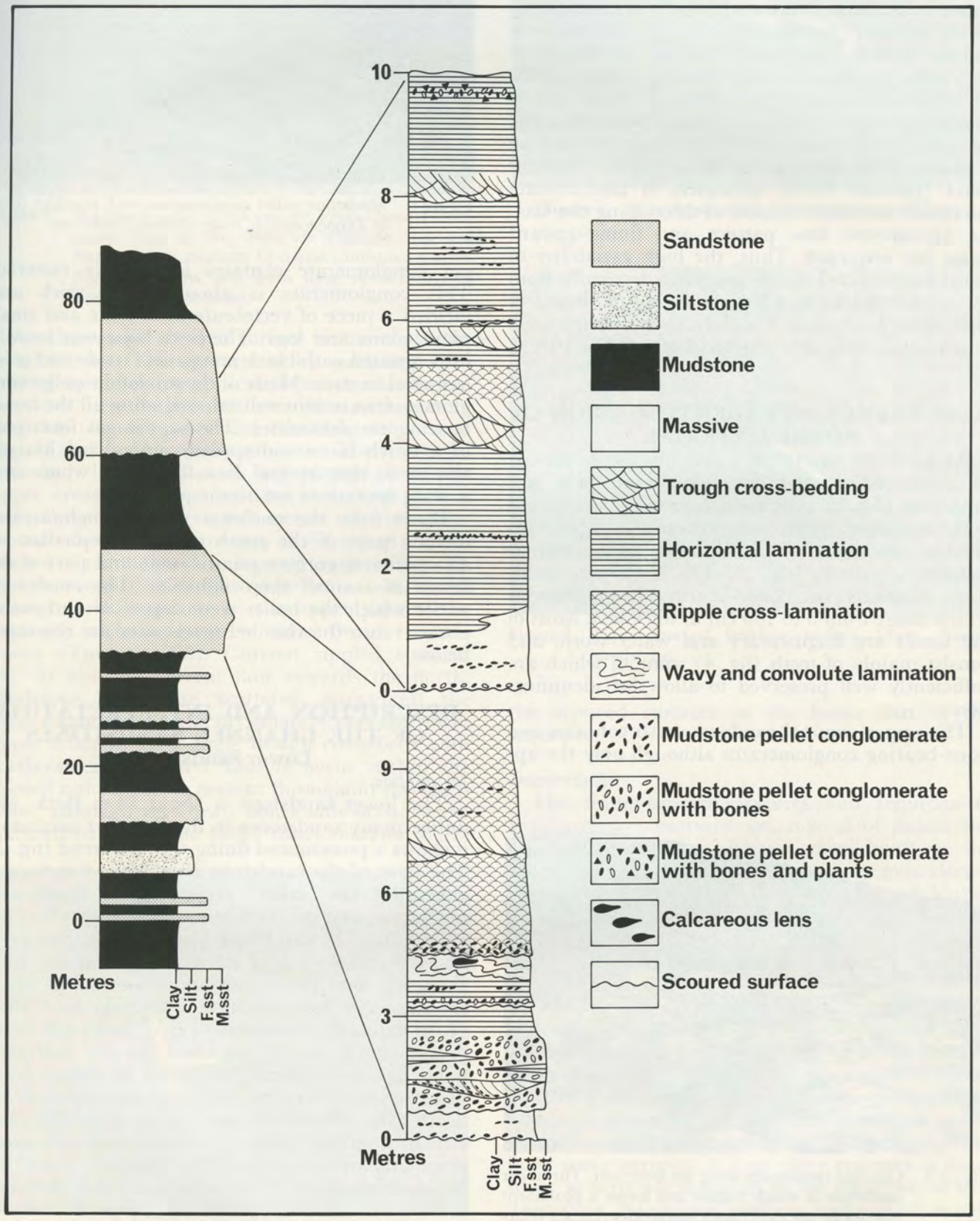

Figure 2. Generalized vertical section of the Beaufort Group sediments along the Bullrivier showing fining-upwards channel sandstone sequences and distribution of bone-bearing mudstone pellet conglomerates.

declining bed shear stress as currents moved obliquely across the bar (Allen 1970). As the point bar accreted laterally, it became overlain by overbank fines, deposited mainly from suspension and subject to periodic desiccation. However, the classic fining-upward meander point bar model of Allen (1965) is seldom developed, probably because of the flashy (unsteady flow pattern) nature of the streams (locally simulates characteristics of braided low sinuosity streams) and the degree of curvature of the meander bends (Turner 1979). Modern studies indicate that tight or gently curved bends are unable to develop a strongly asymmetric flow pattern in which maximum flow velocities are confined to the outer cutbank part of the meander bend (Jackson 1975). Meanders of intermediate curvature are more capable of developing the classic asymmetric flow pattern and fining-upward point bar sequence. Thus, the high variability of point bar channel sands and their departure from the classic fining-upward trend in the Beaufort succession is attributed mainly to the complex geometry of the meander pattern (Turner 1978, 1979).

OCCURRENCE AND IDENTIFICATION OF FOSSIL MATERIAL

At the fossil site the Beaufort sediments consist of about 80 m of interbedded sandstone and mudstone (fig. 2). The fossil material is associated with mudstone pellet conglomerates within two channel sandstones (fig. 3) forming part of fining-upward sequences (fig. 2). The lowermost sandstone contains two bone-bearing conglomerates which range from 6 to 100 cm in thickness. Most of the bones are fragmentary and water worn, and consist mainly of teeth (fig. 4) some of which are sufficiently well preserved to allow for identification.

The upper channel sandstone also contains two bone-bearing conglomerates although only the upper conglomerate contains identifiable material. This conglomerate is about 11 cm thick and yielded a piece of vertebrate limb bone and small plant stems and logs. The limb bone was heavily impregnated with black manganese oxide and is locally radioactive. Many of the mudstone pellet conglomerates are mineralized, including all the bone-bearing conglomerates. The sandstones form part of a much more widespread mineralized horizon similar to that around Beaufort West, where trial mining operations are now in progress.



Figure 3. Channel sandstones along the Bullrivier. The upper sandstone is much thicker and forms a prominent cliff above the river. Both sandstones contain bone-bearing mudstone pellet conglomerates and are locally mineralized.



Figure 4. Mudstone pellet conglomerate with reptilian tooth cf. Dinocephalian, lower channel sandstone.

Bones from the mudstone pellet conglomerates include part of the tooth of a dinocephalian cf. *Anteosaurus*, a gorgonopsian canine and part of the femur of a small therocephalian. The conditions under which the bones were deposited and incorporated into the channel sandstones are discussed below.

DESCRIPTION AND INTERPRETATION OF THE CHANNEL SANDSTONES

Lower Sandstone

Description

The lower sandstone is about 13 m thick, and unlike many sandstones in the Beaufort succession it shows a pronounced fining-upward trend (fig. 2). The base of the sandstone is a scoured surface of generally low relief, incised into bluish-grey mudstone, and overlain by a mudstone pellet conglomerate. The sandstone above the conglomerate and scoured surface is massive and contains a few scattered mudstone clasts. At about 0,5 m above the base is a scoured surface overlain by a thick (1 m) laterally persistent (40 m) mudstone pellet conglomerate. Mudstone clasts are flat and elongate (fig. 5) and locally display a pronounced imbrication with their long axes inclined towards the north-east. Within the conglomerate are thin, lenticular interbeds of horizontally laminated sandstone and trough-shaped scour and fill structures, in which the base of the scour and the foresets are lined with small mudstone clasts, particularly at the upcurrent end. Foreset orientation is towards the north-east.

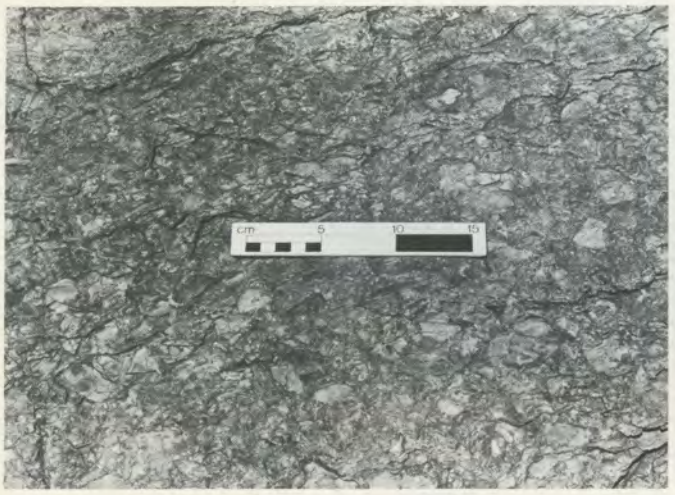

Figure 5. Mudstone pellet conglomerate, lower channel sandstone. Most of the clasts are elongate, flattened discs set in a medium to coarse sandstone matrix. Bone fragments and teeth have been recovered from the conglomerate.

Another major scoured surface occurs above the conglomerate. This is overlain by sandstone containing the following vertical sequence of sedimentary structures: horizontal lamination with parting lineation (fig. 6); wavy and convolute lamination (fig. 7) and ripple cross-lamination. The wavy and convolute laminated unit is separated from the ripple cross-laminated unit by a scoured surface and mudstone pellet conglomerate. A chocolate-brown calcareous lens occurs at the top of the deformed zone, below the scoured surface (fig. 2). The dominance of ripple cross-lamination in the finer-grained sandstone in the upper part of the sequence is characteristic of many Beaufort sandstones (Turner 1978). Current rippled surfaces (fig. 8) indicate current flow towards the north. Mudstone flakes are scattered throughout the rippled sandstones, and occasionally concentrate in ripple troughs. Low angle trough cross-beds with north-easterly directed foresets occur within the rippled unit. Pyrite is present throughout the sandstone, although vertebrate bones only occur in the mineralized mudstone pellet conglomerates above the scoured surfaces in the lower part of the sequence.



Figure 6. Parting lineation on sandstone bedding surface, upper channel sandstone.

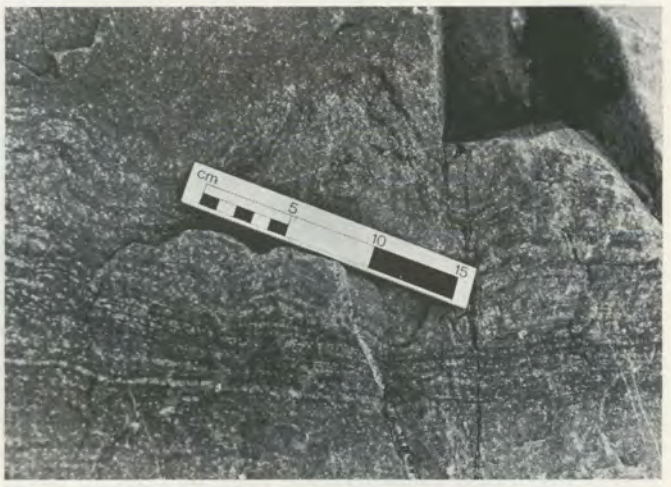

Figure 7. Wavy lamination, lower channel sandstone.



Figure 8. Ripple-marked bedding surface, lower channel sandstone.

Interpretation

The fining-upward textures and sequence of sedimentary structures are typical of fluvial deposits, and show a strong resemblance to the coarse member of the high sinuosity meandering river model (fig. 9) of Allen (1965) and Visher (1972). The lower scoured surface and mudstone pellet conglomerate are attributed to erosion of the floor and cutbank of the channel as it migrated laterally across its floodplain, and the incorporation of the eroded material into a channel lag gravel (Allen 1964, 1970). The structureless sandstone at the base of the sequence implies rapid dumping of sediment from decelerating floodwaters at a rate too fast for sorting processes to cope with. The scoured surface and thick mudstone pellet conglomerate above suggests a prolonged period of flood scour activity; at least three episodes of flood scour activity are apparent in the sequence, as evidenced by the scoured surfaces and mudstone pellet conglomerates. Trough-shaped scour and fill structures probably filled in channel floor depres-

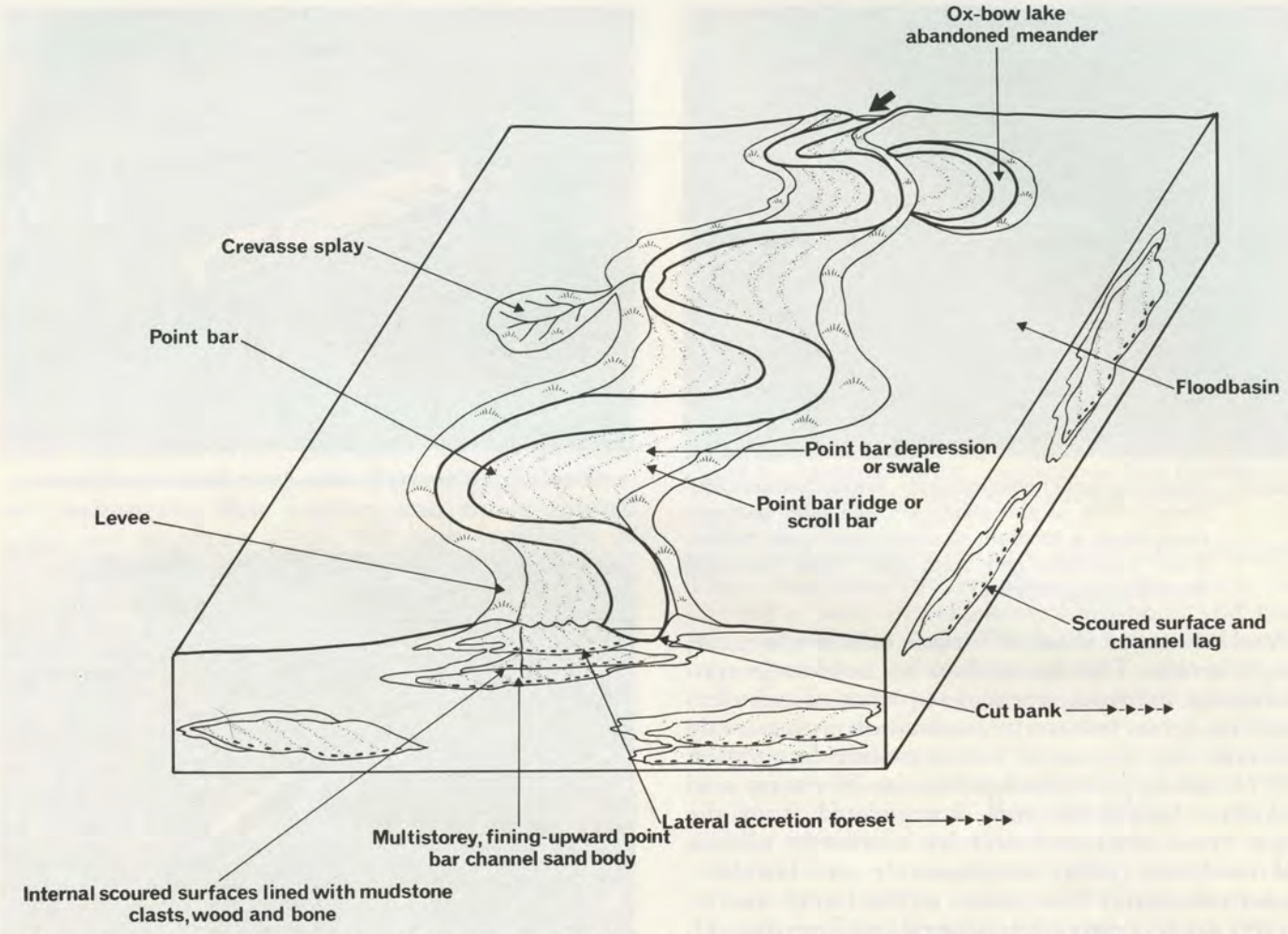

Figure 9. Depositional model of an idealized meander belt fluvial system showing various kinds of fluvial depositional units.

sions immediately following flood activity and scouring, whilst the horizontally laminated sandstone lenses may have been deposited as transitional or low flow regime plane beds (Harms *et al.* 1975).

The scoured surface overlain by horizontal laminations and wavy and convolute laminations suggests a similar pattern with flood scour followed by waning flow and the gradual emergence of the depositional surface. Liquefaction of the sediment due to expulsion of water during late falling stage (Reineck and Singh 1973) could explain the wavy and convolute lamination. Similar deposits have been described from channel sequences by Coleman (1969). Renewed flooding and scour was followed by the development of lower flow regime ripple bedforms during falling water stage, interrupted by the development of sinuous to curve-crested megaripples giving rise to the trough cross-beds in the middle of the rippled unit. The decay of vegetation growing within, and buried with the sediment (cutbank erosion), uses up the available oxygen and forms a reducing environment in which sulphides (pyrite) form. Coleman (1971) notes pyrite forming on the rootlets of living cypress trees along the lower Mississippi River at depths of up to 30 cm.

Upper Sandstone

Description

The uppermost sandstone is about 20 m thick and can be traced laterally for more than 1 km. It is a fine- to medium-grained, moderately sorted, arkosic wacke, with a basal scoured surface of low relief overlain by a mudstone pellet conglomerate. The sandstone immediately above the conglomerate is massive and contains a few scattered mudstone pellet conglomerate lenses, some of which are mineralized. The overlying sandstone shows the following sequence of sedimentary structures (fig. 2): horizontal lamination; trough cross-bedding; ripple cross-lamination; and horizontal lamination with locally developed trough cross-bedding (fig. 10) and scour surfaces associated with mudstone pellet conglomerates. The sequence is dominated by horizontal laminations in contrast to most fining-upward point bar sequences described from modern and ancient meandering river systems (Reineck and Singh 1973). Mudstone pellet conglomerates occur throughout the sandstone, although vertebrate bones are restricted to the thicker conglomerate horizons at the base of the sandstone and in the middle of the sandstone where the bones were found associated with oxidized plant material.



Figure 10. Horizontal lamination overlain by small scale trough cross-bedding, upper channel sandstone.

Interpretation

The general arrangement and type of sedimentary structures within the sandstone correspond with the deposits of modern meandering river channels (Bernard and Major 1963, Allen 1965, 1970). The scoured surface and mudstone pellet conglomerate at the base of the sandstone probably record erosion of the floor and cutbank of the channel during high discharge events, and the deposition of the eroded material as a lag gravel conglomerate (Arnborg 1958). The overlying sandstone has many modern counterparts in the deposits of point bar sands (fig. 9). The sequence from structureless to horizontal lamination, trough cross-bedding and ripple cross-lamination records deposition from decelerating currents during waning flood conditions, as the dominant bedform changed from upper flow regime plane bed to lower flow regime high intensity megaripples and low intensity ripples. Horizontal laminations in the upper part of the sequence may represent upper or lower flow regime plane bed conditions (Harms *et al.* 1975), with flucuating energy levels during decelerating flow resulting in the local development of megaripples. The scoured surfaces and associated mustone pellet conglomerates in the lower part of the horizontally laminated unit probably record minor flood scour events, similar to those described by Picard and High (1973) from modern ephemeral flood streams. The possibility that some of the horizontal laminations developed from downstream migration of megaripples (dunes) overriding the coarser material of the megaripple front (McBride *et al.* 1975) is suggested by their close association with trough cross-bedding.

ORIGIN OF THE BONE-BEARING MUDSTONE PELLET CONGLOMERATES

General

Mudstone pellet conglomerates occur at the base of channel sandstones, where they rest upon mudstone, and within the sandstones. The basal mudstone pellet conglomerates differ from the internal ones in that they are laterally more persistent and associated with major scoured surfaces. They are analogous to the channel floor lag concentrates of modern meandering rivers derived from the erosion of the bank and floor of the channel as it migrates laterally across its own floodplain (Allen 1964, 1965).

The internal bone-bearing mudstone pellet conglomerates probably represent scouring and reworking by floodwaters of consolidated mud layers; the lateral persistence and thickness of the conglomerates implies a major episode of flood scour activity. Modern river systems show that point bar deposition is episodic and composed of more than one flood event (Reineck and Singh 1973). As floodwaters subside the more elevated portions of the river bed may become exposed, leaving behind pools of standing water in hollows and depressions (e.g. swales) away from the thalweg (line of maximum depth). Within such hollows and depressions clays settle out from suspension to form a mud layer, which with further drying may consolidate and form a mudcracked surface. With renewed flooding, scouring of the bed occurs and the mud is incorporated into a mudstone pellet conglomerate along with vertebrate bones and plants picked up by the floodwaters. In some cases turbulence on the downstream side of bones leads to the formation of a scour pit within which the bone accumulates and is then buried on falling river stage. In this situation the bone acts as a bedform modifying the flow, but if buried and preserved it is not normally associated with mudstone pellet conglomerates unless it acts as a sediment trap. Most bones in the conglomerates are too small to act as efficient sediment traps, whilst the larger bones such as ribs and limbs are hydrodynamically unsuitable for trapping because of their shape. These would tend to align in the direction of least resistance to flow with their long axes parallel to flow and the larger end (if present) pointing upcurrent (Blatt *et al.* 1972). In river channel desposits the majority of particles are orientated parallel to flow, particularly when the flow is heavily-laden with sediment, such as during flood events. The fact that many of the larger bones are not associated with highly concentrated mudstone pellet conglomerate zones also argues against sediment trapping by bones as an important mechanism in the formation of mudstone pellet conglomerates. The small size of the clasts and their fragile nature further suggests that they were not transported very far prior to deposition.

Climatic Factors and Contemporary Analogues

Repeated flood scour activity depends on flood periodicity which is largely determined by climatic factors (Friend *et al.* 1979). The presence of desiccation cracks, calcareous concretions of pedogenic origin (Turner 1978), colour mottling, and "desert roses" composed of pseudomorphs of calcite after gypsum (Keyser 1966) in the Beaufort, point to prolonged periods of exposure and desiccation. Comparison of pedogenic calcareous concretions with Quaternary calcretes of similar pedogenic origin (Goudie 1973) provides useful clues to the climatic conditions prevailing during Beaufort times.

The formation of pedogenic carbonate implies not only prolonged exposure, but a warm to hot climate (mean annual temperature of 16–20 °C) and a seasonally distributed rainfall (mean annual rainfall of 100–500 mm) but without any marked seasonality. The maximum monthly rainfall must be less than 25 per cent of the mean annual precipitation for calcrete to form; dry areas with one season of very heavy rainfall tend towards ferricrete and so far no sign of pedogenic iron enrichment has been found in the Beaufort. Other lines of evidence indicative of a warm, dry and possibly arid climate are: (1) the paucity of preserved plant remains (Kitching 1977) and the apparent dwarfism shown by *Glossopteris* leaves from the lower Beaufort (Smith 1978); (2) the catastrophic mass mortality of fish in an ephemeral pool (Keyser 1966); (3) the introduction at this time of new faunal and floral elements consistent with increasing temperatures (King 1963); (4) the presence of a widespread arid zone (desert) to the north of the Beaufort depositional site (King 1963); and (5) the palaeomagnetic data which places this part of Africa during Beaufort times between latitude 30 and 40°S (Creer *et al.* 1973). All this is consistent with rivers draining a dry, arid to semi-arid alluvial plain characterized by fluctuating discharge and periods of low or negligible flow. Such conditions would tend to promote flood scour and fill activity (Leopold *et al.* 1964), intraformational breaks and mudstone pellet conglomerates and the multistorey build-up of channel sands, a feature that is characteristic of most Beaufort channel sandstones (Turner 1979).

Similar conditions occur today in the southern part of the Karoo, between Pearston and Sutherland, which experiences climatic conditions not much different from those envisaged during deposition of the Beaufort sediments (mean annual temperature 15–21°C, and mean annual rainfall 120–380 mm). The rivers draining this part of the Karoo show both braided and meandering characteristics (e.g. Leeurivier) and deposit predominatly fine sand during flood events. The sands are structured mainly by horizontal lamination and ripple cross-lamination and may provide useful contemporary analogues for the Beaufort Group sandstones which are also dominated by these structures. Rivers in humid areas do not show the same frequency of scour and fill because of the removal of fines by perennial flows, leaving the more resistant coarser material behind (Leopold *et al.* 1964).

Derivation and Preservation of Bones

The bones in the mudstone pellet conglomerates are probably derived from upstream sources and from undercutting and reworking of the channel bank deposits during channel migration. Transportation and reworking of the bone in this manner would tend to concentrate the most resistant material such as teeth and compact bone fragments. Some of the bones show suncracking, flaking, rounding and fragmentation consistent with long distance and often turbulent transport, interspersed with periods of subaerial exposure. In most fluvial settings, especially in arid climates, movement of particles is generally intermittent so that weathering during transport may be important.

The similarity in size of the bone (less than 5 cm in length) and its resistant nature suggest that it may represent hydrodynamic accumulations of the chemically most resistant material. Whilst this appears to be true for some of the bone-bearing conglomerates, others contain larger, less resistant bones such as limb bones and ribs (fig. 11). This suggests more locally derived material, probably



Figure 11. Reptilian rib in mudstone pellet conglomerate, lower channel sandstone.

from animals inhabiting the channel and channel bank environments (proximity to water and vegetation). Additional factors, such as the amount of surface weathering to which the bone was subjected prior to its inclusion in the conglomerate, may be important. For example, most bones break down quickly when subjected to surface weathering, especially under dry climatic conditions such as those envisaged for the Beaufort depositional site, unless they are buried quickly or protected from weathering by carbonate concentrations. In the Beaufort both of the latter processes seem to have operated in promoting preservation of bone. Carbonate concentrations are most common in the channel bank (levee) deposits, which contain the best preserved fossil material, as noted by Hotton (1967) and Smith (1978). The bone in some cases serves as a nucleus for $CaCO_3$ concretionary formation with the result that many well-preserved specimens are found within the concretions from channel bank environments. In addition carbonate formation implies alkaline soils which will also favour preservation of fossils (Behrensmeyer 1975). Judging by the internal characteristics of the channel sandstones and the frequent preservation of sandstone palaeosurfaces in overbank environments (Turner 1979), flood periodicity was high and rapid burial and preservation of fossils common.

Hydrodynamic Factors

Bones and clasts carried by the flow will be deposited immediately the flood waters begin to subside and the current is no longer competent to carry the coarsest fraction of its load (bedload). The presence of mudclasts and bones above flood scour surfaces and their association with the coarsest fraction of the sand supports this interpretation. Factors which may increase the depositional potential are: (1) spill resistance and energy loss due to the chaotic deformation of flow around mudclasts and bones in transport (Leopold *et al.* 1964); and (2) the retardation of flow at the bed following the initial deposition of the coarse sand fraction of the bedload (Koster 1978). However, this simple picture of deposition in stream channels according to size grading is not realistic in many cases. For example, deposition often occurs in zones of local flow divergence where conditions are *non-uniform,* in contrast to most field and laboratory studies which have been mainly concerned with uniform flow conditions.

In the present study one important factor which must be explained is the fragile nature of many of the mudclasts and the short distance of transport prior to deposition, despite their association with water-worn bone derived from much farther away. Within alluvial channels preferential sites for the accumulation of bone and mudclasts occur due to local changes in flow conditions induced by bed topography. Hydrodynamic studies show that velocity increases with decrease in depth in the flow direction, whereas the velocity decreases with increasing depth in the flow direction (Allen 1970, Middleton and Southard 1977). These changes are fundamentally linked to two factors, channel shape and bed configuration (Allen 1964). The presence of hollows and depressions on the channel floor of sufficient relief constitute bed configuration which may locally affect flow conditions and the transport and deposition of particles (Leopold *et al.* 1964), assuming channel width and shape are constant. On encountering a hollow or depression lined with mudclasts, the flood waters will suddenly decelerate and tend to deposit the coarsest fraction of their load, including bones, along with the mudclasts as a local lag concentrate (Allen 1964). The sudden deceleration of the floodwaters may be accompanied by a change from upper to lower flow regime conditions and a hydraulic jump. Flume studies have shown that clasts are often deposited where this change takes place, and since these constitute the coarse fraction of the load, lower stage flows are incapable of modifying the deposit, which becomes "fossilized". Under these conditions transport of mudclasts would be short-lived, thereby increasing their potential for preservation. Deposition occurs at such sites because of the loss of competency of the flow to transport all its load due to factors such as particle size, shape and density.

In a situation like this, flume studies on bone transport dynamics and deposition are of limited value. Estimates of transport velocity for bones from their hydrodynamically equivalent quartz grains suffer from the problem that the velocity component at a given point varies with depth. Thus, in principle it is not possible to estimate palaeovelocity from grain or bone size information alone, particularly when mean conditions are specified, since velocity is a probabilistic phenomenon dependent on the frequency and intensity of eddy impingement on a spatially varied bed (Church 1978). The data used by Behrensmeyer (1975) for this purpose was based on experimental work with bed material in a non-dilated state, without imbrication or packing, and with the grains in the uppermost layer available for transport. This condition is seldom found in nature and is not directly applicable to velocity estimates in river channels without introducing probability statements or empirical coefficients into the data base. Two other problems are apparent in attempts to estimate bone transport (as with sands and conglomerates). The first is that what one is measuring is the transport velocity of the bones at their site of deposition and the hydrodynamic conditions are not necessarily the same for deposition as for entrainment (velocity required for initiation of grain movement). Grain size-velocity diagrams such as those used by Behrensmeyer (1975, fig. 8) are based on data for grain entrainment, not deposition, and to date there has been little study devoted to the subject of grain movement once entrainment begins. However, recent studies indicate that sands are deposited at values for the dimensionless shear stress (θ) of 5 per cent lower than those for entrainment. Moreover, since the bones occur only in mudstone pellet conglomerates indicative of major flood events, the floodwaters may have been more heavily laden with sediment than usual, thereby increasing their competence and potential for producing poorly sorted bone debris. Some conglomerates contain bones of varying sizes (including limb bones up to 25 cm long), despite the preponderance of teeth. The absence of bones in the sandstones deposited between major flood events is consistent with the notion of increased competency of the flows (from increased sediment load and/or velocity) necessary for the transport of bone and its inclusion in the conglomerates, the bones coming either from within the channel or from undercutting of the channel bank. In this respect major flood events associated with the conglomerates may have two important effects, they promote channel erosion and undercutting of the bank, and they may be the cause of death among the animal population inhabiting the channel and near-channel environments. Under the dry, arid to semi-arid conditions prevailing at the time, drought and flash floods may have been common occurrences. Periods of drought would tend to concentrate the animals along major water courses, making them easy victims of flash floods. Because of the sparse plant cover and the fact that vegetation capable of colonising and stabilizing the inter-

fluve hillslopes had not yet evolved (Schumm 1968), run-off and sediment yield were exceptionally high. Under these conditions major flood events of the type likely to cause mass drownings would occur frequently — normal flood recurrence interval for most rivers is 2,33 years (Leopold *et al.* 1964). The lack of vegetation beyond the confines of the channel environment may similarly be reflected in the almost complete absence of plant and vertebrate remains in distal floodplain sediments, far removed from the major active channels.

These same general conditions occur today east of Beaufort West where the Salt River drainage system is at present experiencing the effects of a prolonged drought. The drainage system is over 25 km wide and during exceptionally heavy rains the entire system and parts of the surrounding flats are flooded, although normally flow is confined to a narrow central channel.

Current velocities during deposition of the mudstone pellet conglomerate can be estimated from the grain size of the sandstone matrix which averages about 0,2 mm in diameter (medium-grained sand). As discussed earlier, this provides only an "order-of-magnitude" estimate of the flow and suggests that for shallow flows up to 40 cm deep a velocity of about 50 cm/s is required for grain transport (Blatt *et al.* 1972, Harms *et al.* 1975). For deeper flows, velocities up to 100 cm/s are required and during flood events this may increase to between 180 and 300 cm/s (Leopold *et al.* 1964). This is well within the values estimated by Behrensmeyer (1975) for transport of large mammalian bones, including those of hippos and elephants.

CONCLUSIONS

Bone-bearing mudstone pellet conglomerates occur in channel sandstones of the Beaufort Group along the Bullrivier in the Jansenville District, in an area that is extensively mineralized. The sandstones were deposited as point bar sands within a meandering river system flowing towards the north-east. Mudstone pellet conglomerates within the sandstone represent episodes of flood scour and fill activity which were promoted by the flashy (unsteady) nature of the flow and the arid to semi-arid climate. Deposition occurred immediately flood waters began to subside because of the inability of the currents to carry the coarsest fraction of their load (bedload). Depositional potential may have been further increased by: (1) deformation of flow around mudclasts resulting in spill resistance and energy loss; (2) retardation of flow at the bed due to deposition of the coarsest fraction of the bedload; (3) local flow divergence and the development of non-uniform flow conditions; and (4) local changes in flow conditions induced by bed topography.

Estimates of transport velocity for bones from their hydrodynamically equivalent quartz grains are of limited value because: (1) velocity varies with depth; (2) velocity is a probabilistic phenomenon dependent on eddy impingement on a spatially varied bed; (3) experimental work has been carried out on bed material in a non-dilated state which is seldom found in nature; (4) transport velocity is not necessarily the same for deposition as entrainment (initiation of movement); and (5) flood waters are generally heavily-laden with sediment, thereby increasing their competency. Current velocities based on the grain size of the mudstone pellet conglomerate matrix indicate flows of about 50 cm/s for depths of up to 40 cm, and 100 cm/s for deeper flows. During floods, this would probably increase to between 180 and 300 cm/s.

The bone-bearing mudstone pellet conglomerates represent the only known occurrences of vertebrates in this area and include part of the tooth of a dinocephalian cf. *Anteosaurus*, a gorgonopsian tooth and part of the femur of a small therocephalian. The presence of material characteristic of the Dinocephalia biozone has important stratigraphic implications and suggests that the lowermost part of the Beaufort succession, formerly assigned to the *Tapinocephalus* zone, extends much farther east than previously thought (Kitching 1977) and that the uranium mineralization in this area occurs lower down in the Beaufort succession than that around Beaufort West, which belongs mainly to the overlying *Pristerognathus/Diictodon* zone. The presence of a dinocephalian humerus in Beaufort Group strata near Somerset East suggests that the Dinocephalia zone may extend even farther to the east (Keyser 1978), although systematic collecting has still to be carried out in this part of the basin before this can be firmly established. It is also uncertain whether the *Pristerognathus/Diictodon* zone is represented in this area; the only evidence to date is a single pristerognathid and a gorgonopsian specimen with non-Dinocephalia zone affinities. There is considerable scope here for further study.

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FOSSIL HYAENIDAE FROM THE MAKAPANSGAT LIMEWORKS DEPOSIT, SOUTH AFRICA

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ABSTRACT

The remains of three hyaena species have been recovered from the Makapansgat Limeworks deposit. A common small form, *Hyaena hyaena makapani*, and a rare large form, *Pachycrocuta brevirostris*, were recovered from Member 3 (Lower Phase 1 grey breccia). The rare *Crocuta crocuta* was recovered from Member 4 (Upper Phase 1 breccia), and was the only hyaena from this horizon.

Abundant cranial and dental material of *H. h. makapani* facilitated comparisons with extant and fossil forms to confirm its identification as a subspecies of the extant striped hyaena. Despite morphological differences in the skull and teeth, *H. abronia* from Langebaanweg is confirmed as its likely ancestor. Some deciduous teeth of *H. h. makapani* are described and the eruption sequence of permanent cheekteeth deduced. *P. brevirostris* appears to be the largest fossil hyaena from Africa, showing affinities to *P. bellax* from Kromdraai. *C. crocuta* is similar to the extant form and the fossil forms from East Africa. As in the East African deposits, *C. crocuta* appears relatively late in the succession.

The hyaena material has limited value in site faunal correlations for dating purposes, but does not contradict the palaeomagnetic age estimate of more than 2,9 My for Member 3 (grey breccia) (Partridge 1979).

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INTRODUCTION

The family Hyaenidae is well represented in most of the Transvaal cave deposits (Toerien 1952, Ewer 1954, 1955a, Hendey 1974a, Collings *et al.* 1975). The Makapansgat Limeworks deposit is no exception; from there Toerien (1952) described the remains of a small hyaena similar to the extant striped hyaena, *Hyaena hyaena*, which he called *H. makapani*, as well as a large hyaena which he called *Crocuta* cf. *brevirostris*. Since then additional material of both species has been recovered. This material was briefly reported in Collings *et al.* (1975), together with an account of a third species attributed to *C. crocuta*.

The taxonomic and phyletic relationships of the Plio/Pleistocene Hyaenidae have been the subject of many papers (Ewer 1955b, 1967, Kurten 1956, Ficcarelli and Torre 1970, Hendey 1974b, 1978). The close relationship between the Makapansgat small hyaena and the extant striped hyaena is generally acknowledged, and in a review of the African fossil hyaenids Ewer (1967) concluded that they were only subspecifically different. Ewer (1955b) suggested that the Pliocene hyaena *H. namaquensis* might be a possible ancestor of *H. h. makapani*, but this was later considered unlikely (Ewer 1967). The late Miocene/early Pliocene deposit at Langebaanweg has yielded much hyaenid material including the species *H. abronia*, which has been proposed as the likely ancestor of the Makapansgat form and the extant striped hyaena (Hendey 1978).

This paper presents a detailed account of the hyaena material reported in Collings *et al.* (1975), and it covers all the cranial material on hand at the Bernard Price Institute for Palaeontological Research in 1972. The relationships of the hyaenas and their significance is discussed primarily in relation to finds elsewhere in Africa.

MATERIAL AND METHODS

The fossil material was mechanically prepared, mostly by staff preparators at the Bernard Price Institute, using hammer and punch. A few specimens were also prepared by the author using a "Vibro-tool" and emery disc.

With the exception of the carnassials, where additional measurements were taken, two measurements were taken on all teeth. These were the mesiodistal and buccolingual distances, corresponding to the length (L) and breadth (B) respectively. The measurements were taken at the level of the cingulum, and the mean of three measurements was recorded each time. Use was made of ratio diagrams in comparisons between species, and in particular those based upon percentages.

In references to the stratigraphy of the Limeworks the sequence and terminology of Partridge (1979) and Brain (1958) is followed.

RESULTS AND DISCUSSION

Hyaena hyaena makapani

Except for specimen M244 from Member 2 (basal red mud), all *H. h. makapani* specimens were recovered from Member 3 (Lower Phase 1 grey breccia) (J.W. Kitching, pers. comm.).

Skull (table 1; figs. 1, 2)

The skull is morphologically similar to the two extant *Hyaena* species, but is smaller than either *H. hyaena* or the fossil *H. abronia* (table 2).

TABLE 1

Skull measurements of *Hyaena hyaena makapani* from the Makapansgat Limeworks deposit

Dimension	Sample	Mean (mm)	Std. Dev. (mm)	Range (mm)
Condylobasal length	5	200,4	6,5	194,0–210,0
Zygomatic width	1	138,0		
Palate width	4	63,3	3,4	60,3–68,1
Interorbital width	6	45,3	2,9	40,4–47,8

TABLE 2

Comparison of mean skull measurements: *Hyaena hyaena makapani, Hyaena abronia* and extant *Hyaena hyaena*

Species	Condylobasal length (mm)	Zygomatic width (mm)	Interorbital width (mm)
H. h. makapani [a]	200,4	138,0	45,3
H. abronia [b]	217,0	*c.* 145,0	47,7
H. hyaena [b]	211,0	*c.* 146,0	44,0

a = composite reconstruction (figs. 1, 2) based on M 2530, M 299, M 8348
b = Hendey (1974b)

A comparison of *H. h. makapani* with the illustration and description of *H. abronia* in Hendey (1974b) revealed a few cranial differences. In *H. h. makapani* the palate (fig. 2a) is relatively shorter and narrower, and there appears to be a slightly longer precanine diastema. In lateral view (fig. 1a) the angular process of the mandible in *H. h. makapani* is not bulbous as it is in *H. abronia*, and it has a slightly dorsally directed distal end. In all these features *H. h. makapani* is similar to the striped hyaena.

Permanent dentition (table 3)

The dental formula 3/3:1/1:4/3:1/1 = 34 is identical to that in *H. hyaena* and *H. brunnea* (Ewer 1973).

With the exception of the robust caniniform I^3, the incisors are small teeth and are seldom recovered. Of the 28 canines recovered one upper and two lower were still in their alveoli. Upper and lower canines could be distinguished because upper canines are straighter and more elliptical in cross-section. Premolars, both loose and in their alveoli, were the most common hyaenid teeth recovered. Upper and lower premolars could be distinguished because lower premolars have their cusps arranged in a straight line parallel to the jaw ramus, whereas upper premolars have the first cusp offset lingually.

The cusp terminology used for the carnassials is taken from Gromova (1968), and is illustrated in Figure 3. The talonid of M_1 has a mean value of

TABLE 3

Measurements of teeth of *Hyaena hyaena makapani* from the Makapansgat Limeworks deposit

Tooth	Dimension	Sample	Mean (mm)	Std. dev. (mm)	Range (mm)
I^1	length	2	3,1		2,8–3,4
	breadth	2	4,4		
I^2	length	3	4,6		4,1–5,6
	breadth	3	6,6		6,2–7,2
I^3	length	6	7,5	0,4	7,1–8,0
	breadth	6	8,9	0,6	8,2–9,7
C	length	12	13,0	0,5	12,3–14,0
	breadth	12	9,1	0,5	8,3–9,9
P^1	length	5	6,4	0,4	6,0–7,0
	breadth	5	5,9	0,5	5,4–6,6
P^2	length	21	14,6	1,1	12,6–16,1
	breadth	20	9,4	0,5	8,6–10,2
P^3	length	29	19,6	1,1	16,5–21,1
	breadth	31	12,6	0,7	11,0–13,8
P^4	length	28	28,8	1,1	25,8–31,2
	breadth	26	17,1	1,1	15,6–19,5
	length metastyle	26	10,5	0,5	9,3–11,5
M^1	length	16	5,6	0,5	4,7–6,6
	breadth	16	12,8	0,7	12,0–14,1
I_3	length	4	5,6	0,2	5,4–5,8
	breadth	4	6,2	0,1	6,1–6,3
C	length	15	12,9	0,6	11,6–13,9
	breadth	15	9,8	0,5	8,9–10,5
P_2	length	13	13,6	0,7	11,9–14,8
	breadth	14	8,1	0,6	7,2–9,1
P_3	length	20	17,9	0,7	16,7–19,1
	breadth	21	10,8	0,5	9,7–11,5
P_4	length	23	19,2	0,7	17,4–20,4
	breadth	21	10,9	0,5	9,7–12,1
M_1	length	17	20,8	0,9	19,1–22,0
	breadth	19	10,1	0,6	9,3–11,0
	length talonid	15	4,3	0,3	3,7–4,7

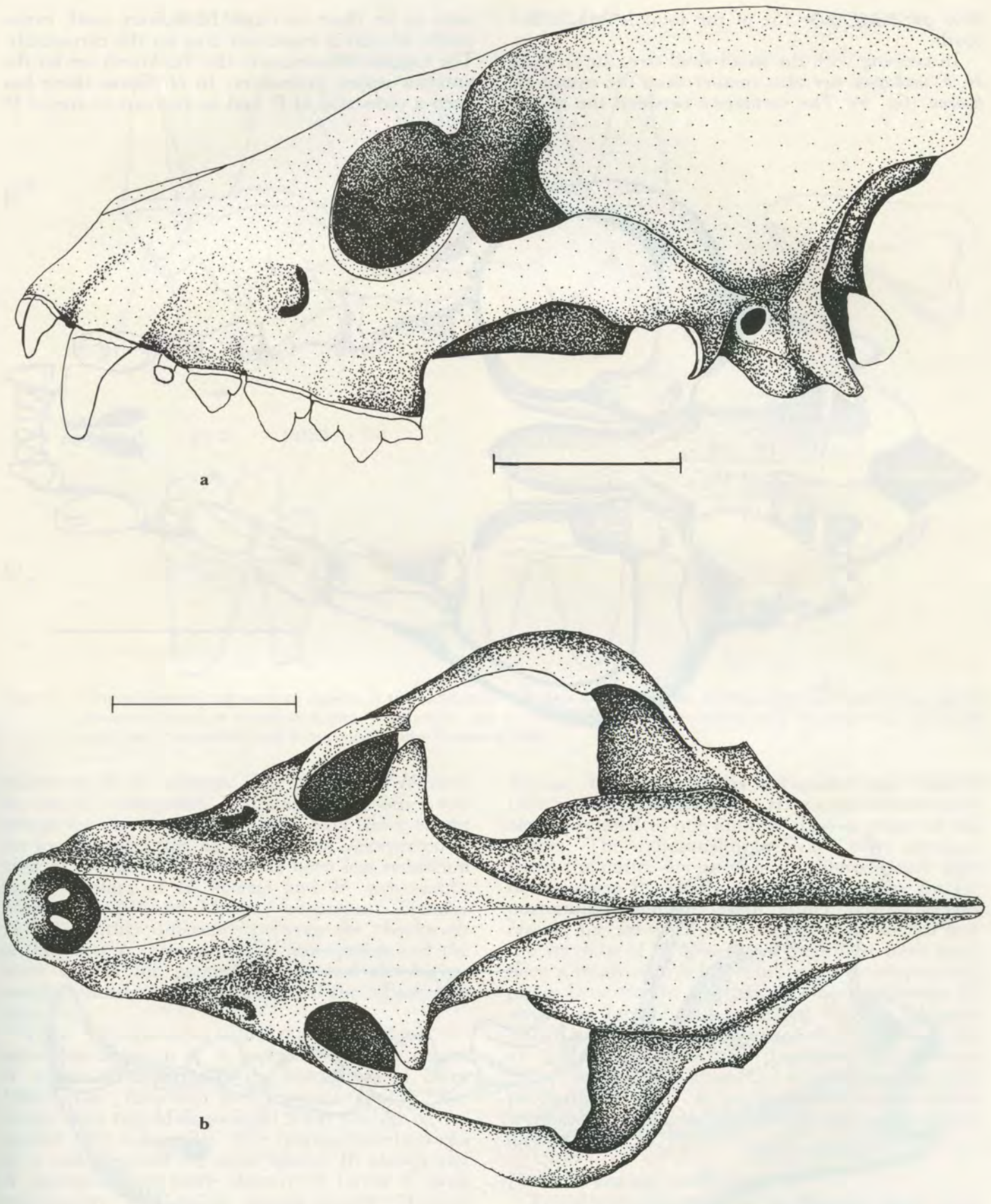

Figure 1. Skull of *Hyaena hyaena makapani* showing (a) lateral and (b) dorsal aspects (scale bar = 5 cm). (Composite reconstruction based mainly on M 2530, M 8348 and M 299.)

20,6 per cent (n = 15) of the total length of the tooth.

In keeping with the small skull size, the teeth of *H. h. makapani* are also smaller than the extant *H. hyaena* (fig. 4). The similarity between the two is seen to be close in terms of various tooth ratios (table 4); this is especially true for the carnassials. The biggest differences in the cheekteeth are for the anterior upper premolars. In *H. hyaena* there has been a reduction of P^1 and an increase in size of P^2

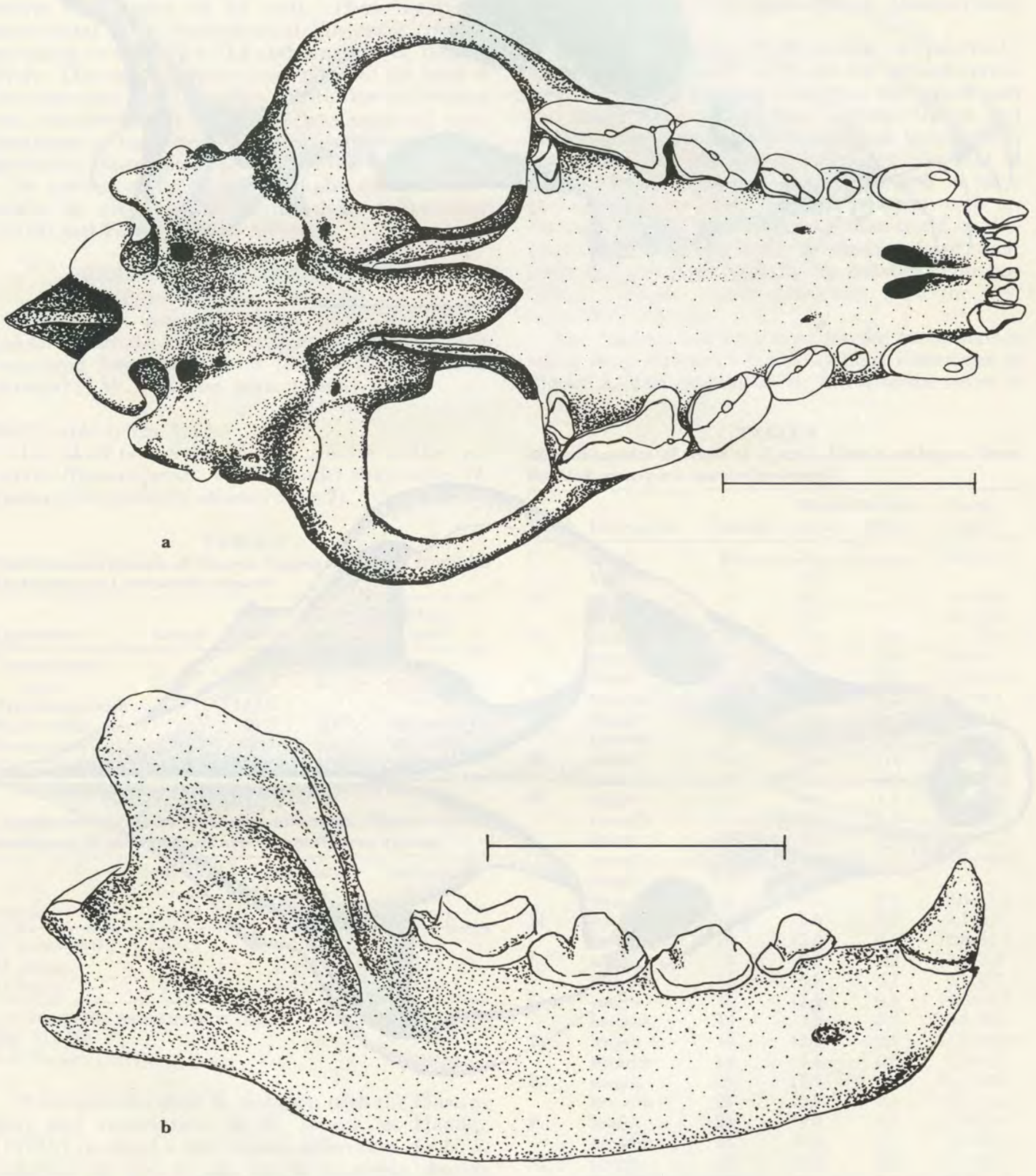

Figure 2. Reconstructed skull and mandible of *Hyaena hyaena makapani* showing (a) ventral aspect of skull and (b) lateral aspect of mandible (scale bar = 5 cm). (Skull reconstruction as in Figure 1; mandible based on M 262.)

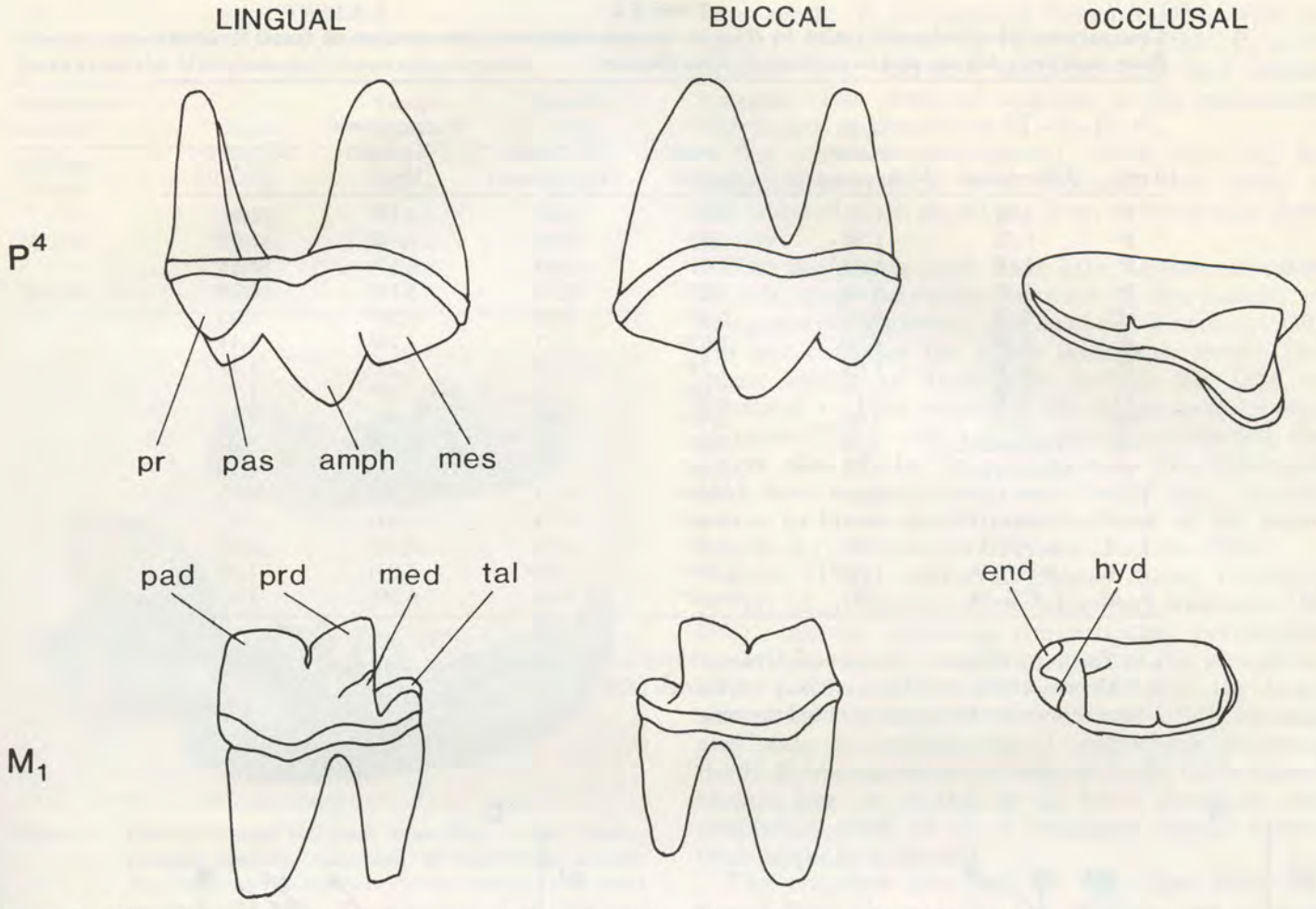

Figure 3. Lingual, buccal and occlusal aspects of the carnassials of *Hyaena hyaena makapani*. Terminology: pr= protocone, pas = parastyle, amph = amphicone, mes = metastyle, pad = paraconid, prd = protoconid, med = metaconid, tal = talonid, end = entoconid, hyd = hypoconid (after Gromova 1968).

relative to *H. h. makapani*. The pattern for *H. abronia* and *H. namaquensis* is similar to the other two except for the upper molar, and to a lesser extent the lower molar (fig. 4). This is not unexpected in view of the fact that there has been less reduction in the molars of *H. abronia* and *H. namaquensis,* where both M^2 and M_2 may be present (Hendey 1978). Another difference between the cheekteeth of the older *H. abronia* and *H. namaquensis* and the other two is the presence of P_1 and the higher length:breadth ratio of most of the cheekteeth (table 4).

These comparisons illustrate the close relationship between *H. h. makapani* and the extant *H. hyaena*, and supports the contention of Ewer (1967) that they are not separate species, but rather that the Makapansgat form should be regarded as a subspecies. The relationship between *H. h. makapani* and the older species *H. abronia* and *H. namaquensis* is more obscure in terms of skull morphology and tooth measurements. Hendey (1978) also noted differences in postcranial elements, where *H. abronia* had relatively longer hind limbs than the extant *H. hyaena*. Hendey (1978) concluded that *H. abronia* was the likely ancestor of *H. hyaena,* with *H. h. makapani* the intermediate form, and *H. namaquensis* the possible ancestor of *H. brunnea*. The comparisons in Figure 4 and Table 4 indicate that *H. abronia* and *H. namaquensis* are more closely related to one another than to either of the others. The relationship appears even stronger when the entire dentition is considered, since they both possess P_1, M^2 and M_2 and have more similar postcranial elements than either of the extant *Hyaena* species or *H. h. makapani*. If *H. abronia* was the ancestor of *H. h. makapani* then there must have been a relatively rapid evolutionary developmental phase between the late Miocene/early Pliocene *H. abronia* at Langebaanweg, dated 4–5 My (Hendey 1978), and the first appearance of *H. hyaena,* dated at 3 My in East Africa (Coppens and Howell 1976). A form from East Rudolf exhibiting the dental characters of *H. hyaena* and many of the cranial features of *H. abronia* may well be an intermediate form (Leakey 1976).

Deciduous dentition (table 5, fig. 5)

The deciduous dentition of hyaenas bears little resemblance to the permanent dentition, and without good comparative material it is unlikely that deciduous teeth would be correctly identified. Fortunately, two specimens from the Limeworks contained deciduous teeth with permanent teeth erupting. By working the surrounding bone away

TABLE 4

Comparison of cheektooth ratios in *Hyaena hyaena makapani*, two species of fossil hyaenas from southern Africa, and two extant hyaena species

Teeth	Dimensions	*H. h. makapani* (Makapansgat)	*H. hyaena* (extant)	*H. abronia* (Langebaan)	*H. namaquensis* (Namaqualand)	*H. brunnea* (extant)
P^1	L/B	1,09	1,04[a]	1,08[c]	1,18[d]	1,04[a]
P^2	L/B	1,56	1,64[c]	1,82[c]	1,78[d]	1,49[c]
P^3	L/B	1,54	1,61[c]	1,64[c]	1,57[d]	1,43[c]
P^4	L/B	1,69	1,62[b]	1,73[c]	1,70[d]	1,70[b]
M^1	L/B	0,44	0,50[c]	0,62[c]	0,56[d]	0,44
P_2	L/B	1,70	1,55[c]	1,77[c]	1,75[d]	1,41[c]
P_3	L/B	1,65	1,74[c]	1,82[c]	1,77[d]	1,47[c]
P_4	L/B	1,77	1,82[c]	1,90[c]	1,88[d]	1,71[c]
M_1	L/B	2,06	2,00[b]	2,02[c]	2,20[d]	2,05[b]
M_1	Trigonid/L	0,79	0,80[f]		0,75[d]	0,84[f]
P^4	Metastyle/L	0,37	0,36[f]			0,38[f]
P^3, P^4	L P^3/L P^4	0,68	0,68[b]	0,71[c]	0,71[d]	0,65[b]
M^1, P^4	W M^1/L P^4	0,44	0,46[c]	0,54[c]	0,54[d]	0,37[c]
P_3, P_4	L P_3/L P_4	0,92	0,93[b]	0,92[c]	0,92[d]	0,87[b]
P_3, P_4	B P_3/B P_4	1,01	0,99[c]	0,96[c]	0,97[d]	1,04[c]
P_4, M_1	L P_4/L M_1	0,92	0,98[b]	0,90[c]	0,89[d]	1,01[b]

Key:
a = Toerien (1952), b = Ficcarelli and Torre (1970), c = Hendey (1974b), d = Hendey (1978), e = Ewer (1955a), f = Kurten (1956).
Unless otherwise stated = own measurements.

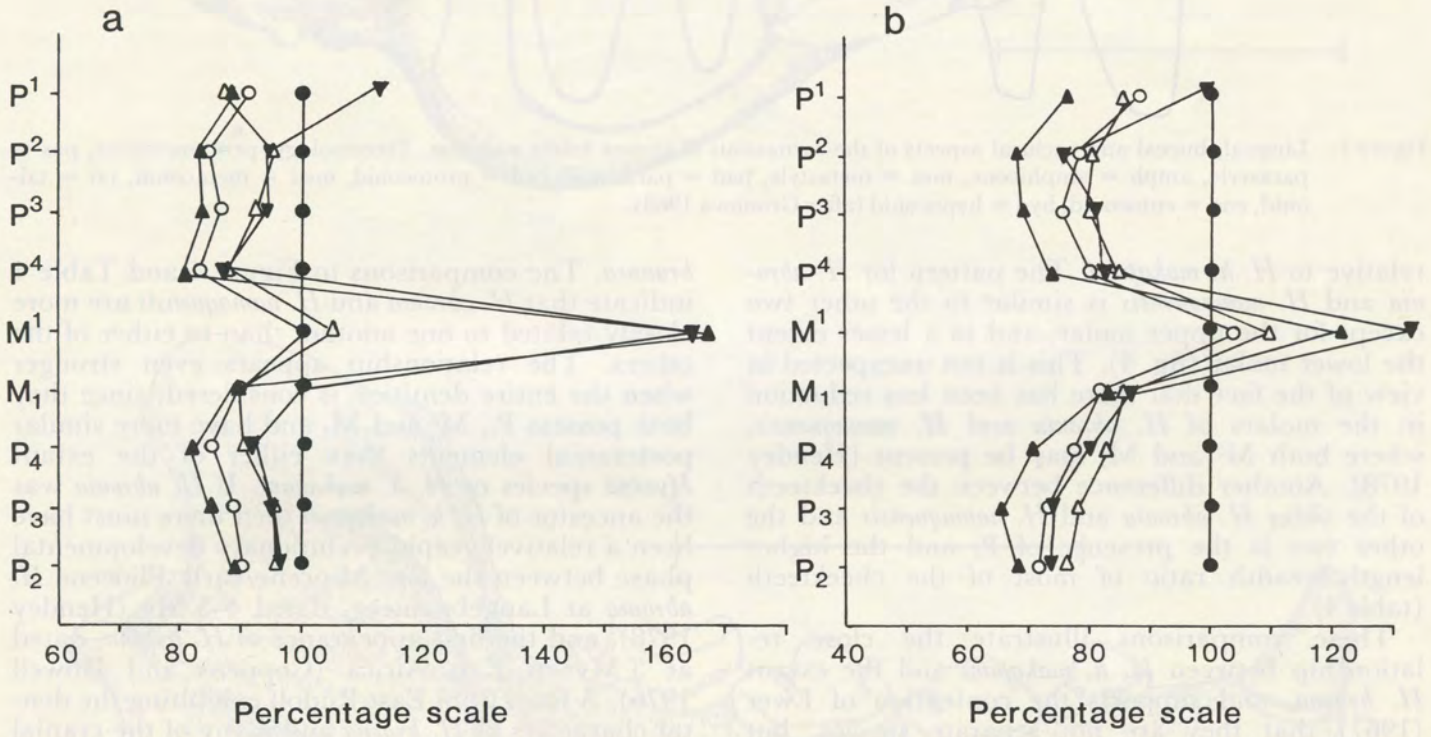

Figure 4. Ratio diagram comparing (a) mean crown lengths and (b) mean crown widths in *Hyaena hyaena makapani* (○), *Hyaena hyaena* extant (△), *Hyaena abronia* (▲) and *Hyaena namaquensis* (▼). Standard of comparison (100 per cent) *Hyaena brunnea* extant (●). Data from Toerien (1952), Kurten (1956), Hendey (1974b, 1978) and own measurements.

with an emery disc and "Vibro-tool" the permanent teeth were exposed and identification as *H. h. makapani* confirmed.

Specimen M 603 is a portion of a right maxilla with DM^3, DM^4 and M^1 *in situ*, with P^4 starting to erupt, and P^3 about to do so. DM^4 resembles M^1 in having a similar crown pattern and being located in a comparable position. Like M^1, it also has a greater breadth (buccolingual axis) than length (mesiodistal axis). DM^3 is a slender shearing tooth functioning as the upper carnassial, and it is comparable to P^4. It has three cusps and a blade arranged roughly in a straight line, meaning that it has one more cusp than P^4, its functional replace-

TABLE 5
Measurements of *Hyaena hyaena makapani* deciduous teeth from the Makapansgat Limeworks deposit

Specimen number	Tooth	Length (mm)	Breadth (mm)
M 2340	DM^3	21,3	
M 603	DM^3	20,2	12,0
	DM^4	7,6	12,3
M 2284	DM_2	*c.* 14,0	*c.* 5,7
	DM_3	15,0	6,3
M 2342	DM_3	14,7	5,8



Figure 5. *Hyaena hyaena makapani* mandibles from Makapansgat showing specimen M 2284 with deciduous teeth, and permanent teeth erupting, and adult paratype (M 252). The mandible of M 2284 was worked away to expose the permanent teeth.

ment tooth. The extra cusp on DM^3 is the paracone which is separate from the metacone, unlike in P^4 where these two cusps have fused to form the amphicone. The DM^3, therefore, has a parastyle, paracone, metacone and metastyle in a line proceeding from the mesial to the distal end. It also has a large protocone situated lingually relative to the paracone and metacone. The amphicone of P^4 was erupting immediately distal to DM^4, and the tip of the protocone of P^4 had erupted anterior to the lingual extension of DM^4. When the permanent premolars were exposed by working away the maxilla, the parastyle of P^4 could be seen erupting immediately lingual to the metastyle of DM^3, and P^3 beneath the paracone and parastyle of DM^3. It appears that P^4 would have erupted before P^3, and the order of eruption of the three hindmost permanent cheekteeth was M^1–P^4–P^3.

Specimen M 2284 consists of the major portion of a right mandible with DM_2 and DM_3 *in situ*, and the permanent teeth C, P_2, P_3 and P_4 about to replace. M_1 had been lost prior to fossilization and DM_4 had either been shed, or like M_1 had been lost. Unlike in the adult, the mandible is short, shallow and comparatively fragile. Both DM_2 and DM_3 are unlike the permanent teeth, being high and narrow. The mandible was worked away on both lingual and buccal sides to expose the permanent teeth. P_2 is erupting beneath DM_2 with its main cusp between the two roots of DM_2. P_3 is replacing DM_3, and P_4 is replacing DM_4 in a similar manner. The order of eruption of the permanent cheekteeth appears to be M_1–P_2–P_4–P_3.

The state of development of the roots of the erupting permanent teeth indicates that many of the isolated teeth found are from animals of a similar age.

The deciduous teeth have little taxonomic value at this stage primarily because of the paucity of comparative material, and because Kurten (1956) did not consider the lower deciduous teeth. The mean length of 14,85 mm (n = 2) for DM_3 is identical to that recorded for the striped hyaena (Kurten 1956), which is surprising considering the larger size of the striped hyaena. The damaged DM_2 has an approximate length of 14 mm, but this seems to be an overestimate in view of the mean length of 11,76 mm for *H. hyaena* (Kurten 1956).

Ewer (1967) expressed doubts about Toerien's (1952) identification of the maxillary fragment (M 603), but by exposing the erupting permanent teeth it has been possible to confirm the identification. Toerien (1952) drew attention to the large size of DM^3 compared to specimens of *H. brunnea*, and also to morphological differences between them. It has not been possible to verify these observations but, in relation to the lower dentition, the deciduous teeth of *H. h. makapani* appear larger than might be expected.

The eruption sequence for the upper teeth deduced from the maxilla (M 603) fits the pattern shown by examples from the families Felidae, Mustelidae and Viverridae (Ewer 1973). In these families the eruption sequence of the lower teeth is M_1–P_2–P_3–P_4, and not M_1–P_2–P_4–P_3 as it appears to be in specimen M 2284.

Pachycrocuta brevirostris

All *Pachycrocuta brevirostris* material obtained came from Member 3 (Lower Phase 1 grey breccia) (J.W. Kitching, pers. comm.).

Since Toerien's (1952) description of the remains of a large hyaena from the Limeworks three additional specimens attributed to the same species have been found. The isolated left lower canine (M 606) described by Toerien fits into the canine alveolus of specimen M 2565, and may be from the same individual. The specimens were mostly fragmentary and the teeth extensively worn, so that accurate measurements could not always be obtained (table 6, fig. 6).

The most noteworthy feature of this form relates to its size, and only *P. brevirostris* has teeth of a comparable size (Howell and Petter 1980). It is principally on this basis that the Makapansgat specimens are assigned to the genus *Pachycrocuta*. The features considered most characteristic of the genus relate to details of M_1, P_4 and P^4 (Ficcarelli and Torre 1970, Howell and Petter 1980). Unfortunately, in the Makapansgat specimens neither M_1 nor P_4 is present, and in neither of the P^4 specimens

TABLE 6
Measurements of *Pachycrocuta brevirostris* teeth from the Makapansgat Limeworks deposit

Specimen number	Tooth	Length (mm)	Breadth (mm)
M 2565	P_2	18,4	13,0
	P_3	23,0	17,1
M 604	P_3	24,9	19,4
M 6010	P^4	42,0	
M 2533	P^3	*c.* 25,2	*c.* 16,1
	P^4	*c.* 44,0	*c.* 20,5
	M^1	*c.* 6,0	*c.* 11,5



Figure 6. *Pachycrocuta brevirostris* mandible fragments from Makapansgat. (a) Specimen M 604 and (b) specimen M 2565.

available can details of the crown pattern be discerned. Nevertheless the Makapansgat form has the robust premolars found in *Pachycrocuta*. In particular, the breadth:length ratios of 0,71 and 0,74–0,78 for P_2 and P_3 respectively are closer to *P. brevirostris* than to other species of *Pachycrocuta* or *Hyaena* (Howell and Petter 1980).

The only hyaena of comparable size from South African Plio/Pleistocene deposits is *Hyaena bellax* from Kromdraai (Ewer 1954). Ewer (1967) concluded that the closest relative of the Kromdraai form was *Hyaena brevirostris* from Europe, a viewpoint supported by Ficcarelli and Torre (1970) when they grouped them as two species under the genus *Pachycrocuta*. Howell and Petter (1980) went further and synonymized the Makapansgat and Kromdraai forms as *P. bellax*. There are, however, differences, notably the larger teeth in the Makapansgat form, particularly P^4. In addition the breadth:length ratios in the Kromdraai form are smaller — 0,67 and 0,72 for P_2 and P_3 respectively. The M^1 is less developed in the Makapansgat form, being considerably smaller in relation to P^4. These differences seem sufficient to warrant separation at the specific level and consequently the Makapansgat form has been assigned to *P. brevirostris*.

Large hyaenas of the *Pachycrocuta* type have therefore twice appeared in southern Africa. As far as can be established the only other site in Africa where these large hyaenas have been recovered is Ain Brimba in Tunisia (Howell and Petter 1980).

Crocuta crocuta

One specimen (M 2567) attributed to *C. crocuta* was obtained from Member 4 (Upper Phase 1 breccia) (J.W. Kitching, pers. comm.) (fig. 7). No other hyaena material has been recovered from this horizon.



Figure 7. *Crocuta crocuta* mandible M 2567 from Makapansgat.

The specimen is the major part of a left mandible with P_2, P_3, P_4 and M_1. Part of the talonid of M_1 was damaged, but otherwise the teeth are well preserved and could be measured (table 7). The trigonid comprises about 87 per cent of the total length of M_1. The damage to the talonid is such that it is impossible to establish if a metaconid was present. Absence of a metaconid would have confirmed identification as *Crocuta,* although its presence would not have excluded the possibility that the specimen belongs to *Crocuta* (Kurten 1956).

TABLE 7
Measurements of *Crocuta crocuta* teeth (specimen M 2567) from the Makapansgat Limeworks deposit

Tooth	Length (mm)	Breadth (mm)	Trigonid (mm)
P_2	14,2	9,1	
P_3	19,3	13,7	
P_4	21,5	13,1	
M_1	*c.* 26,3	11,4	23,0

The teeth are slightly smaller than those of the extant *C. crocuta,* but their similarity is immediately apparent, particularly when compared to the genus *Hyaena* (fig. 8). Ficcarelli and Torre (1970) established several useful dental characters for separating the genera *Crocuta* and *Hyaena,* including two based upon the lower dentition — P_4 length:M_1 length, and M_1 breadth:M_1 length. Both of these ratios for specimen M 2567 fall within the *Crocuta* range (table 8) and outside the *Hyaena* range (table 4).

A comparison of tooth dimensions between the extant *C. crocuta* and the specimens from Makapansgat, East Rudolf, Olduvai, and Swartkrans plus Kromdraai combined shows the similarity between the forms (table 8). The most marked change is seen in M_1, where there has been a trend towards a relative increase in the length up to the extant form. There appears to have been little change in the lower dentition since the earliest occurrence of *C. crocuta.* Leakey (1976) stated that there had been little change in cranial or postcranial morphology of *C. crocuta* for 2 My.

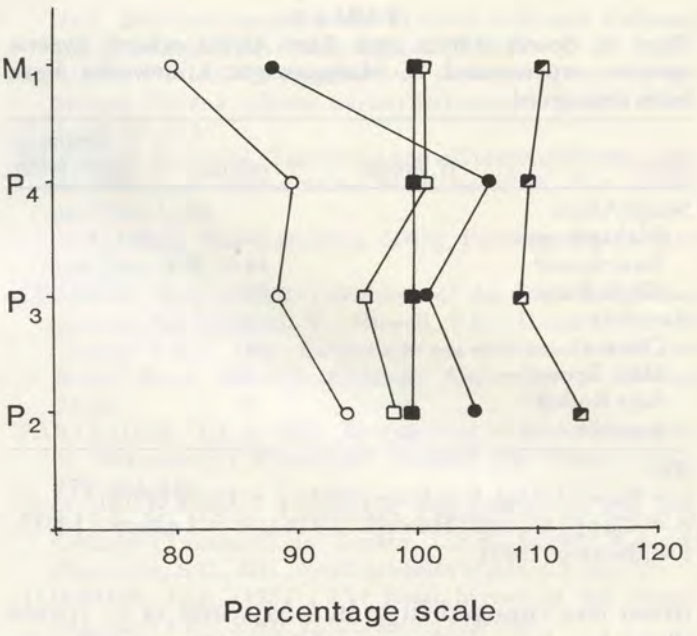

Figure 8. Ratio diagram comparing mean crown lengths in *Crocuta crocuta* from Makapansgat (□), *C. crocuta* from Swartkrans plus Kromdraai (◩), *Hyaena hyaena makapani* (○) and *Hyaena brunnea* (●). Standard of comparison (100 per cent) *Crocuta crocuta* extant (■). Data from Ewer (1954, 1955a), Kurten (1956), Leakey (1976) and own measurements.

TABLE 8
Comparison of cheektooth ratios in *Crocuta crocuta* from several Plio/Pleistocene deposits in Africa, and the extant form

Teeth	Dimension	Makapansgat	East Rudolf [a]	Olduvai [b]	Swartkrans and Kromdraai [c]	Extant [d]
M_1	L/B	2,31	2,26	2,27	2,32	2,39
P_4	L/B	1,64	1,66	1,61	1,72	1,77
P_3	L/B	1,41	1,44	1,44	1,50	1,44
P_2	L/B	1,56	1,41	1,43	1,43	
P_4, M_1	L P_4/L M_1	0,82	0,77	0,76	0,80	0,81
P_3, P_4	L P_3/L P_4	0,90	0,94	0,95	0,94	0,94

Key:
a = Leakey (1976), b = Petter (1973), c = Ewer (1954, 1955a), d = Ficcarelli and Torre (1970).

Correlations and dating

Both *H. hyaena* and *C. crocuta* have been recovered at several sites of Plio/Pleistocene age in East Africa and South Africa (table 9). These include some sites in East Africa for which K-Ar dates have been obtained. The earliest datable deposits at which a small hyaena similar to the Makapansgat form have been recovered are the lower member of the Koobi Fora Formation, East Rudolf (Leakey 1976), and the Usno Formation and Member B of the Shungura Formation, Omo Group (Howell and Petter 1976). The earliest dated deposits containing *C. crocuta* are the lower member of the Koobi Fora Formation, East Rudolf (Leakey 1976) and Member G of the Shungura Formation, Omo Group (Howell and Petter 1976). Dates for these formations are: lower member Koobi Fora 2,61–3,18 My (Fitch and Miller 1976); Usno Formation > 2,97 My, Member B Shungura Formation 2,95–2,97 My, and Member G Shungura Formation 1,83–1,93 My (Coppens and Howell 1976). It must be emphasized that *H. hyaena,* and to a lesser extent *C. crocuta,* occurred in later horizons from both East Rudolf and the Omo Group (Leakey 1976, Howell and Petter 1976). Leakey (1976) drew attention to the fact that the Hyaenidae, especially *H. hyaena,* have little value in site comparisons and correlations because the den-

TABLE 9
Sites in South Africa and East Africa where hyaena species represented at Makapansgat Limeworks have been recovered

Sites	*H. hyaena*	*C. crocuta*	*P. brevirostris and P. bellax*
South Africa			
Makapansgat	x	x	x
Swartkrans[a]		x	
Kromdraai[b]		x	x
East Africa			
Olduvai[c]	x	x	
Omo Group[d]	x	x	
East Rudolf[e]	x	x	
Laetolil[f]	x	x	

Key:
a = Ewer (1955a), b = Ewer (1954), c = Petter (1973), d = Coppens and Howell (1976), e = Leakey (1976), f = Dietrich (1942).

tition has changed little in 3 My, and in *C. crocuta* there has been little cranial or postcranial change in 2 My. Thus, based upon the hyaena material, Member 3 (Lower Phase 1 grey breccia) could be any age up to 3 My and Member 4 (Upper Phase 1 breccia) up to 2,6 My but, because of their conservatism, hyaenas appear to have limited use in correlations for dating purposes. Consequently there is nothing in the hyaena material to contradict the palaeomagnetic age estimate of > 2,9 My for the Makapansgat Limeworks grey breccia (Member 3) (Partridge 1979).

CONCLUSIONS

Cranial and dental characters confirm the identification of the abundant remains of the small hyaena in Member 3 (Lower Phase 1 breccia) as a subspecies of the extant striped hyaena. Comparisons support Hendey's (1978) suggestion that its likely ancestor is *H. abronia* from Langebaanweg. However, the relationship between *H. h. makapani* and extant *H. hyaena* seems to be closer than the relationship between *H. h. makapani* and *H. abronia; H. abronia* seems to be more closely related to *H. namaquensis*.

Fragmentary remains of a large hyaena in Member 3 (Lower Phase 1 grey breccia) are identified as *P. brevirostris*. This large hyaena shows affinities to *P. bellax* from Kromdraai, and these specimens seem to be the only records of these large hyaenas from Africa.

Hyaenas are represented by one specimen from Member 4 (Upper Phase 1 breccia), here identified as *C. crocuta*. This form is similar to the extant form and to fossil Plio/Pleistocene forms from East Africa.

C. crocuta seems to have replaced *H. h. makapani* and *P. brevirostris* in the upper horizons. Kurten (1956) documented replacement of *P. brevirostris* by *C. crocuta* at several deposits in Europe and China, which he believed was due to direct competition. A similar replacement of *H. hyaena* by *C. crocuta* occurred in the Upper Pleistocene of Palestine, with *H. hyaena* only reappearing after the extinction of *C. crocuta* (Kurten 1965). By contrast, in several East African deposits both *H. hyaena* and *C. crocuta* have been recovered from the same horizon (Leakey 1976, Howell and Petter 1976), and the ranges of the extant forms overlap (Kruuk 1976). Consequently the apparent disappearance of *H. h. makapani* in later horizons at Makapansgat is unlikely to be due only to competition with *C. crocuta*.

H. h. makapani and *C. crocuta* are morphologically similar to forms from datable deposits in East Africa. Correlations indicate that the age of Member 3 (Lower Phase 1 grey breccia) could be up to 3,0 My, and Member 4 (Upper Phase 1 breccia) up to 2,6 My. The hyaena material therefore provides general support for the palaeomagnetic age estimate of > 2,9 My for the grey breccia (Partridge 1979). However, because the Hyaenidae, especially *H. hyaena* and to a lesser extent *C. crocuta*, are so conservative they have limited value in site correlations for dating purposes.

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REVISED STRATIGRAPHY OF THE BEAUFORT GROUP IN THE SOUTHERN KAROO BASIN

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ABSTRACT

The Beaufort Group in the southern Karoo Basin between Graaff-Reinet and Sutherland has been divided into three formations based primarily on the changing ratio of sandstone to mudstone. The former Abrahamskraal Formation is elevated to subgroup status and divided into two new formations, the Lootskloof Formation and the Verlatenkloof Formation, whilst the Teekloof Formation is retained but more precisely defined. The Verlatenkloof Formation includes two members, the Jakhals Valley Member and the Paalhuis Member. The Teekloof Formation includes the Oukloof Member in addition to the previously defined and described Oudeberg Sandstone Member. Stratotypes are erected for the new formations and members in accordance with the recommendations of the South African Committee for Stratigraphy.

Subdivision of the formations and their relationship to the established biostratigraphy and facies patterns provides a means of fixing and correlating the most important uranium mineralised units in the succession with greater accuracy. These comprise the Paalhuis Member, the Oukloof Member and the Jakhals Valley Member, although the most important mineralised unit is the Paalhuis Member which contains up to 90 per cent of all known uranium occurrences in the Beaufort West area.

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INTRODUCTION

The main Karoo Basin in South Africa (fig. 1) contains one of the most extensive and well exposed sequences of Gondwana rocks in the southern hemisphere. The middle part of the succession, or Beaufort Group, which is the most extensively exposed stratigraphic unit in the Basin, contains a rich reptilian fauna that allows for a fairly refined scheme of biostratigraphic zonation (Keyser and Smith 1979). In comparison, little is known about the lithostratigraphy of the group; a situation occasioned to some extent by the vast and apparently monotonous succession of sandstones and mudstones lacking any well-defined lithostratigraphic markers. This problem is compounded by the lenticularity of most sandstones and the extensive dolerite intrusions which make correlation difficult. At the same time attempts to match straight lithologies rather than general lithological sequences have to contend with diachronism.

Uranium mineralisation occurs in the Beaufort Group in the southern Karoo Basin, usually as widely dispersed local concentrations within lenticular sandstones (Turner 1978, 1979). Because of this mode of occurrence and lack of adequate stratigraphic guides, the relationship between different mineralised horizons is uncertain (Turner 1981). A more detailed stratigraphic subdivision and correlation is therefore essential in order to try and overcome these problems. The main purpose of this paper is to attempt to establish a more detailed formal lithostratigraphic subdivision and correlation of the Beaufort Group in the southern Karoo Basin between Graaff-Reinet and Sutherland (fig. 1) based on the regional lithostratigraphic relationships outlined by Keyser and Smith (1979) and Turner (1979). All new formations and members are described in accordance with the requirements of the South African Stratigraphic Code (1971) and the International Subcommission on Stratigraphic Classification (1970).

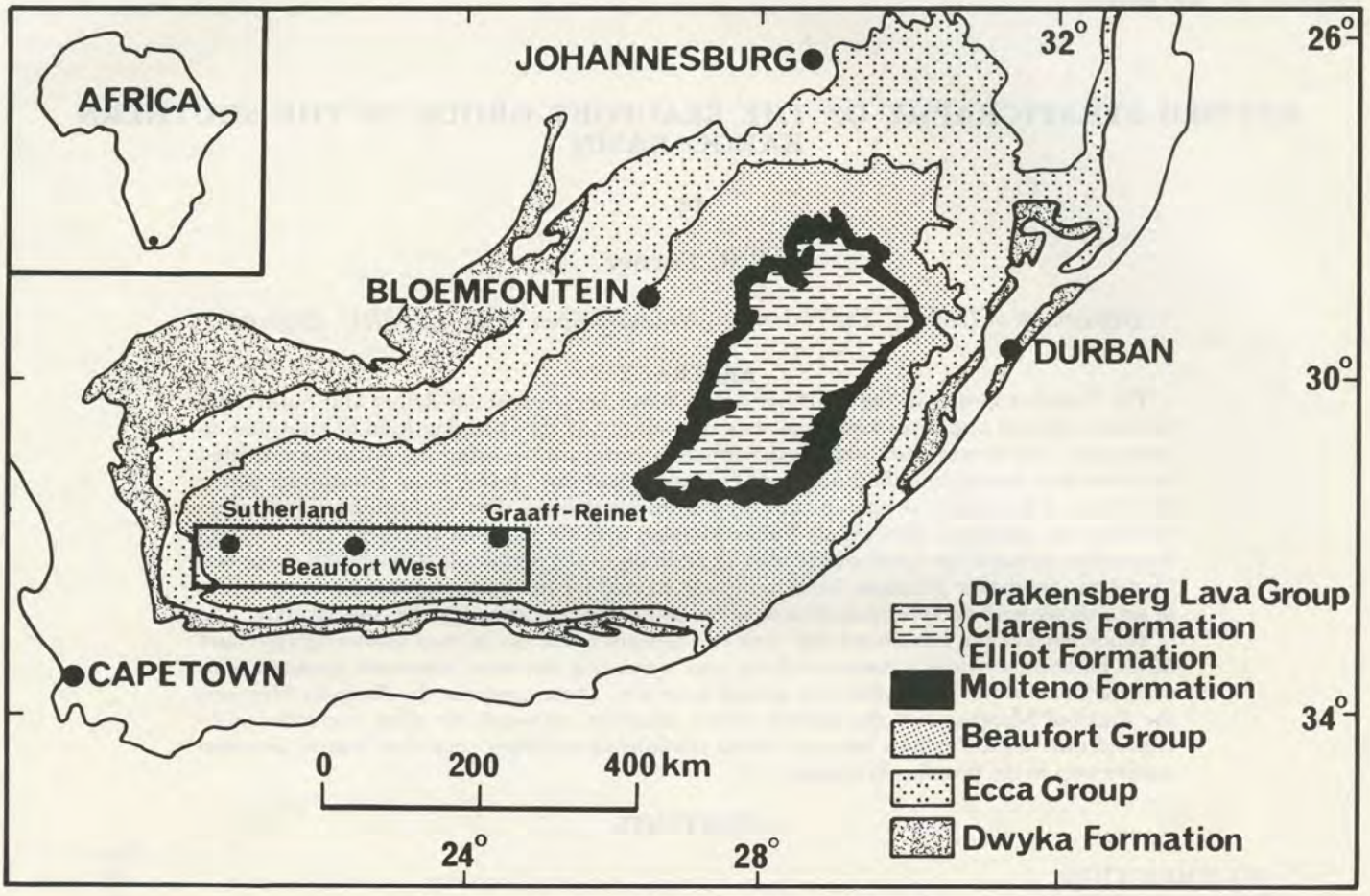

Figure 1. Karoo Basin and location of study area.

STRATIGRAPHY

General

Beaufort Group sediments were deposited in an intracratonic basin receiving detritus from a source area located to the south and west (Ryan 1967, Martini 1974, Turner 1975). Sedimentation was initiated by source area uplift (especially in the south), possibly due to collision between two lithospheric plates reproducing a cordilleran type orogenic event as predicted by modern plate tectonic theory (Dewey and Bird 1970). The sediments consist mainly of mudstones, siltstones and sandstones, and along the southern margin of the basin they have been caught up in the Cape Orogeny and extensively folded. Northwards the folding decreases in intensity and dies out completely on approaching the northern boundary of the study area (fig. 1) where the sediments are flat-lying.

The Beaufort Group lies conformably on the Ecca Group, the contact between them records a gradual change from a deltaic depositional system to a fluvial depositional system in response to source area uplift and the northward progradation of Beaufort sediments, accompanied by a gradual shallowing and shrinkage of the Ecca Basin in the same general direction. Thus argillaceous sediments assigned to the Ecca Group in the northern part of the basin may be the time equivalent of the Beaufort Group in the south (Turner 1978) and the boundary on a basinwide scale must be diachronous. The Ecca–Beaufort boundary is generally defined and mapped on the basis of the first occurrence of red and purple mudstones characteristic of the Beaufort Group. Unfortunately this definition cannot be applied in many areas because of the sporadic distribution of red and purple mudstones in the lower part of the Beaufort succession, as pointed out by Ryan (1967). A more reliable and accurate indication of the boundary is the presence of thick, laterally persistent sandstones of delta front origin that Johnson (1976) included in his Waterford Formation at the top of the Ecca Group. These sandstones can be distinguished from those in the Beaufort on the basis of their internal structure (presence of deformation structures and lack of cross-bedding), coarsening-upwards as opposed to fining-upwards grain-size trends, and the interbedded shales, which are generally darker, more carbonaceous and better laminated than the argillaceous rocks in the Beaufort.

A lithostratigraphic subdivision of the Beaufort Group in part of the eastern Cape Province was proposed by Johnson (1976). Although this scheme, with minor modifications, was accepted by the Karoo Working Group of the South African Committee for Stratigraphy, it is uncertain as to how it relates to areas farther west. This arises largely from facies changes and the fact that the scheme depends mainly on the presence or absence of red mudstones which are only sporadically

TABLE 1
Beaufort Group stratigraphy and facies associations in the southern Karoo Basin between Sutherland and Graaff-Reinet

Sequence*	Group	Subgroup	Formation West	Formation East	Member West	Member East	Biozones† West Keyser and Smith (1979)	Biozones† East Kitching (1977)	Facies Associations	Correlations with Eastern Cape‡
Karoo	Beaufort		Teekloof		Steenkampsberg§		*Dicynodon lacerticeps-Whaitsia*	*Daptocephalus*	Flood basin	Balfour Formation
					Oukloof		*Aulacephalodon-Cistecephalus*	*Cistecephalus*		
					Hoedemaker§	Oudeberg Sandstone	*Tropidostoma-Endothiodon*			
		Abrahamskraal	Verlatenkloof		Paalhuis		*Pristerognathus Diictodon*	*Tapinocephalus*	High Sinuosity Channel	Middleton Formation
					Jakhals Valley		Dinocephalian			
			Lootskloof						Low Sinuosity Channel	Koonap Formation

* Terminology according to recommendations of Karoo Working Group, South African Committee for Stratigraphy.
† The biozones in the west are assemblage zones whereas those in the east are essentially range zones.
‡ Terminology according to Johnson (1976).
§ Informal terminology according to Stear (1980).

present in the succession farther west. Thus, as a means of defining stratigraphic boundaries on both a local and regional scale, colour change is of little value, especially in the lower part of the succession where rapid changes in colour are particularly common. For this reason Keyser and Smith (1979) divided the Beaufort Group in this part of the Karoo Basin into two formations, the Abrahamskraal Formation and the Teekloof Formation. The Abrahamskraal Formation is distinguished from the overlying Teekloof Formation mainly in the presence of chert bands, the more numerous sandstones and the paucity of red mustone. Unfortunately, a twofold division recognises only broad lithostratigraphic trends and is inadequate in many areas where the Beaufort succession may comprise up to three lithostratigraphic divisions of formational status, which can be further divided, in some cases, into members based essentially on the changing ratio of sandstone to mudstone.

In view of this it is proposed that the Abrahamskraal Formation should be divided into two units of formational status, and the term Abrahamskraal elevated to subgroup status within the Beaufort Group, in accordance with the recommendations of the International Subcommission on Stratigraphic Classification (1970). The Teekloof Formation retains its name and status (table 1).

Stratigraphic studies reveal that all the formations within the Beaufort Group are of regional extent. However, the degree of exposure is poor in the Camdeboo Flats west of Pearston with the result that the formations in this area are of a composite nature based on borehole data and measured sections. Since both the Lootskloof and Verlatenkloof formations have been affected by the Cape Folding in this area, the relationship between stratigraphy and structure was determined prior to section measurement in order to try, as far as possible, to eliminate repetition of beds and anomalous thickness values. The location of stratotypes and reference sections is shown in Figure 2 and the generalised lithostratigraphic relations in Figure 3.

Lootskloof Formation

The formation is well exposed along Lootskloof River south of Pearston (fig. 2) where up to 400 m of continuous section is exposed in the northern limb of a large syncline. The formation attains a maximum thickness of about 490 m, but in the west in Verlatenkloof Pass, it thins to less than 100 m (fig. 5). To the east it grades laterally into the Koonap and possibly the lower part of the Middleton Formation (table 1). It is underlain by arenaceous deposits of the Waterford Formation at the top of the Ecca Group, and overlain by sediments of the Verlatenkloof Formation (fig. 3). The lower boundary is transitional and diachronous, being based primarily on differences in character of the sandstones and associated argillaceous strata. The upper boundary, which is not markedly diachronous, is transitional and arbitrarily defined on the changing ratio of sandstone to mudstone (mudstone increases at the expense of sandstone)

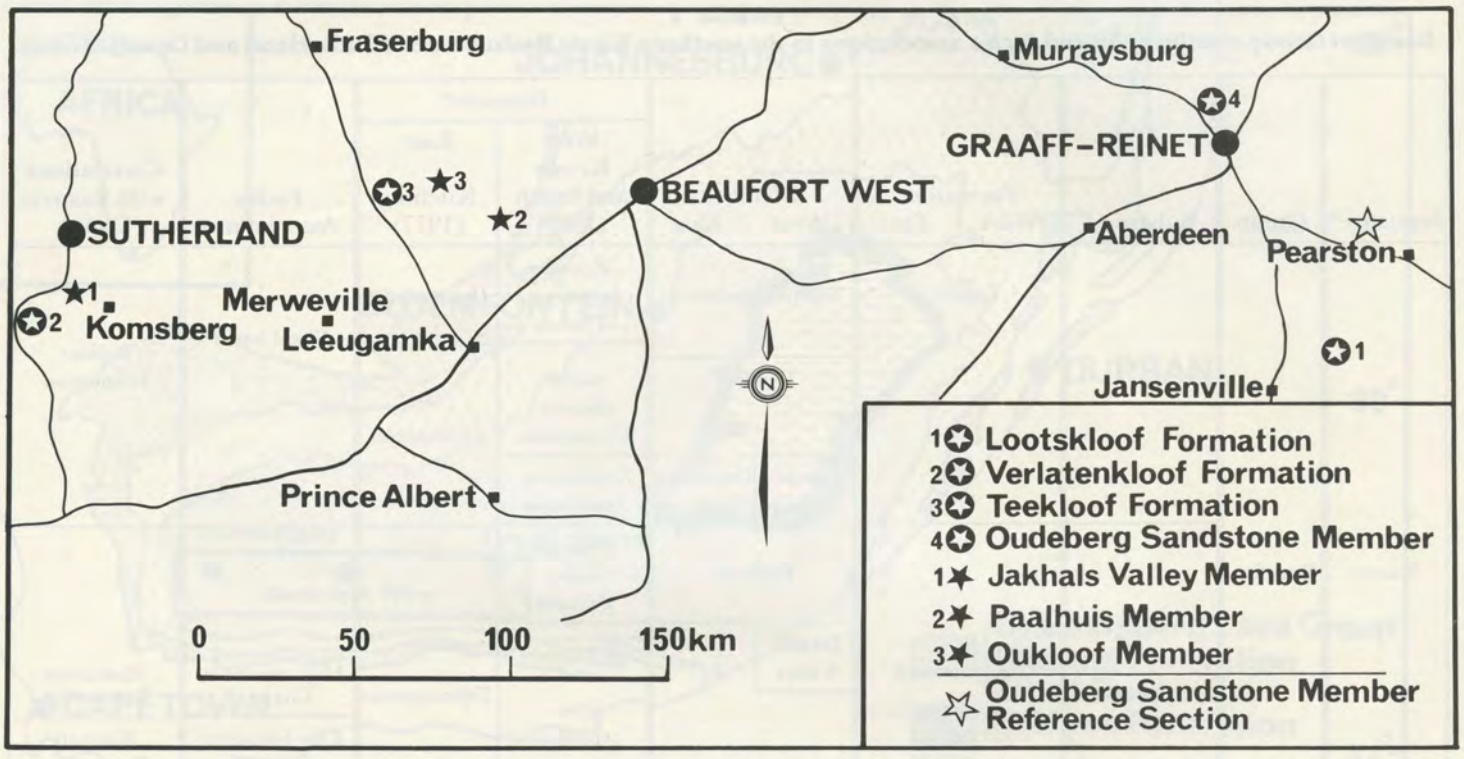

Figure 2. Location of stratotypes and reference section.

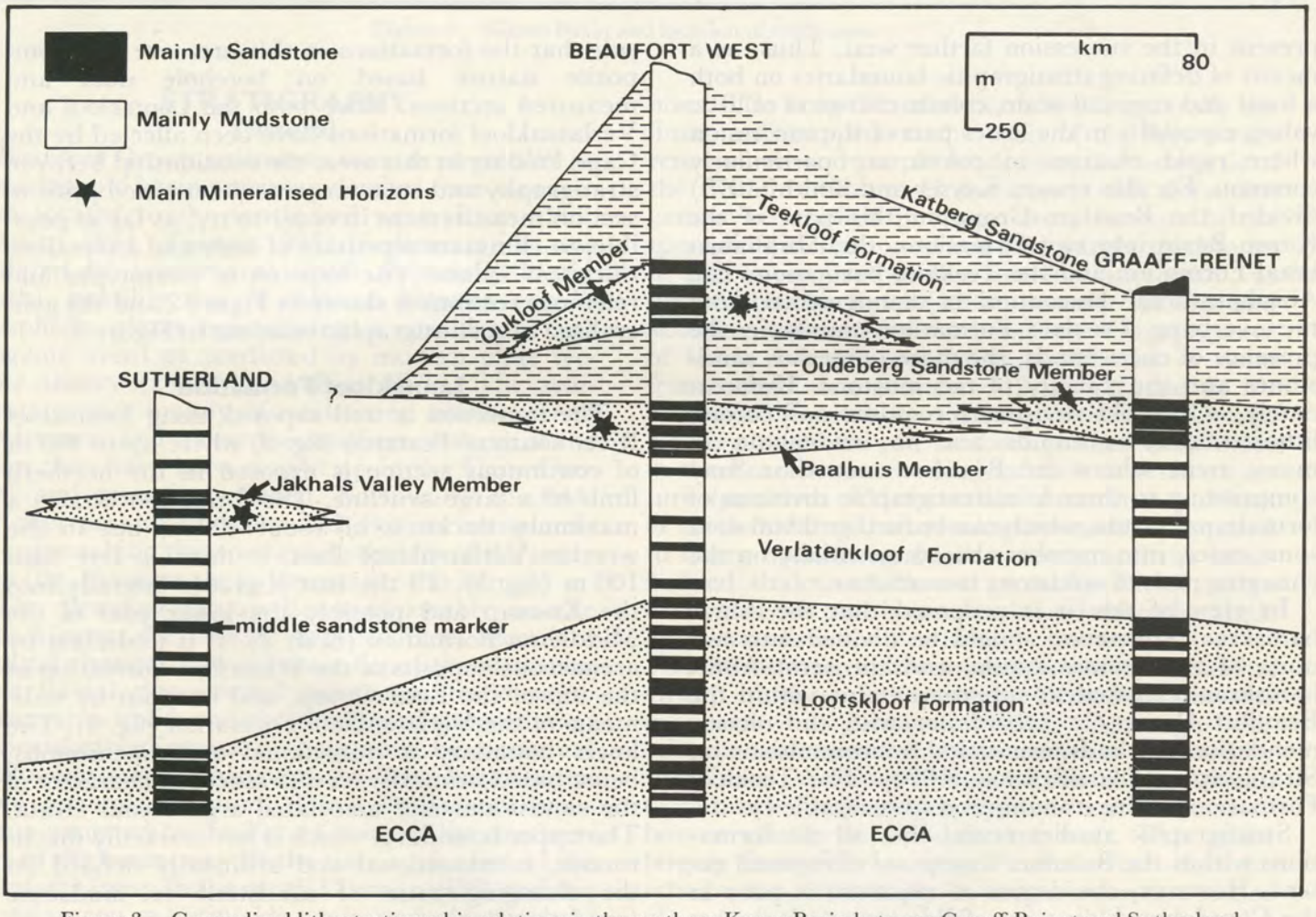

Figure 3. Generalised lithostratigraphic relations in the southern Karoo Basin between Graaff-Reinet and Sutherland.

and the increased red coloration of the mudstones (Turner 1978). The formation coincides with the lower part of the Abrahamskraal Subgroup (table 1). Chert bands are, however, not regarded as being diagnostic of the formation because they are absent in the Lootskloof section, and throughout most of the western part of the outcrop investigated, and occasional chert lenses have been found in the overlying formation.

Lithologically the formation consists of sandstones and subordinate interbedded siltstones and mudstones (figs. 5, 6). The sandstones attain thicknesses of up to 25 m, and are predominatly fine-grained, dark grey and calcareous. Many of them have a characteristically speckled appearance on both fresh and weathered surfaces, particularly in the eastern part of the basin around Jansenville and Graaff-Reinet. Characteristic sedimentary structures in the sandstones are horizontal lamination, ripple cross-lamination and cross-bedding (fig. 5). Sole structures, mudcracks, sandstone dykes and rill marks are present but less common. The sandstones are interbedded with mudstone and siltstone pellet conglomerates (sometimes associated with plant material and vertebrate bones), and contain pyrite and large brown-weathering calcareous nodules and lenses.

The argillaceous sediments consist of bluish-grey, occasionally maroon and purple mudstones and silty mudstones, interbedded with ripple cross-laminated greenish-grey siltstones. The mudstones

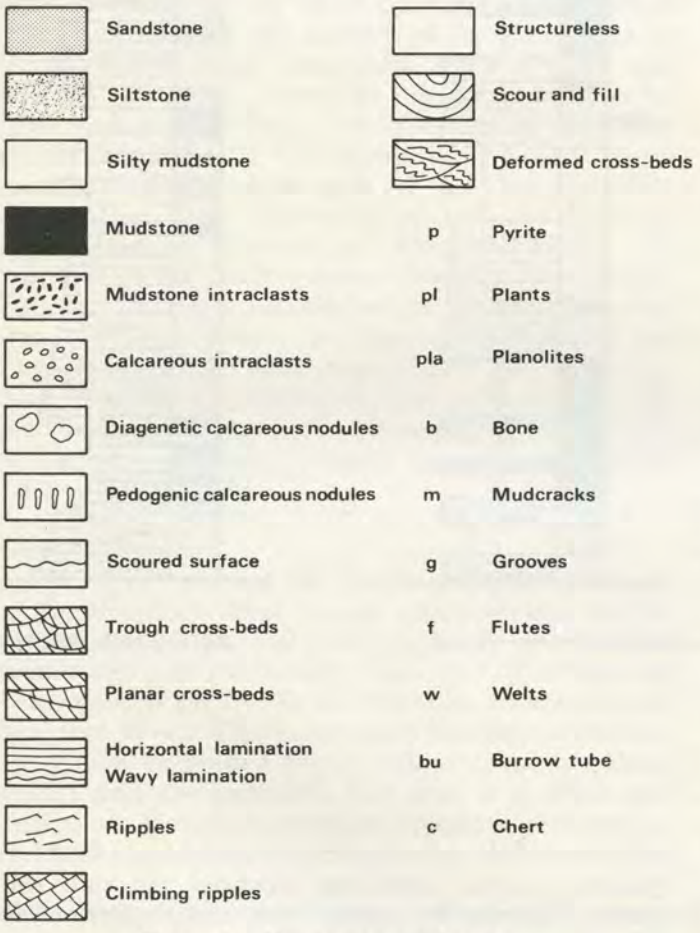

Figure 4. Key to measured sections.

contain calcareous nodules from 3 to 6 cm in diameter, which locally form nodular layers. Siltstones also occur as gradational units between the thicker sandstones (those more than 3 m) and mudstones, and may be ripple cross-laminated or horizontally laminated. Towards the top of the formation the following changes occur: (1) the ratio of sandstone to mudstones decreases (from 1 : 1 at the base to 1 : 4 at the top); (2) the sandstones become more lenticular and less speckled in appearance; (3) the maroon and red coloured mudstones become more common; (4) the number of calcareous nodules in the mudstones increases; and (5) the chert bands become less common. Biostratigraphically the formation falls within the Dinocephalian Assemblage Zone which is of Middle to Upper Permian age and comprises the lowermost part of the Beaufort Group in the southern Karoo Basin, west of longitude 25°E (Keyser and Smith 1979). It corresponds approximately with the low sinuosity channel facies association of Turner (1978) (table 1).

Verlatenkloof Formation

This formation is well exposed along the escarpment between Verlatenkloof and Ouberg Pass, south of Sutherland. The stratotype is located on the east side of Verlatenkloof (fig. 2) where the measured section is about 1 000 m thick (fig. 7). The top of the formation is not encountered in this area and when traced eastwards it thins to about 400 m in the vicinity of Beaufort West, thickening slightly in the Graaff-Reinet area to about 600 m (fig. 3). However, exposure in the east is generally poor (especially on the Camdeboo Flats between Aberdeen and Pearston) with the result that an understanding of the formation in this area is based mainly on borehole data, augmented by a few measured sections from road cuttings and river valleys.

The formation is underlain by the Lootskloof Formation (fig. 3), and merges laterally with the Middleton Formation east of Pearston (table 1). Moving eastwards across the basin from the Beaufort West area the formation is overlain by the Teekloof Formation and the Oudeberg Sandstone Member at the base of the Teekloof Formation (fig. 3). Lithologically the Verlatenkloof Formation consists of mudstone and silty mudstone with subordinate interbeds of siltstone and sandstone (fig. 8). It shows a lower degree of diagenesis than the underlying Lootskloof Formation and is less resistant to weathering. The mudstones are bluish grey to maroon or red, the red coloration becoming more pronounced towards the top of the formation, for example, at Libertas along the foothills of the escarpment west of Pearston. Calcareous nodules occur in the mudstones, sometimes concentrated into nodular layers. Chert lenses and septarian nodules have also been recorded from the mudstones, but according to Keyser and Smith (1979) the cherts differ from those in the overlying formation in that they are generally green, and also pink weathering.

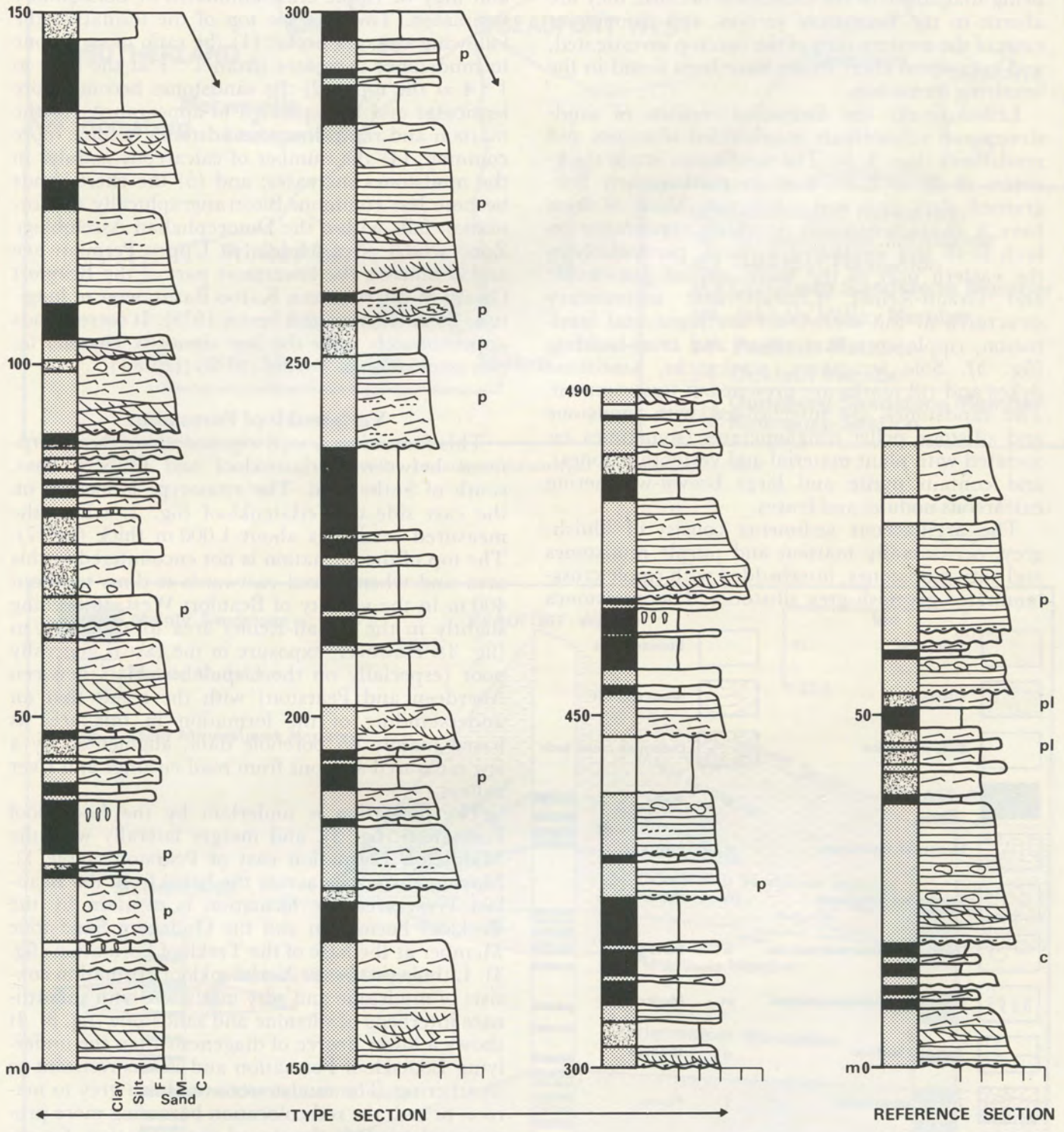

Figure 5. Type section and reference section of the Lootskloof Formation. The reference section is located at the foot of Verlatenkloof Pass, and is conformably overlain by the Verlatenkloof Formation (see fig. 2 for location).



Figure 6. Thick, laterally persistent sandstones interbedded with subordinate amounts of siltstone and mudstone, Lootskloof Formation, south of Pearston.

Siltstones are typically greenish-grey and characterised by ripple cross-lamination, horizontal lamination, lenticular bedding, burrows, root marks and purple red mottling. The siltstones occur as thin lenticular beds with scoured bases and gradational tops within the mudstones, or they form part of fining-upward sequences comprising sandstone, siltstone and mudstone. The sandstones are fine- to very fine-grained, greyish-green and structured mainly by horizontal lamination and ripple cross-lamination. They differ from the sandstones in the underlying formation in that they are slightly finer-grained, thinner, and more markedly lenticular in character. Within the middle of the formation in Verlatenkloof is an unusually thick (30 m) and laterally persistent sandstone that provides a useful local marker, here designated the middle sandstone marker (figs. 3, 7). The formation broadly corresponds with the upper part of the Dinocephalian Assemblage Zone, extending up into the *Pristerognathus-Diictodon* Assemblage Zone. However, the presence of the *Pristerognathus-Diictodon* Assemblage Zone is not firmly established in the Graaff-Reinet area, although Keyser and Smith (1979) record the *Tropidostoma-Endothiodon* Assemblage Zone outcropping south of Graaff-Reinet and extending to the east beyond Pearston. The formation is equivalent to the high sinuosity channel facies association of Turner (1978) (table 1).

Paalhuis Member

The upper part of the Verlatenkloof Formation in the Beaufort West area is characterised by the presence of about 140 m of regularly interbedded sandstones and mudstones (figs. 3, 7, 9) which are well exposed on the farm Paalhuis, 45 km west of Beaufort West. The sandstones weather a distinctive yellow or golden-brown colour (zone of golden sands) and are generally less than 8 m thick and lenticular. However, abutting contacts between individual sandstones sometimes give the impression that they are laterally persistent units, especially when seen from a distance. Horizontal laminations, ripple cross-laminations and cross-bedding are the dominant internal sedimentary structures. Calcareous pods and lenses are infrequently present within the sandstones, which also contain trace fossils *(Planolites?)* and possible pustular algal mats (Turner 1979). The interbedded mudstones are bluish-grey to maroon and locally silty in character with occasional calcareous nodules. The mudstones are massive and unlaminated and locally contain burrow tubes. Biostratigraphically the member falls within the *Pristerognathus-Diictodon* Assemblage Zone, and is the most important mineralised horizon in the succession, containing about 90 per cent of all known uranium occurrences. The member is possibly equivalent to the Poortjie Sandstone (Rossouw and De Villiers 1953) and includes the Rietkuil sandstone and the Rystkuil sandstone.

Jakhals Valley Member

A prominent feature of the formation in the west is the presence of about 110 m of interbedded sandstones and mudstones (figs. 3, 7) which are well exposed along the edge of the escarpment south of Sutherland on the farm Jakhals Valley. The sandstones are much thicker (25 m) than those in adjacent parts of the formation and form resistant ledges which stand out from the more easily weathered mudstones. These ledges are clearly visible on aerial photographs and form a distinct geomorphological expression of the member in this area. The sandstones are fine-grained and pale grey, often with a distinct speckled appearance similar to some of the sandstones in the Lootskloof Formation. They contain mudstone lenses, intraformational conglomerates, calcareous nodules and a little pyrite. Clasts within the conglomerates include mudstone, silty mudstone and reworked small calcareous nodules. The sandstones are locally rich in plant material and profusely cross-bedded, and are well exposed at the top of Verlatenkloof. Other structures present in the sandstones include horizontal lamination and ripple cross-lamination. The mudstones are bluish-grey to maroon in colour and contain minor interbeds of siltstone and fine sandstone up to 30 cm thick. The siltstone and sandstone interbeds fine upwards and are internally structured by horizontal lamination and ripple cross-lamination. The member wedges out to the east between Komsberg and Merweville (fig. 2); a similar wedging effect occurs west of Sutherland (fig. 3).

Teekloof Formation

This formation is named for exposures in Teekloof Pass, 30 km south of Fraserburg (fig. 2) where it attains a thickness of about 1 000 m. Details of the stratotype are given by Keyser and Smith (1979) and are not repeated here. The top of the formation is not encountered in the Beaufort West area where it is underlain by the Verlatenkloof Formation. Eastwards, between Graaff-Reinet and Pearston, the Teekloof Formation is underlain by the Verlatenkloof Formation (Paalhuis Member?)

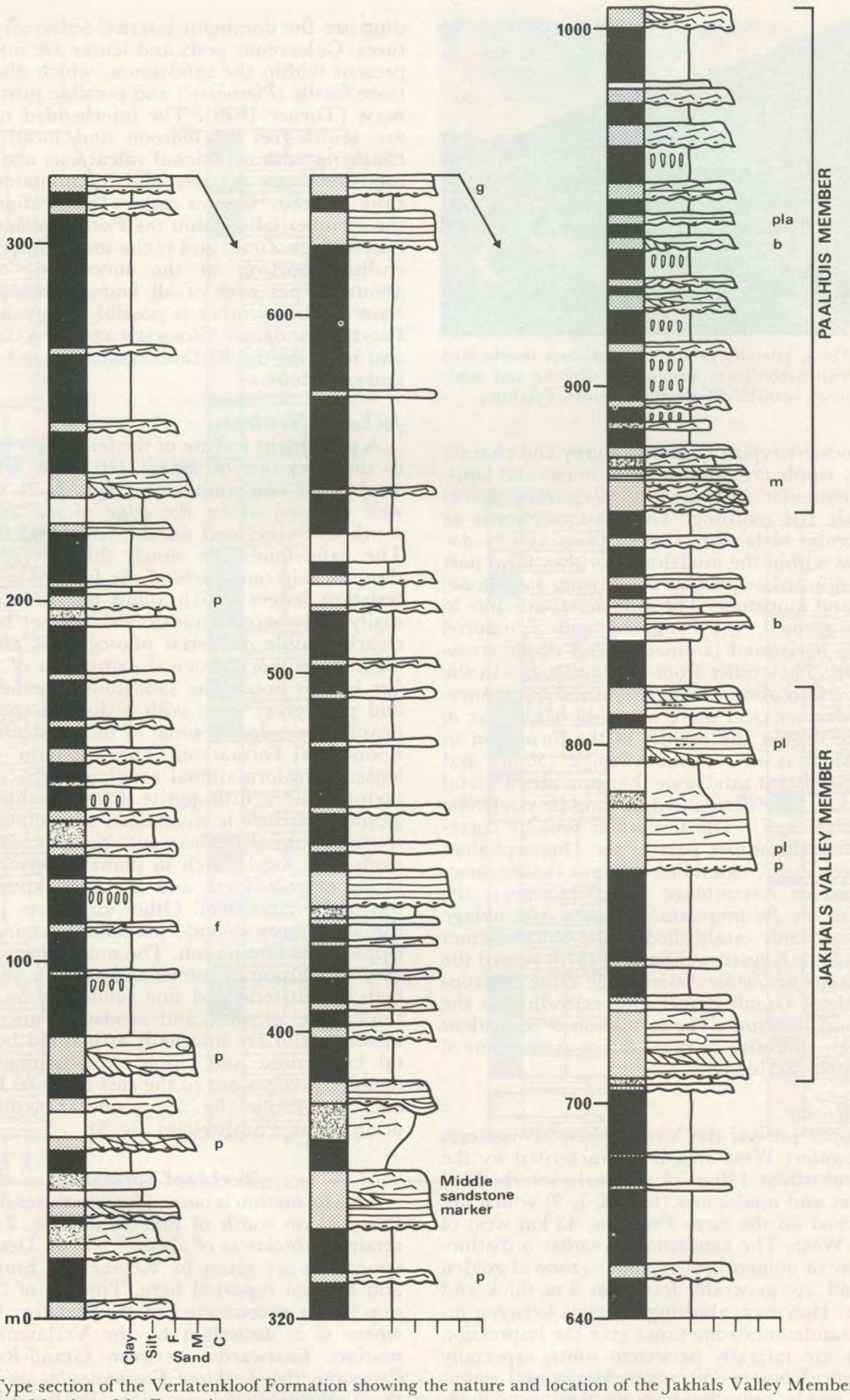

Figure 7. Type section of the Verlatenkloof Formation showing the nature and location of the Jakhals Valley Member and Paalhuis Member of the Formation.



Figure 8. Mudstones and silty mudstones with subordinate interbeds of sandstone and siltstone, Verlatenkloof Formation, west of Verlatenkloof, Sutherland District.



Figure 9. Thin sandstones and interbedded mudstones of the Paalhuis Member of the Verlatenkloof Formation (a) along the lower slopes of Gifberg, west of Beaufort West. The top of the Paalhuis Member is defined by a small plateau feature (b), overlain by the slope-forming mudstones of the Teekloof Formation (c), which contains a prominent sandy horizon, the Oukloof Member (d), towards the top (see fig. 11). The mountain is capped by a thick dolerite sheet (e).

and overlain by the Katberg Sandstone Formation (fig. 3). Between Fraserburg and Sutherland the formation appears to wedge out, whilst to the east it grades laterally into the Balfour Formation (table 1).

The formation consists predominantly of maroon and bluish-grey, massive, and locally silty mudstone with occasional interbeds of siltstone and fine-grained sandstone (Fig. 9). The mudstones are much more prominent than in the formation below, forming sequences up to 30 m thick between the siltstone and sandstone beds. Calcareous nodules are common in the mudstones, often concentrated into nodular layers and associated with vertebrate fossils (Kitching 1977). "Desert roses", representing pseudomorphs of calcite after gypsum are characteristic of the formation, especially in the east where they form distinct horizons (Keyser 1966).

The sandstones are generally less than 3 m thick (Turner 1978), fine-grained and graded, with a scoured base that is commonly associated with fine mudstone clasts. Internally, the sandstones are horizontally laminated and ripple cross-laminated with the tops of the beds frequently ripple-marked. The siltstone beds are less than 1 m thick. They have sharp or slightly scoured bases, internal cross-lamination, and grade into silty mudstone and mudstone at the top. Desiccation cracks are common along the bases of siltstone and sandstone beds which are less common and thinner than most arenaceous divisions in the Verlatenkloof Formation. The formation falls within the *Tropidostoma-Endothiodon*, *Aulacephalodon-Cistecephalus*, and *Dicynodon lacerticeps-Whaitsia* Assemblage Zones, and is equivalent to the flood basin facies association of Turner (1978) (table 1).

Oukloof Member

This member is particularly well exposed in Oukloof Pass, 39 km south of Fraserburg (fig. 2) where it attains a thickness of about 125 km (fig. 10). It consists of 28 m thick laterally persistent (more than 1 km) sandstones with minor amounts of mudstone and silty mudstone (figs. 10, 11). The sandstones are grey to yellow-grey, fine- to medium-grained, interbedded with mudstone pellet conglomerates and contain occasional bone fragments. Characteristic internal sedimentary structures are horizontal lamination, ripple cross-lamination and cross-bedding. The sandstones form prominent cliffs and ledges between the less resistant argillaceous strata. Mudstones and silty mudstones are typically bluish-grey or maroon and contain calcareous nodules and occasional burrow tubes (fig. 10). The member falls within the *Aulacephalodon-Cistecephalus* Assemblage Zone of Keyser and Smith (1979).

Recently Stear (1980) informally introduced the terms Hoedemaker and Steenkampsberg member for the mudstone-dominated sequences below and above the Oukloof Member. The Hoedemaker member coincides with the *Tropidostoma-Endothiodon*

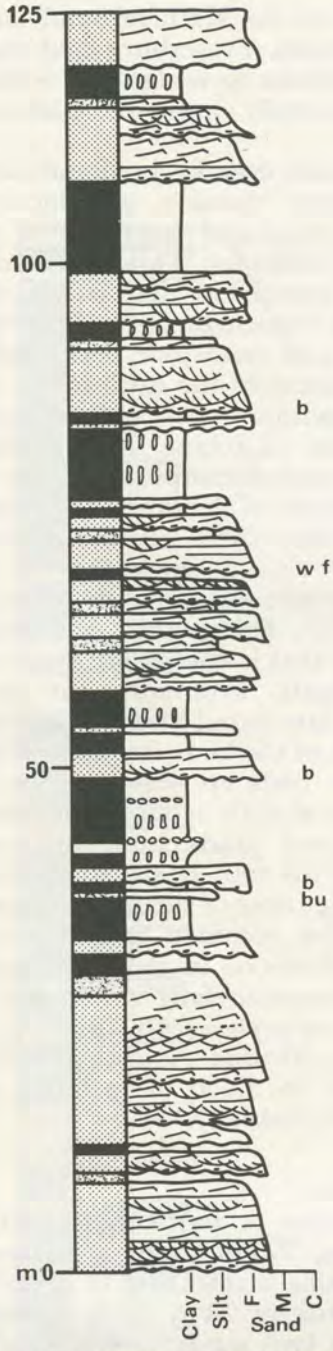

Figure 10. Type section of the Oukloof Member of the Teekloof Formation.

Assemblage Zone and the Steenkampsberg member with the *Dicynodon lacerticeps-Whaitsia* Assemblage Zone and the uppper part of the *Aulacephalodon-Cistecephalus* Assemblage Zone (table 1).

Oudeberg Sandstone Member

The name Oudeberg Sandstone was first used by Keyser (1973) for exposures of Beaufort Group strata to the north-east of Oudeberg Pass between Graaff-Reinet and Murraysburg (fig. 2). Within the pass itself the section is faulted and extensively intruded by dolerite, making it unsuitable as a stratotype. Good exposures occur farther east towards Pearston, particularly along the foothills of the escarpment on the farm Libertas where a reference section was measured (fig. 12).



Figure 11. Thick laterally persistent sandstones with subordinate mudstones and siltstones of the Oukloof Member, Oukloof Pass, south of Fraserburg. The base of the member is the base of the lowermost laterally persistent sandstone.

The member, which is about 120 m thick, defines the base of the Teekloof Formation, and is underlain by the Verlatenkloof Formation (fig. 3). It consists of sandstones with minor amounts of mudstones and silty mudstone (fig. 12). Individual sandstones are laterally persistent and attain thicknesses of up to 20 m, particularly in the lower and middle part of the formation (fig. 12). They are fine- to medium-grained sandstones structured by horizontal lamination, ripple cross-lamination and occasional cross-bedding. Mudpellet conglomerates, pyrite and plant material are present in the sandstones, which weather out from the softer more argillaceous formations above and below to form prominent ledge features (fig. 13). The formation dips eastwards at about 2–3°, probably as a result of an underlying dolerite intrusion. Its upper and lower boundaries are taken at the first and last appearance of thick, laterally persistent sandstones. The formation wedges out between Graaff-Reinet and Aberdeen; to the east its extent is uncertain, but it probably extends as far as East London. The formation falls within the *Tropidostoma-Endothiodon* Assemblage Zone of Keyser and Smith (1979), which places it stratigraphically just below the Oukloof Member of the Teekloof Formation in the Beaufort West area (table 1). The formation represents a sandstone dominated fluviatile sequence at the base of the floodbasin facies association (table 1) which has been compared to the low sinuosity channel facies association of Turner (1978).

CONCLUSIONS

The proposed lithostratigraphic subdivision of the Beaufort Group in the southern Karoo Basin between Graaff-Reinet and Sutherland, and its relationship to the established biostratigraphy (Keyser and Smith 1979) and facies patterns (Turner 1978, 1979,) enables the more important uranium mineralised horizons in the succession to be fixed and correlated with greater accuracy. For

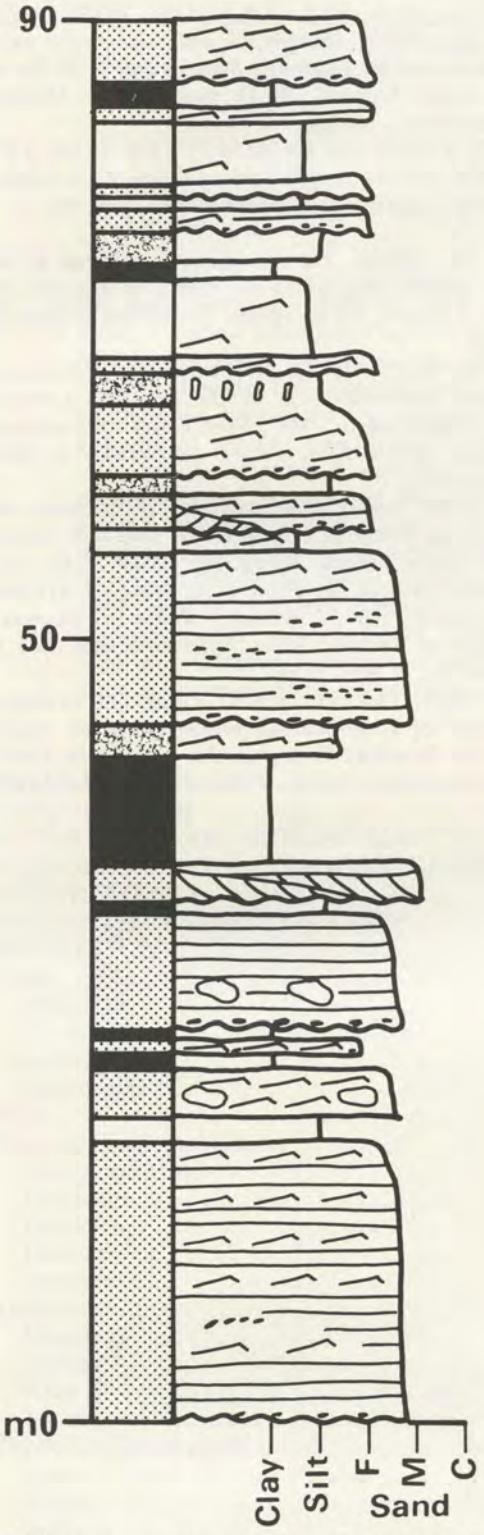

Figure 12. Reference section of the Oudeberg Sandstone Member of the Teekloof Formation.

example, in the Beaufort West area the most important mineralised horizon (containing 90 per cent of all known uranium occurrences) coincides approximately with the Paalhuis Member at the top of the Verlatenkloof Formation which falls within the *Pristerognathus-Diictodon* Assemblage Zone (Keyser and Smith 1979) and the top of the high sinuosity channel facies association (Turner 1978, 1979) (fig. 3). The base of this member includes the Rietkuil and possibly the Rystkuil sandstones, two of the most important mineralised sandstones in the Beaufort West area. Westwards, the extent of the Paalhuis Member is uncertain; it may wedge out or extend around the outcrop towards the north as depicted on the geological map of Sutherland. Nevertheless, the *Pristerognathus-Diictodon* Assemblage Zone is still present and suggests that biostratigraphically the main mineralised horizon at Sutherland is the same as that around Beaufort West, whether it coincides with the Paalhuis Member or not.



Figure 13. Prominent, ledge-forming sandstones of the Oudeberg Sandstone Member, between Graaff-Reinet and Pearston. The sandstones are located at the base of the Teekloof Formation along the contact with the underlying Verlatenkloof Formation which forms the lower slopes of the mountain and the flats in the foreground. Capping the mountain is a thick dolerite sheet.

Important occurrences of uranium mineralisation occur within the Oukloof Member of the Teekloof Formation (fig. 3), especially south of Fraserburg, although they tend to be more localised than those in the Paalhuis Member of the Verlatenkloof Formation. Other important occurrences of uranium mineralisation are associated with the sandy Jakhals Valley Member lower down in the Verlatenkloof Formation (fig. 3) along the edge of the escarpment south of Sutherland (Turner 1975). The way in which the main mineralised horizon relates to areas farther east is not firmly established because of the poor outcrop and lack of adequate borehole and biostratigraphic control. However, recent vertebrate finds in Beaufort sandstones along the Bullrivier in the Jansenville District, in an area that is extensively mineralised, indicate the presence of the Dinocephalian Assemblage Zone (Turner 1981). This suggests that the main mineralised horizon in this area occurs lower in the succession than around Beaufort West.

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

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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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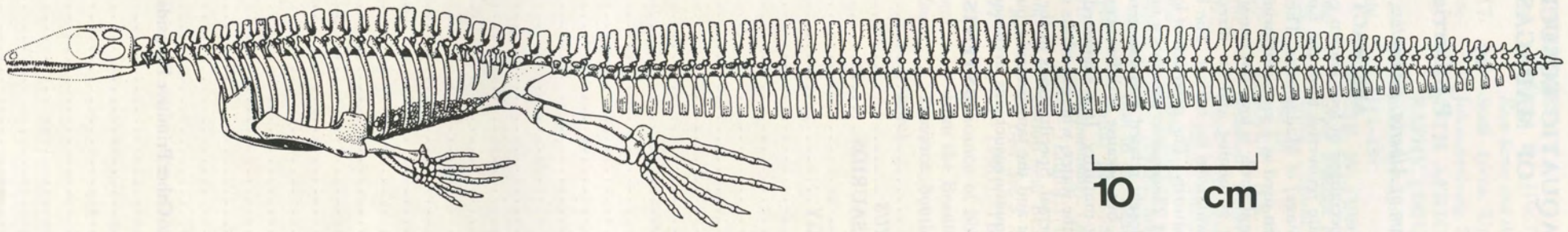

Reconstruction of the skeleton of *Hovasaurus boulei*, an aquatic eosuchian from the Late Permian of Madagascar.

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

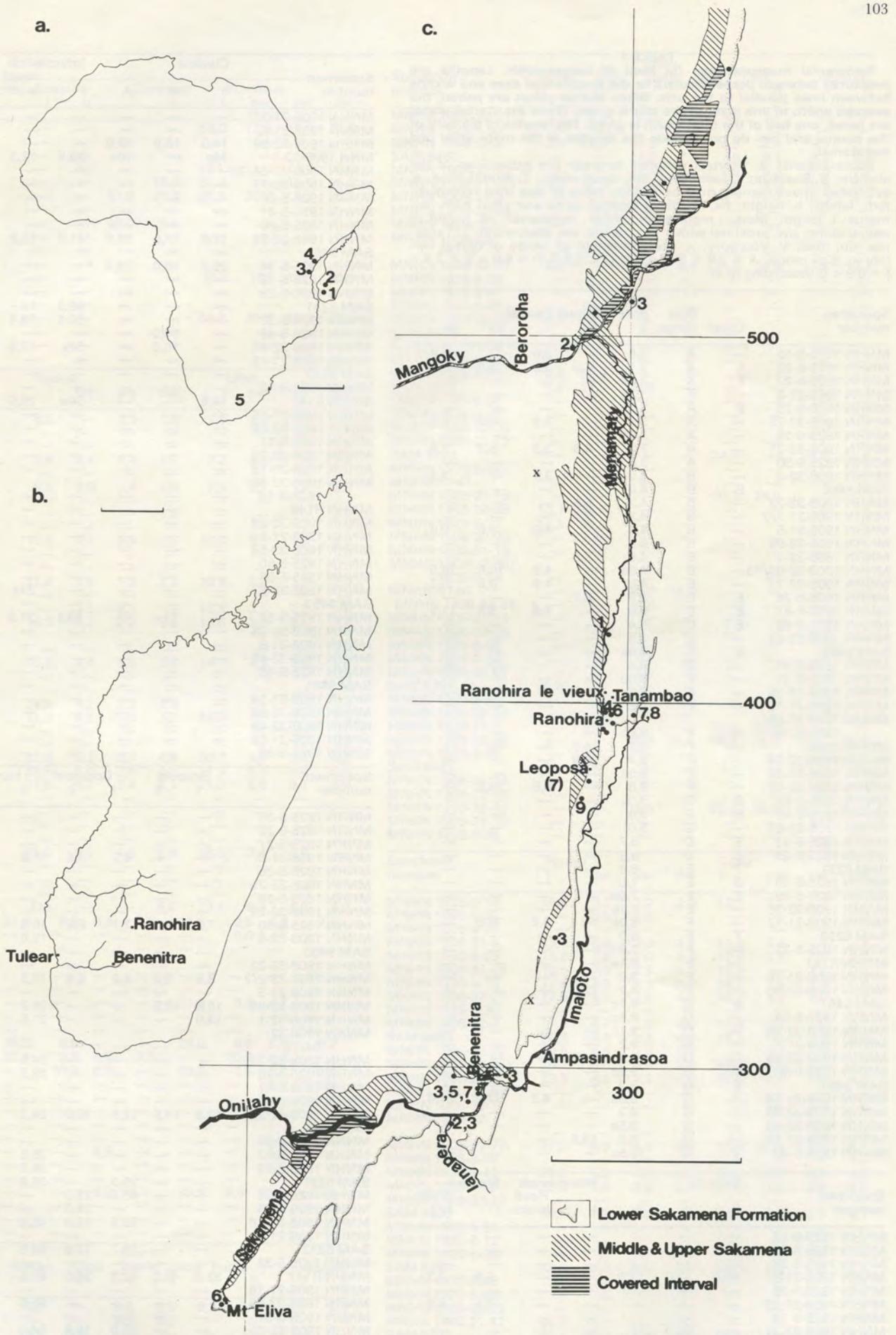

Figure 1. Eosuchian localities of Africa and Madagascar. a, Madagascar has been moved on the map to its probable position at the end of the Permian. 1, Mount Eliva. 2, Ranohira. 3, Tanga, Tanzania. 4, Mariakani, Kenya. 5, *Youngina* Localities. Scale = 1 000 km; b, the island of Madagascar; c, collecting 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

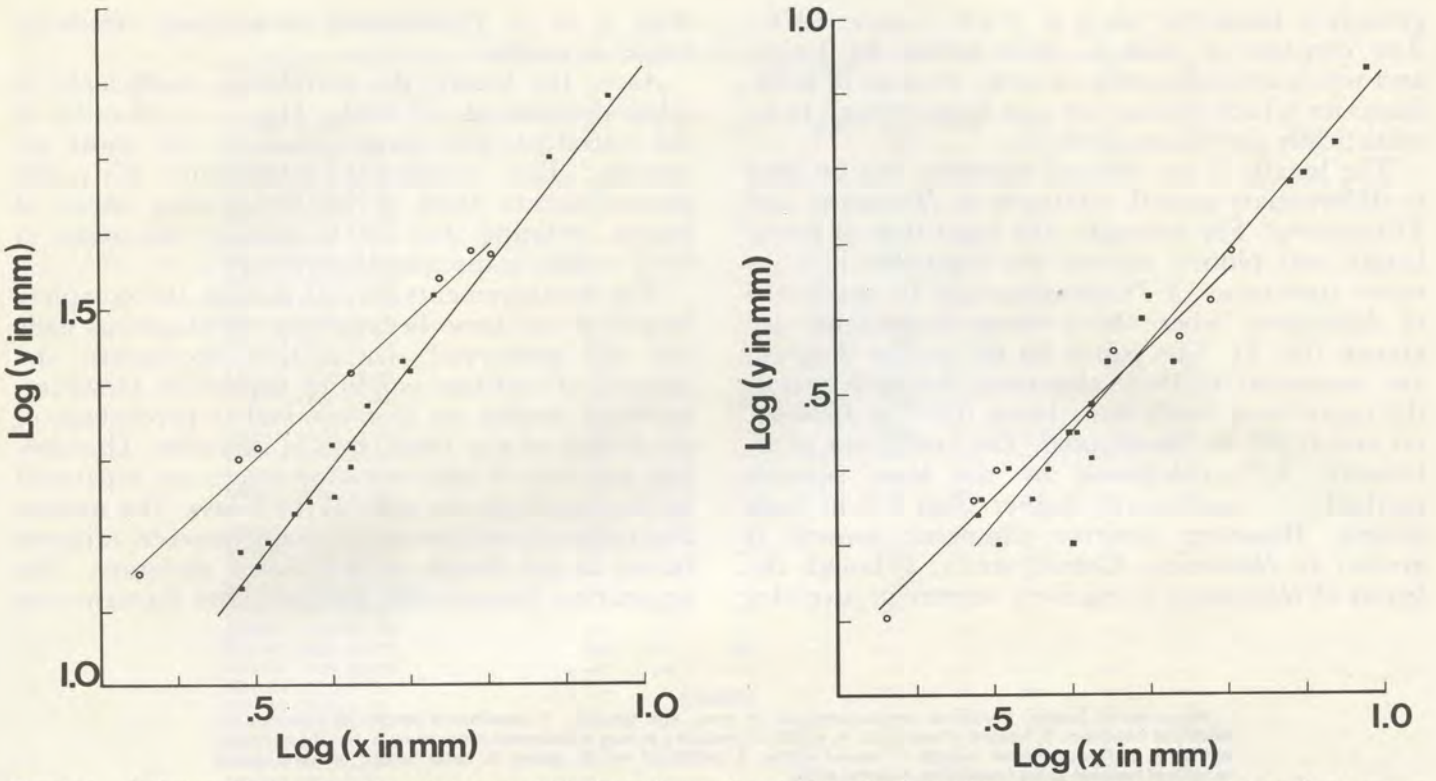

Figure 2. Relationship between length (a) or width (b) of femur (y) and length of associated thoracic centrum (x) in *Thadeosaurus* (circles) and *Hovasaurus* (squares). All measurements converted to logarithms. Data from Currie 1981b.

(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

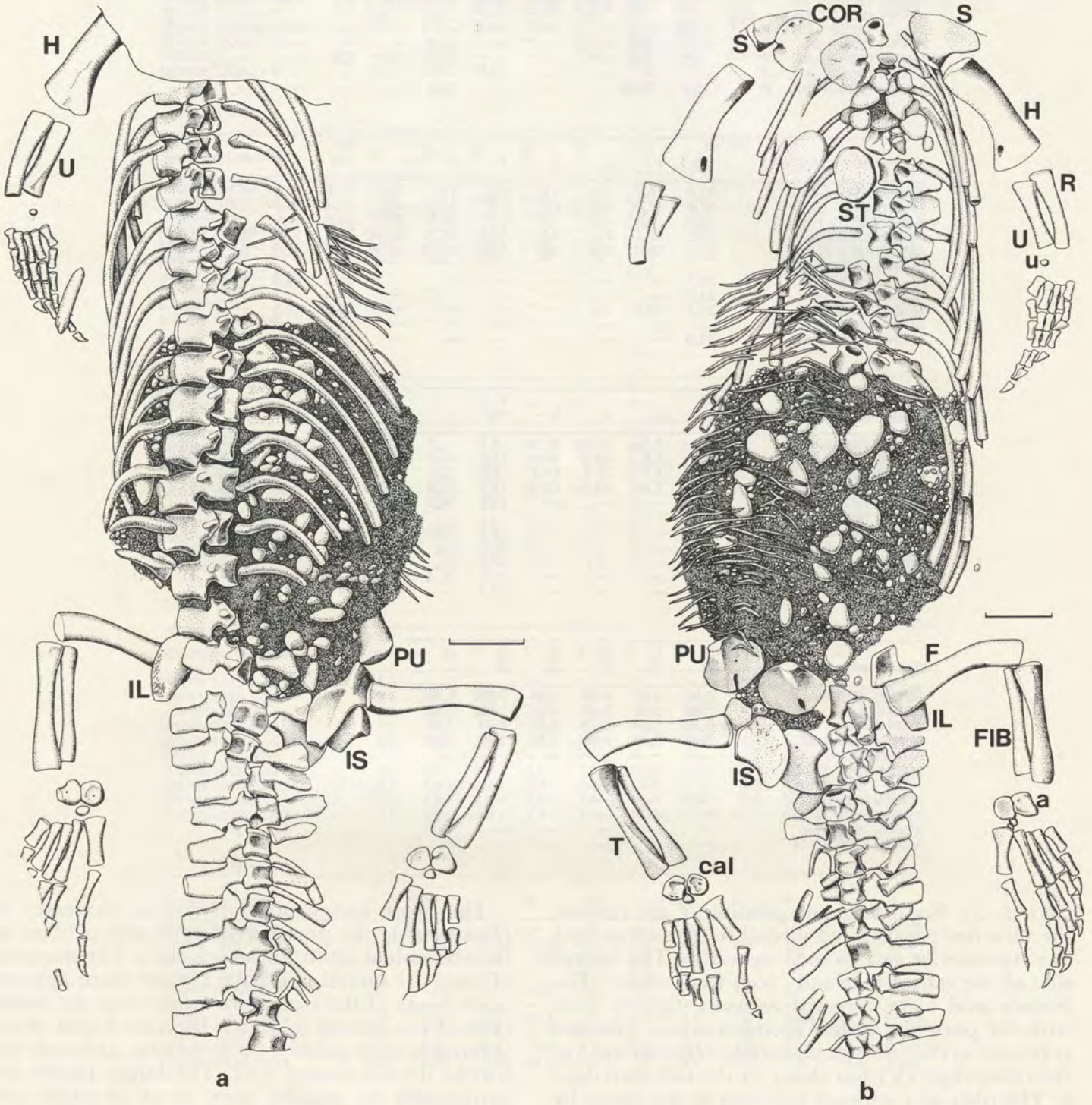

Figure 3. *Hovasaurus boulei*, lectotype. a, MNHN 1908-21-2; b. MNHN 1908-21-7; counterpart of MNHN 1908-21-2. Scale = 1 cm.

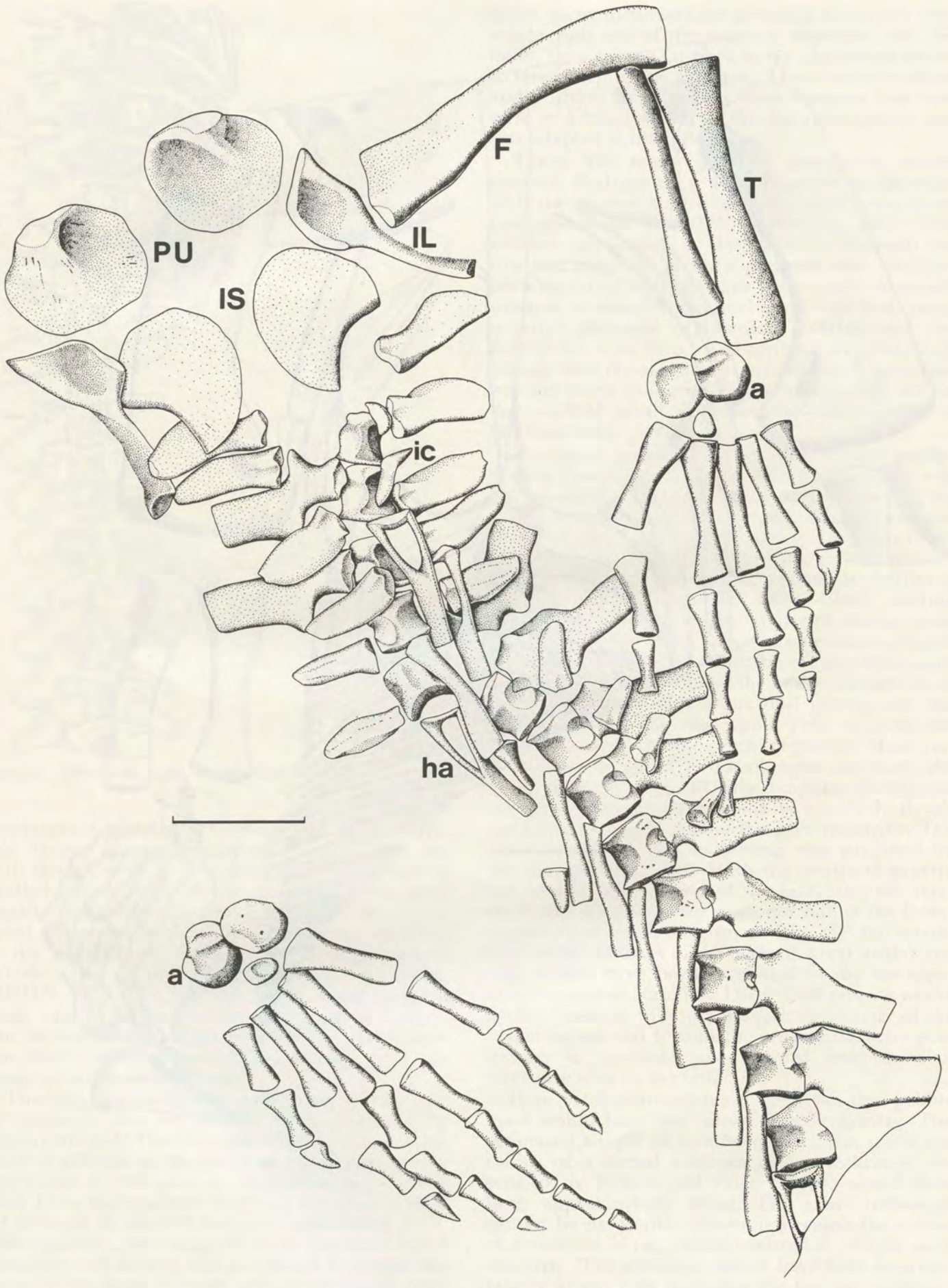

Figure 4. *Hovasaurus boulei*, MNHN 1908-32-77. Scale = 1 cm.

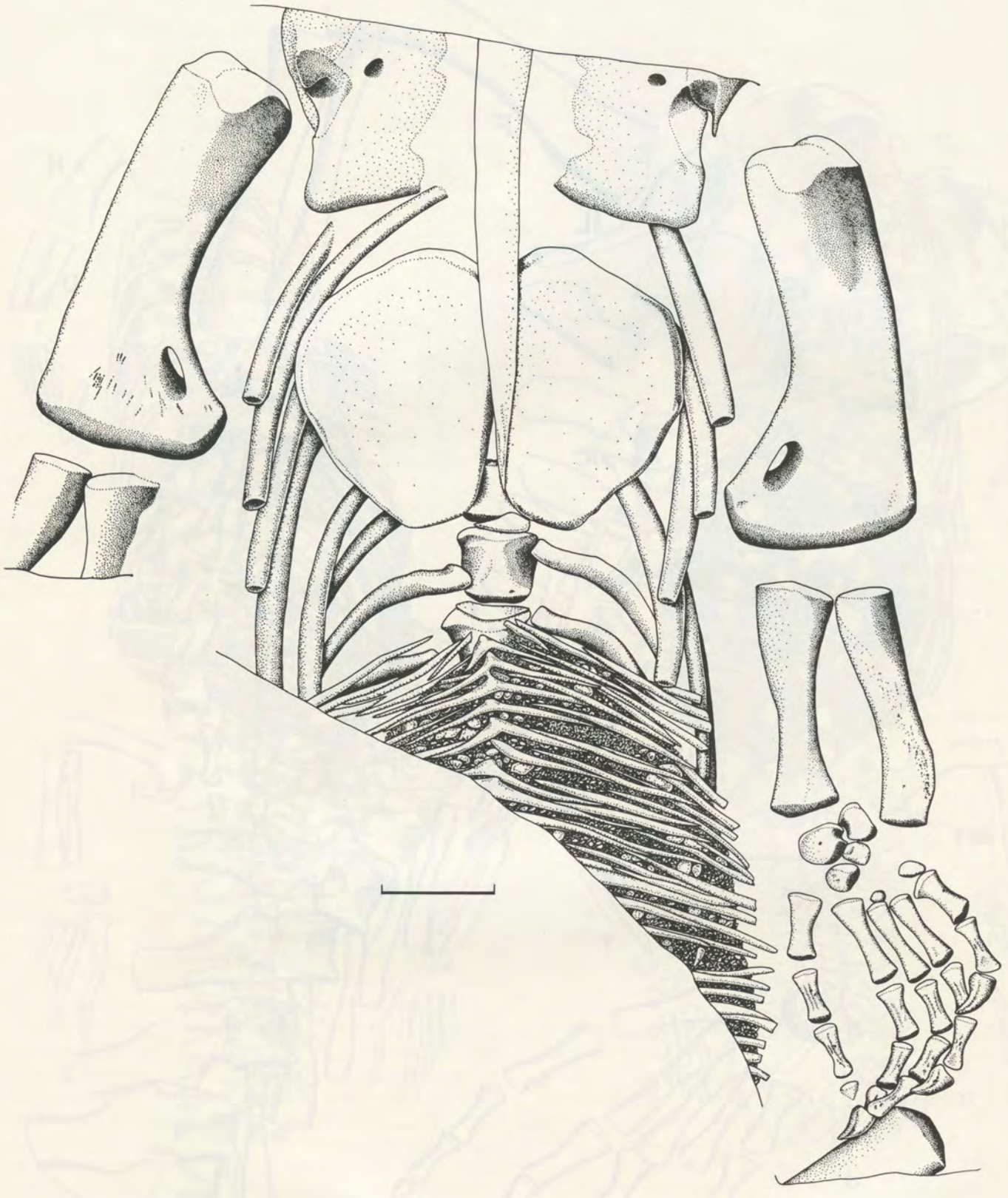

Figure 5. *Hovasaurus boulei*, MNHN 1925-5-12. Scale = 1 cm.

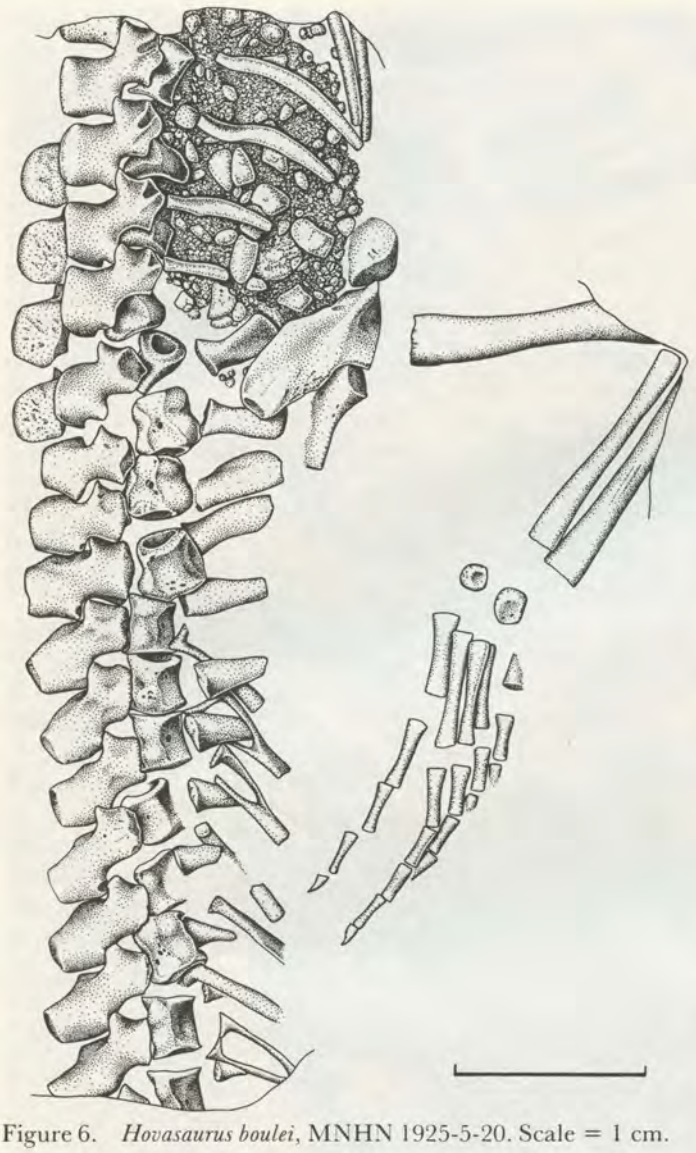

Figure 6. *Hovasaurus boulei*, MNHN 1925-5-20. Scale = 1 cm.

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

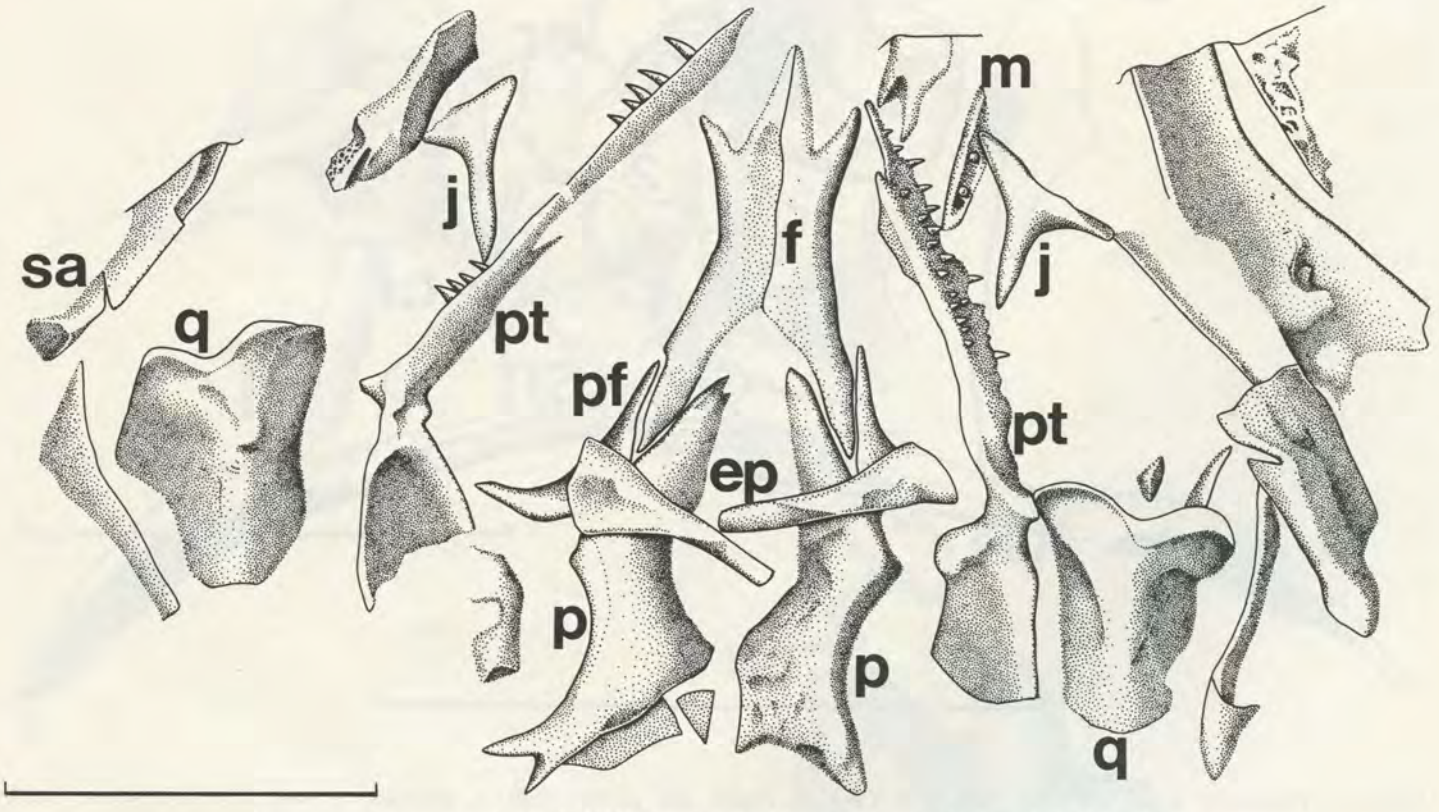

Figure 8. *Hovasaurus boulei*, MNHN 1925-5-34. Ventral view of skull roof. Scale = 1 cm.

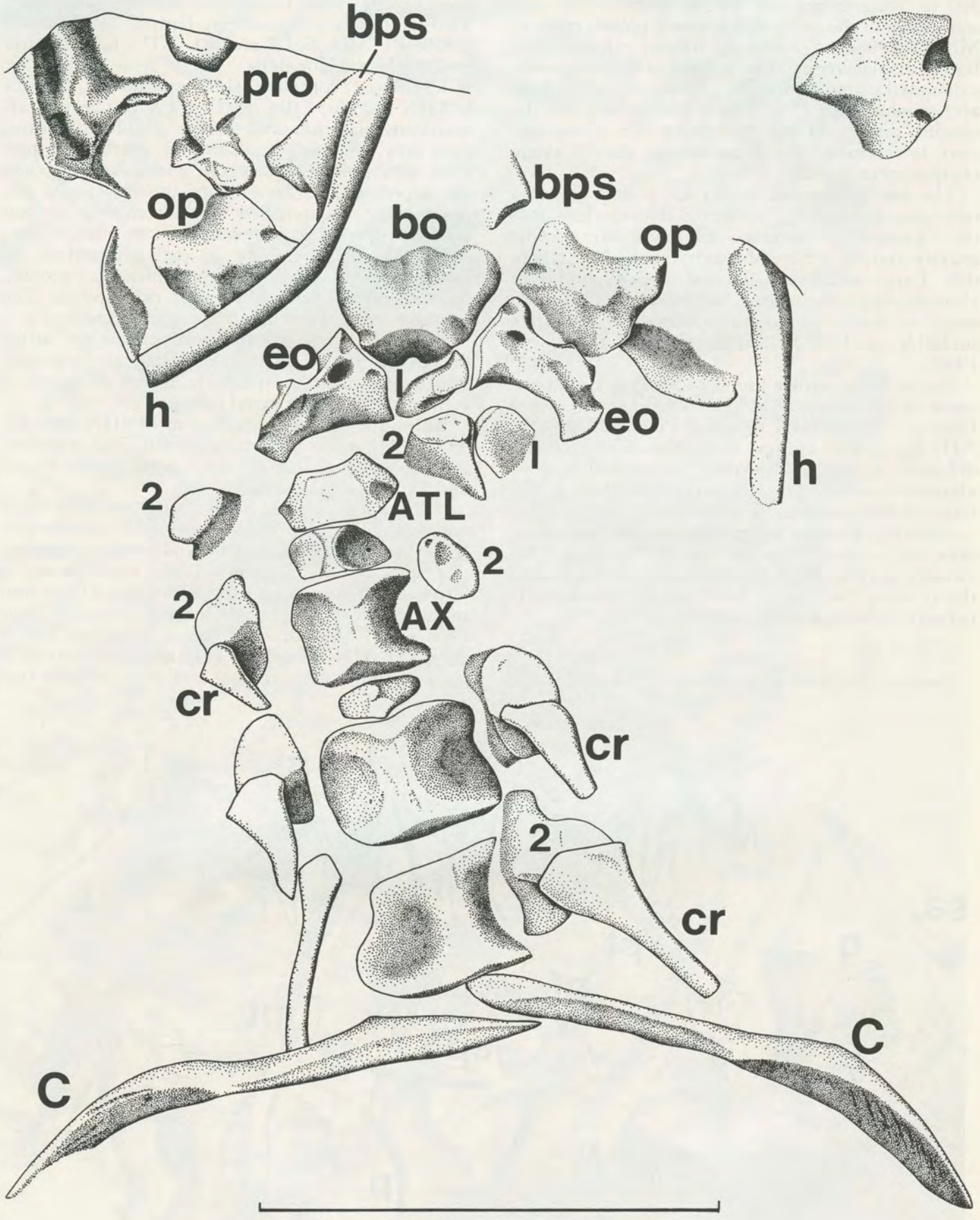

Figure 9. *Hovasaurus boulei*. MNHN 1925-5-30. Cervical region and partial skull, 1, proatlas; 2, base of neural spine. Scale = 1 cm. Upper right, reconstruction of left opisthotic (posterior view).

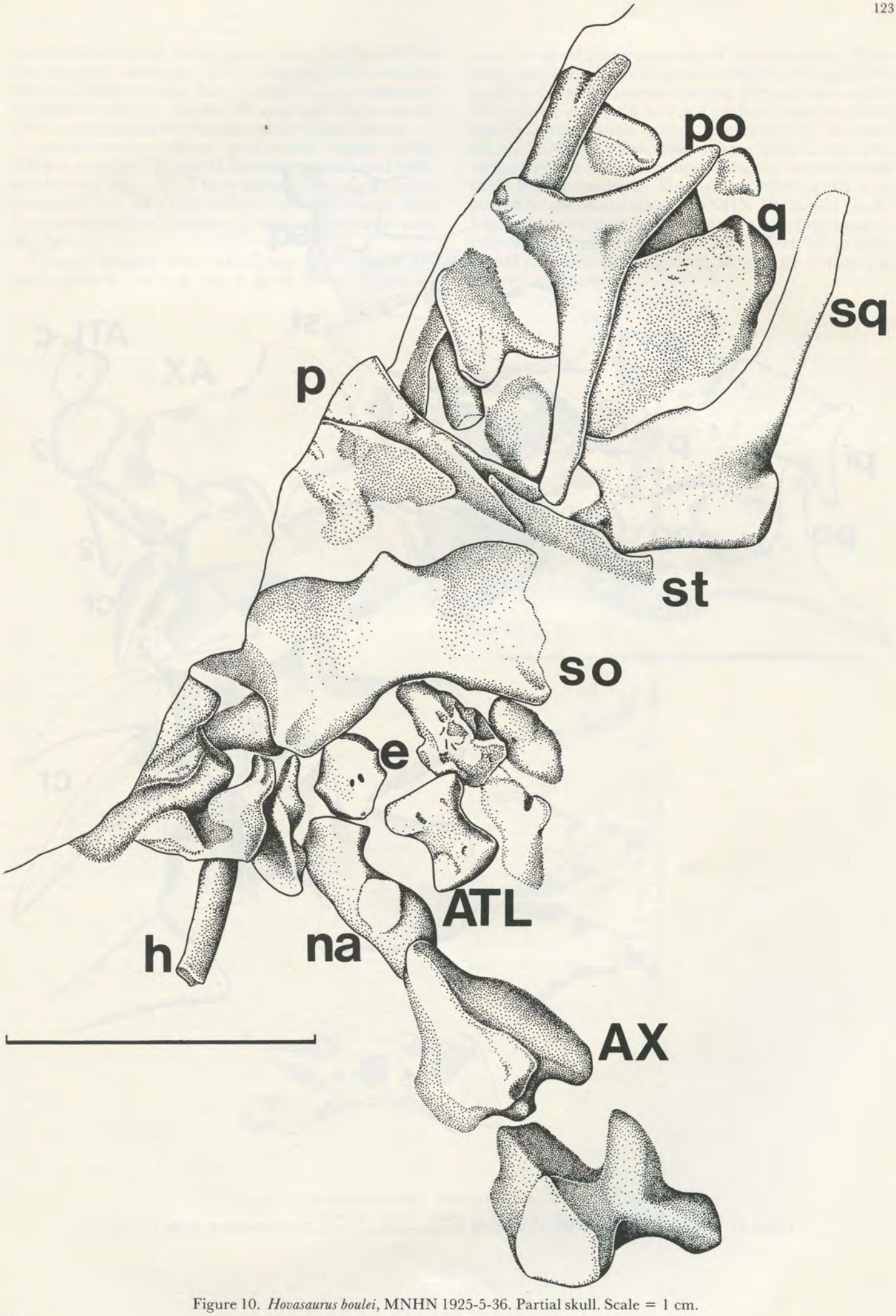

Figure 10. *Hovasaurus boulei*, MNHN 1925-5-36. Partial skull. Scale = 1 cm.

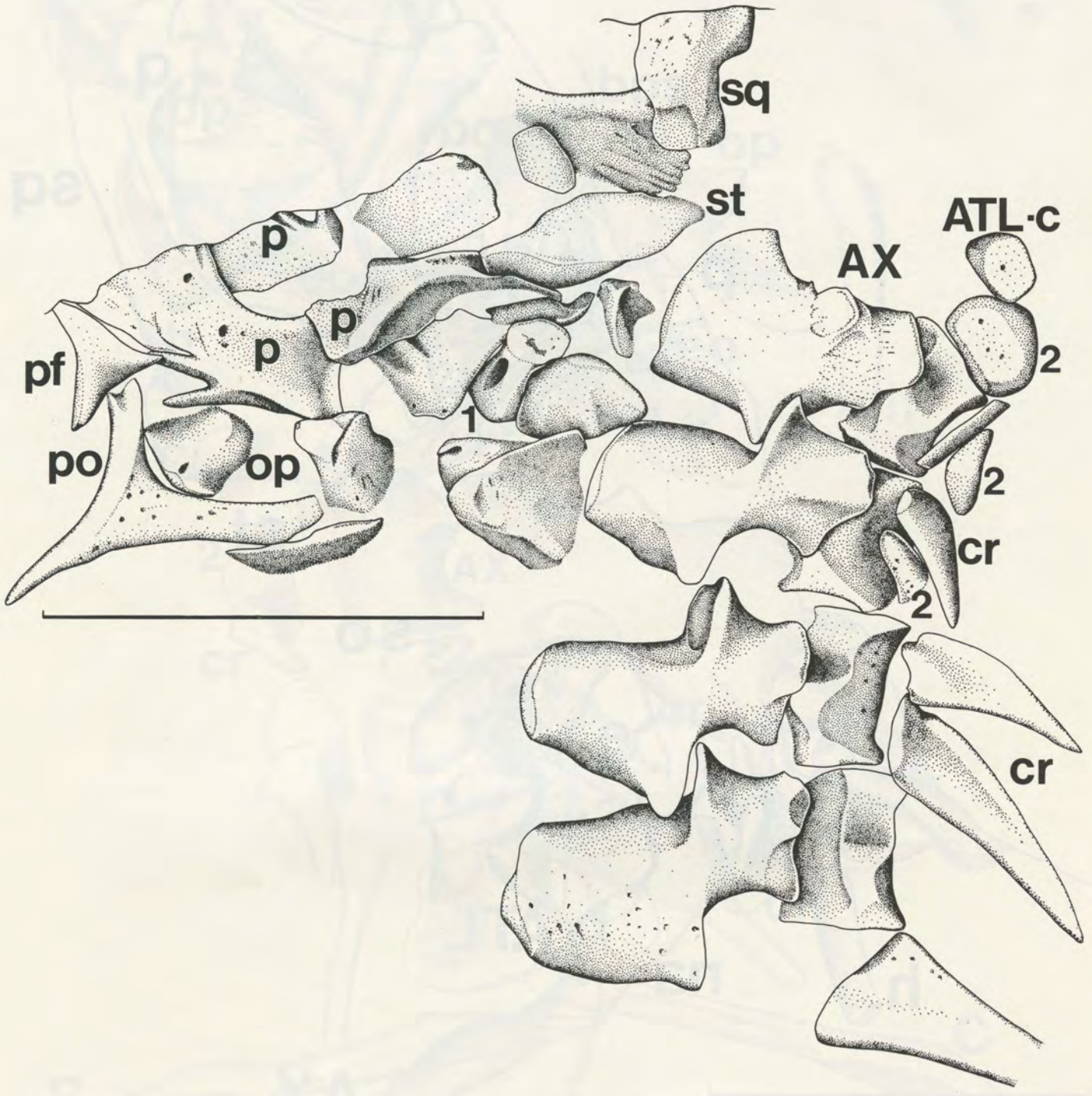

Figure 11. *Hovasaurus boulei*, MNHN 1908-32-99. Partial skull. 1, stapes; 2, intercentrum. Scale = 1 cm.

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.

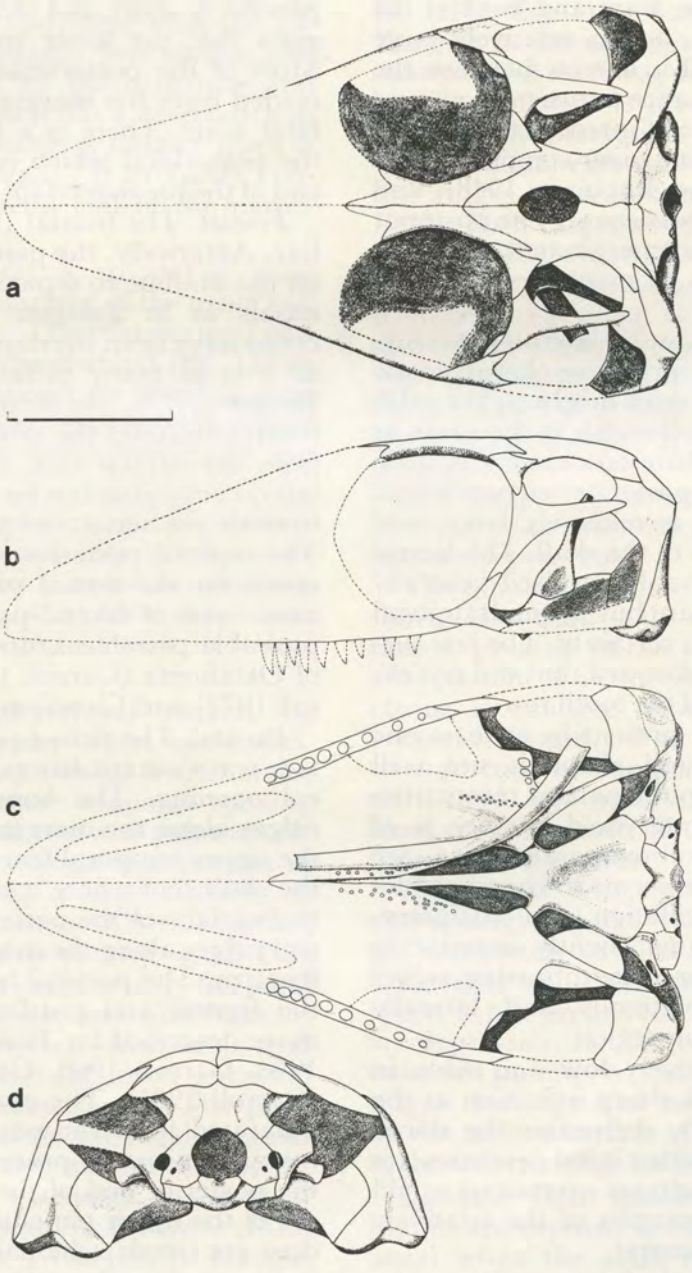

Figure 12. *Hovasaurus boulei*. Reconstruction of skull. a, dorsal view; b, lateral view; c, palatal view; d, occipital view. Scale = 1 cm.

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).

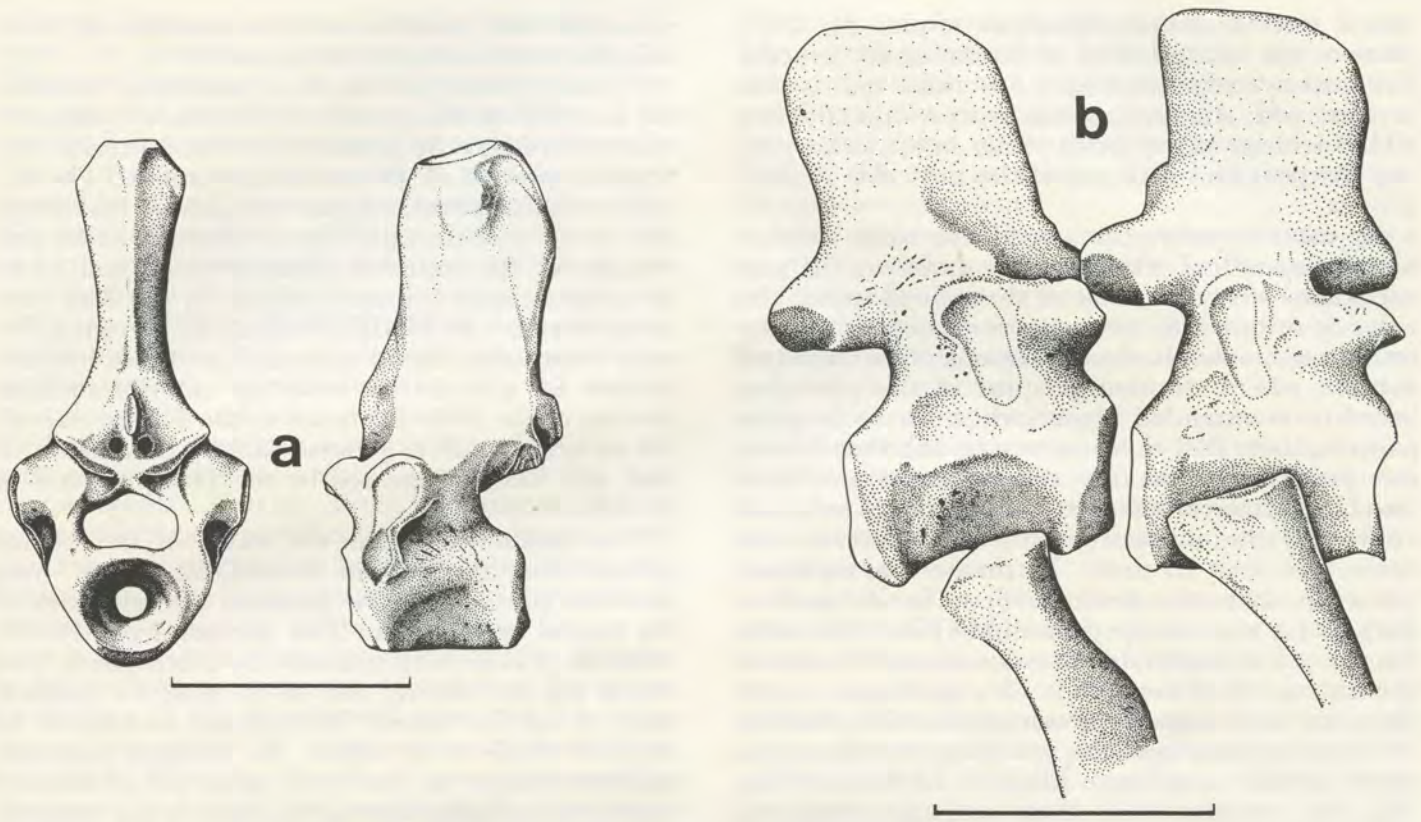

Figure 13. *Hovasaurus boulei*, dorsal vertebrae. a, SAM 9463, partially restored, posterior and lateral views of 13th dorsal vertebra; b, MNHN 1908-32-60, 16th and 17th dorsal vertebrae. Scale = 1 cm.

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.

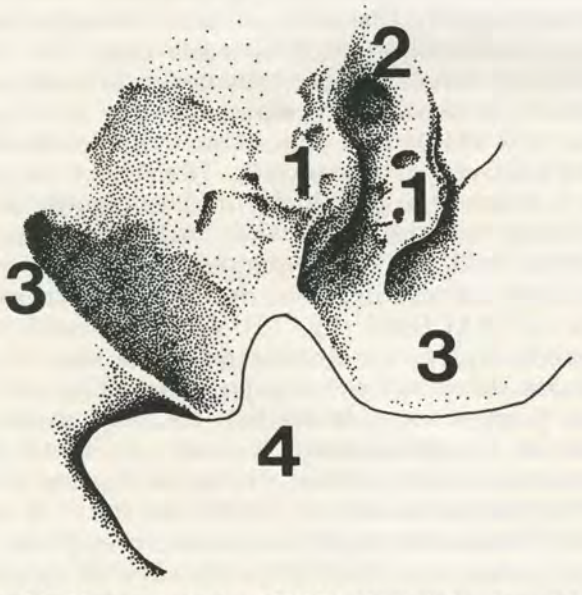

Figure 14. *Hovasaurus boulei*, MNHN 1908-32-24. Accessory articulations on anterior surface of 12th neural spine. 1, processes; 2, pit; 3, anterior zygapophyses; 4, neural canal. X9.

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

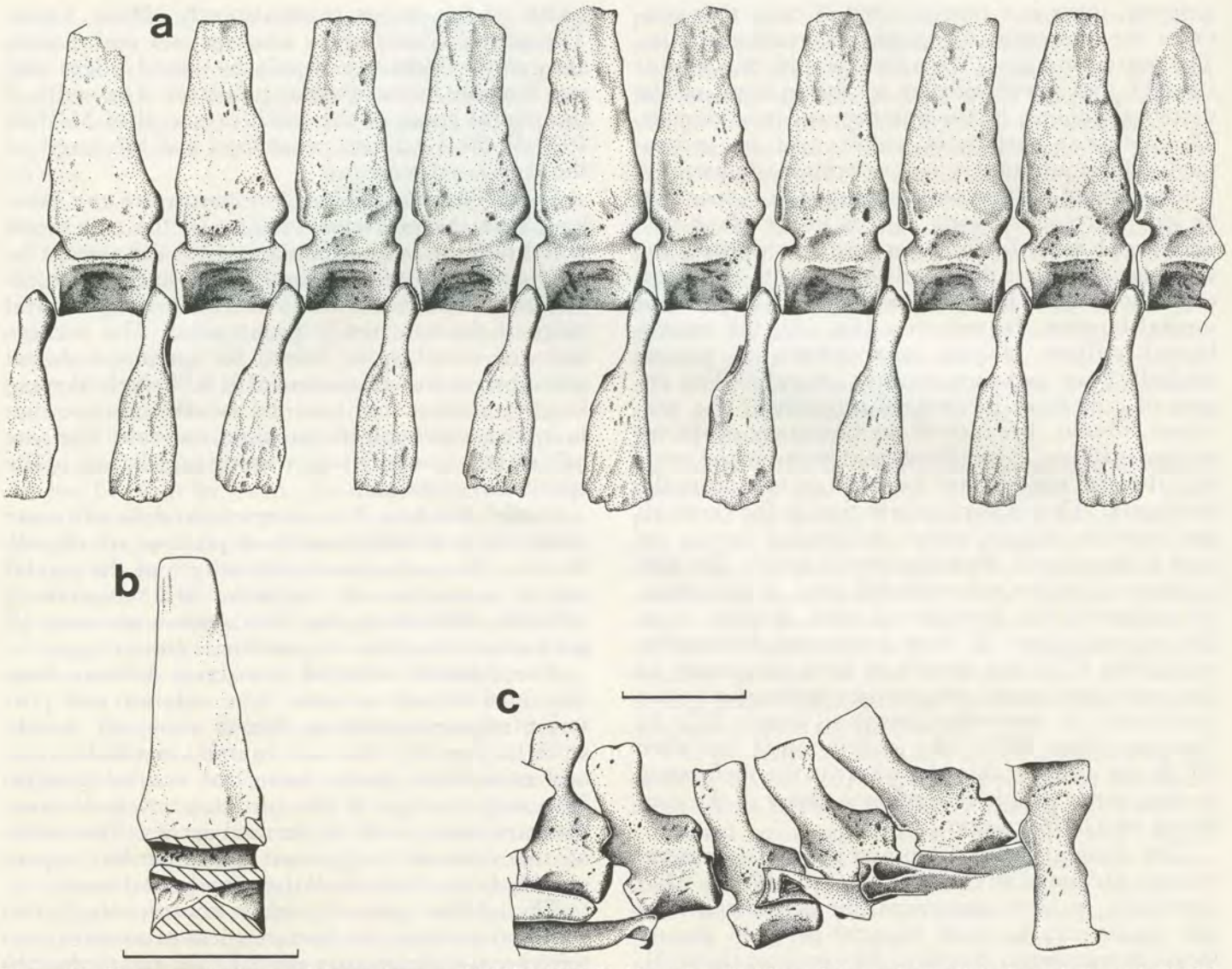

Figure 15. *Hovasaurus boulei*, caudal vertebrae. a, MNHN 1908-21-11, series of mid-caudal vertebrae (right lateral view); b, SAM 9462, mid-caudal vertebra, broken open to show neural and notochordal canals; c, SAM 9456, distal caudals, approximately 58th–63rd. Scale = 1 cm.

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*.

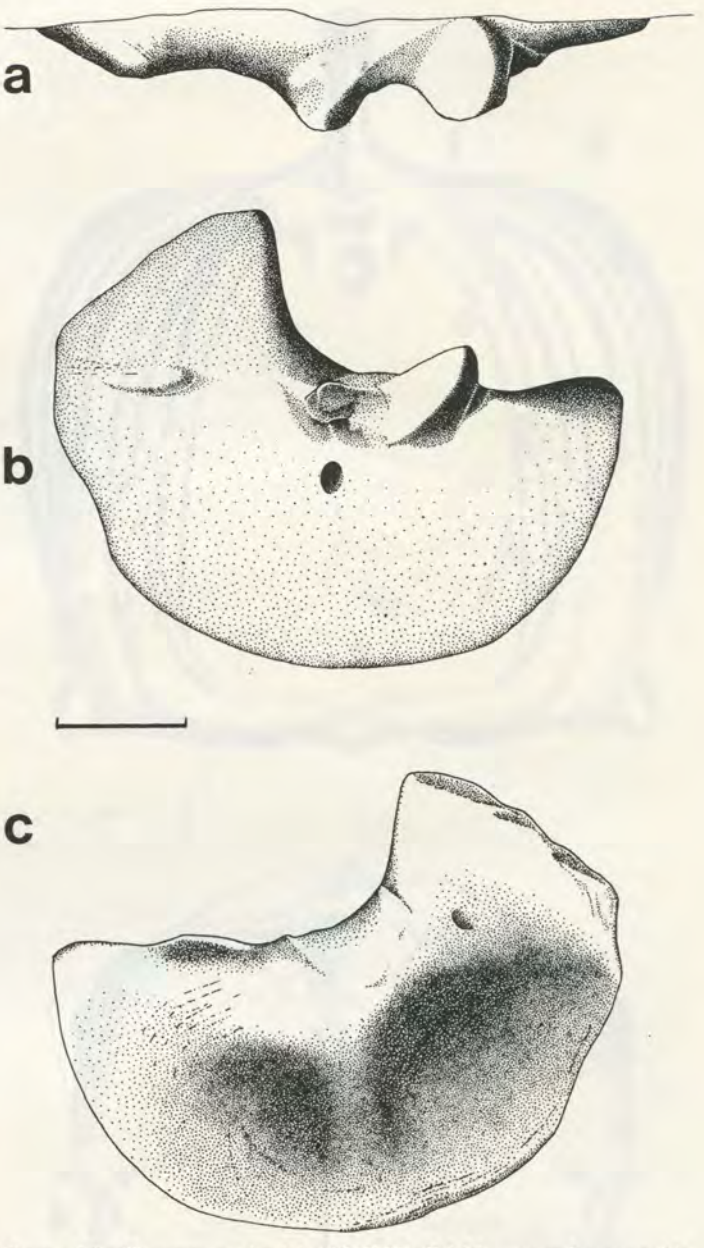

Figure 16. *Hovasaurus boulei*, MNHN R147, scapulocoracoid. a, lateral view; b, ventral view; c, dorsal view. Scale = 1 cm.

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

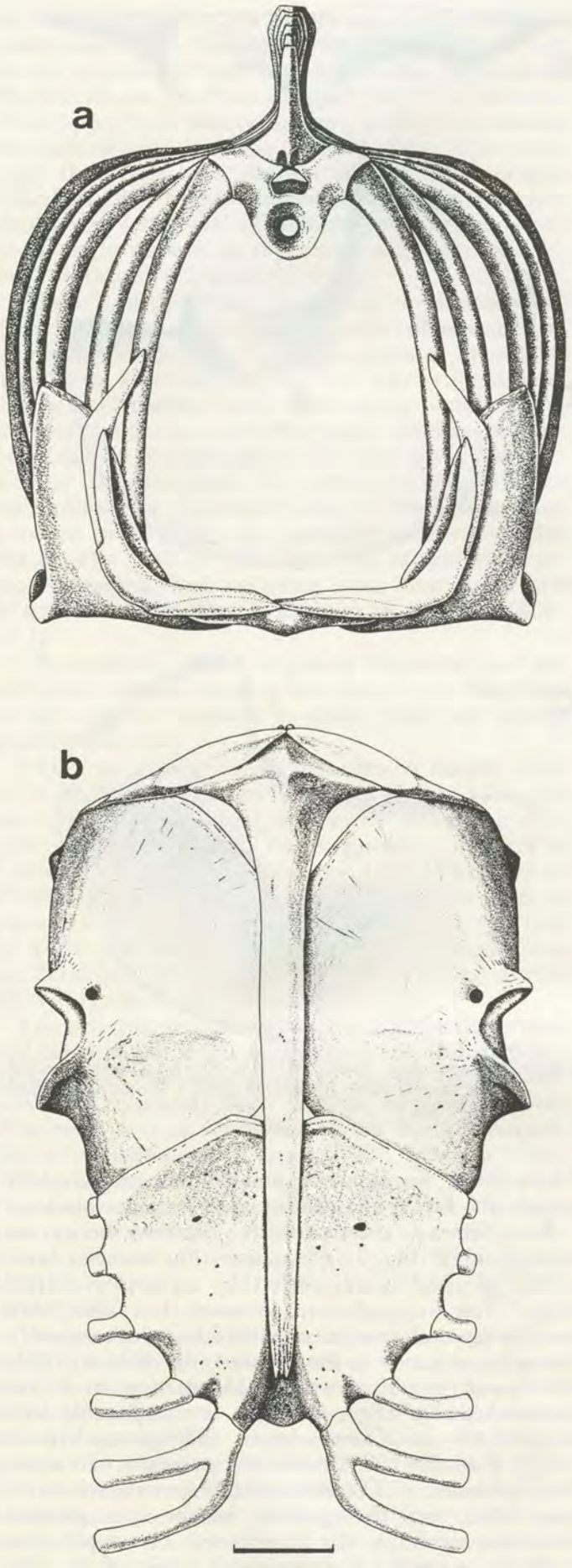

Figure 17. *Hovasaurus boulei*, reconstruction of pectoral region, a, anterior view; b, ventral view. Scale = 1 cm.

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*

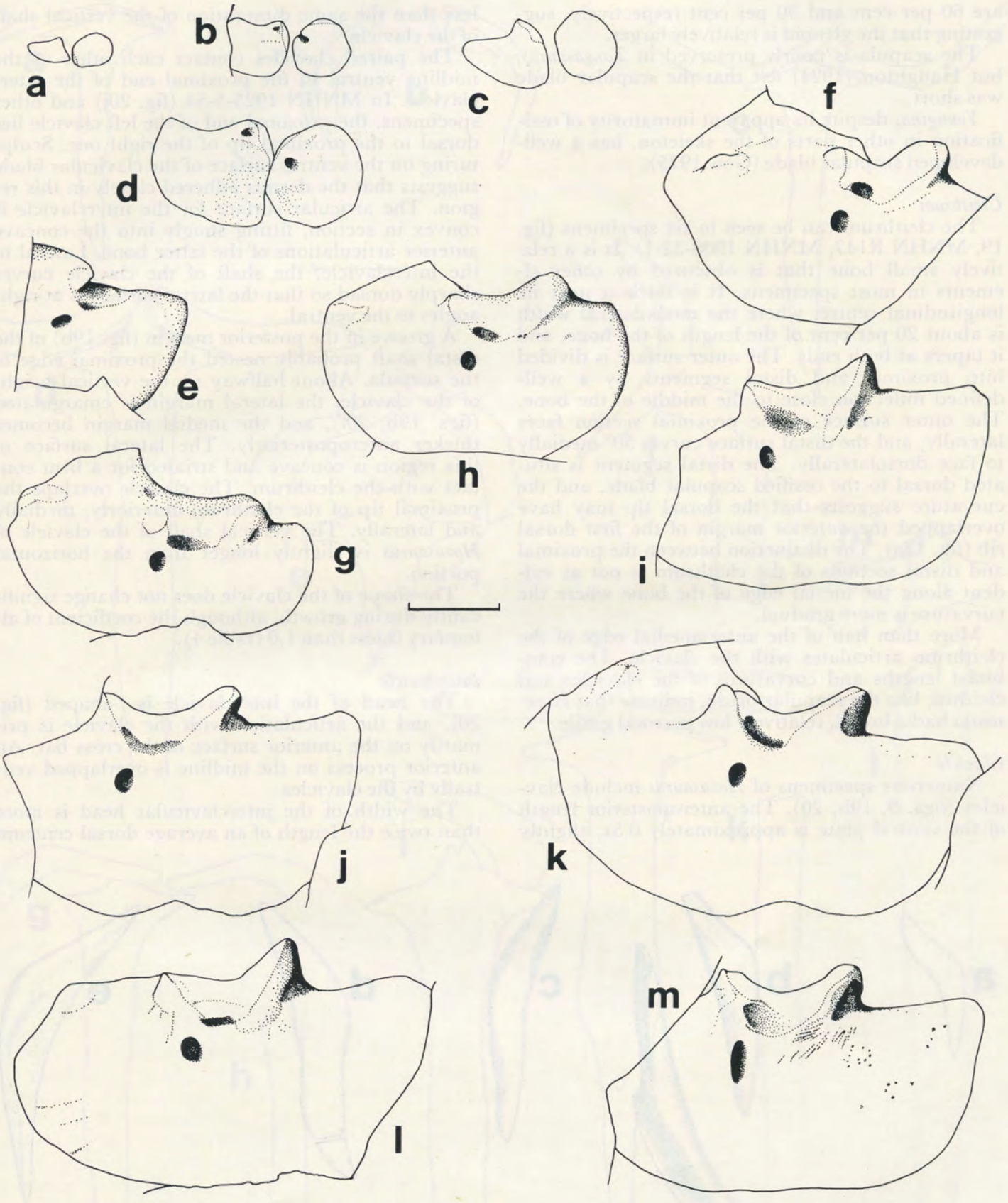

Figure 18. *Hovasaurus boulei*, scapulocoracoid, ventral view. a, MNHN 1908-21-8; b, MNHN 1925-5-30; c, MNHN 1908-21-7; d, MNHN 1908-32-23; e, MNHN 1925-5-12; f, MNHN 1925-5-49, partially restored from right side; g, MNHN 1908-32-26; h, MNHN 1908-32-27; i, MNHN 1925-5-56; j, MNHN 1908-21-18; k, MNHN 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

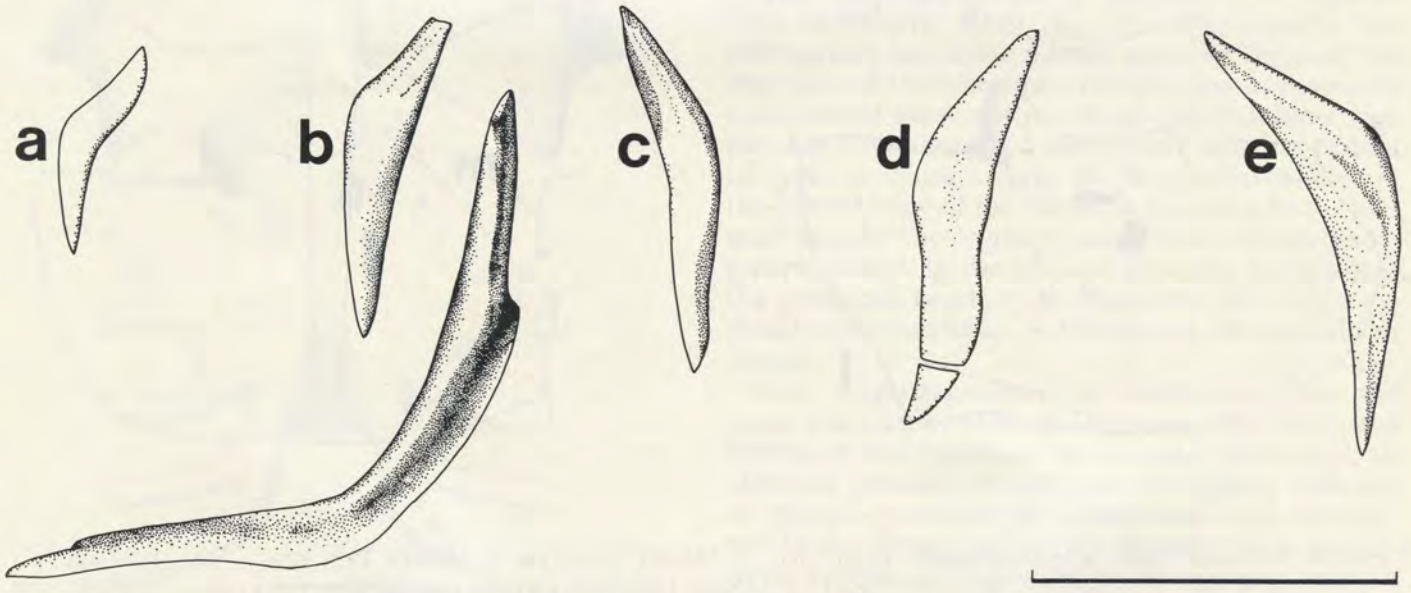

Figure 19. *Hovasaurus boulei*, cleithrum. a, MNHN 1908-21-8, posterior view of left cleithrum; b, MNHN 1908-32-99, anterior view of right cleithrum and posterior view of right clavicle; c, MNHN 1908-32-99, anterior view of left cleithrum; d, MNHN 1908-32-23, anterior view of right cleithrum; e, MNHN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

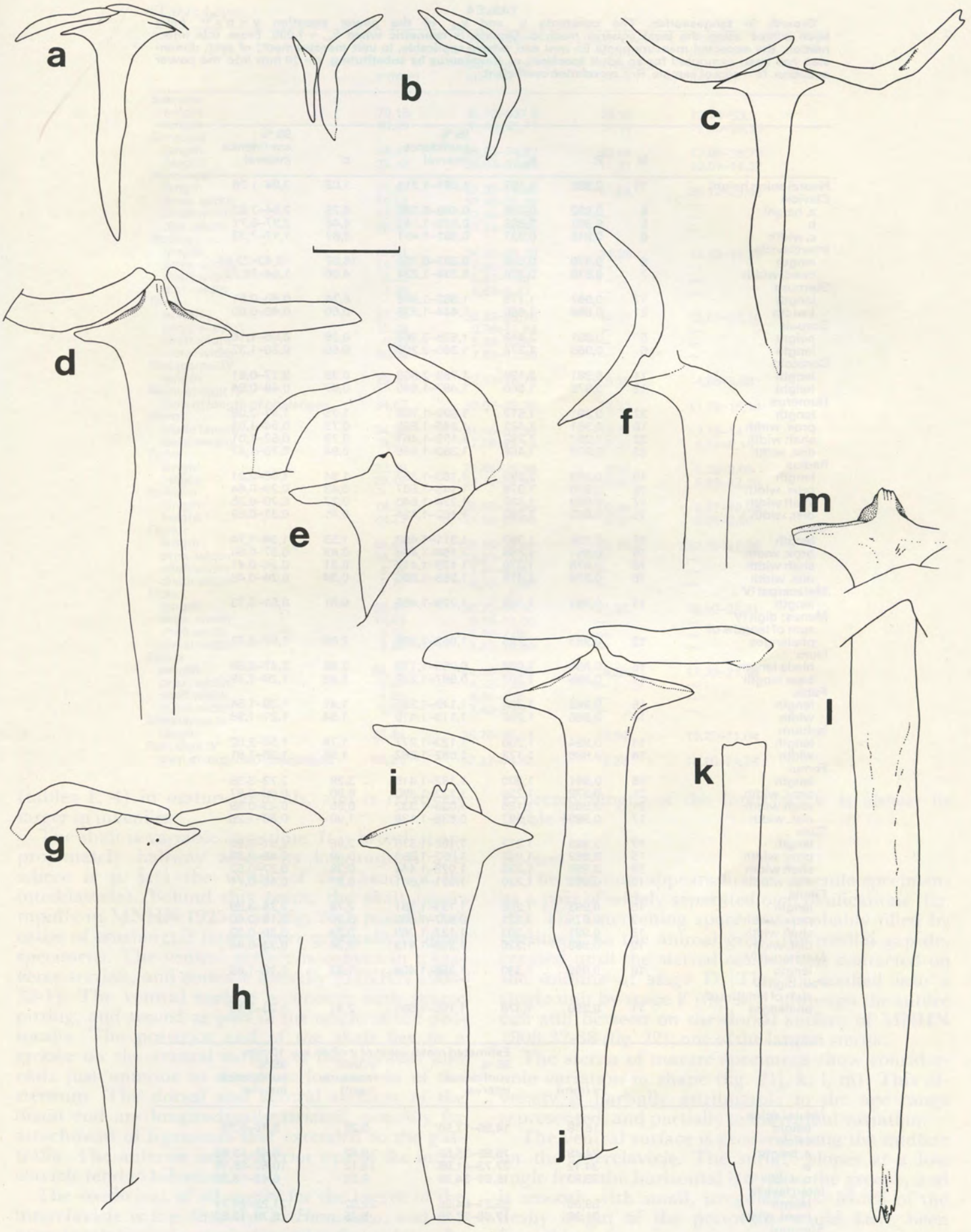

Figure 20. *Hovasaurus boulei*, dermal elements of pectoral girdle. a, MNHN 1925-5-30, interclavicle and clavicles; b, MNHN 1908-32-99, clavicles and cleithra; c, MNHN 1908-32-23, interclavicle and clavicles; d, MNHN 1925-5-38, interclavicle and clavicles; e, MNHN 1925-5-49, interclavicle and clavicles; 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-

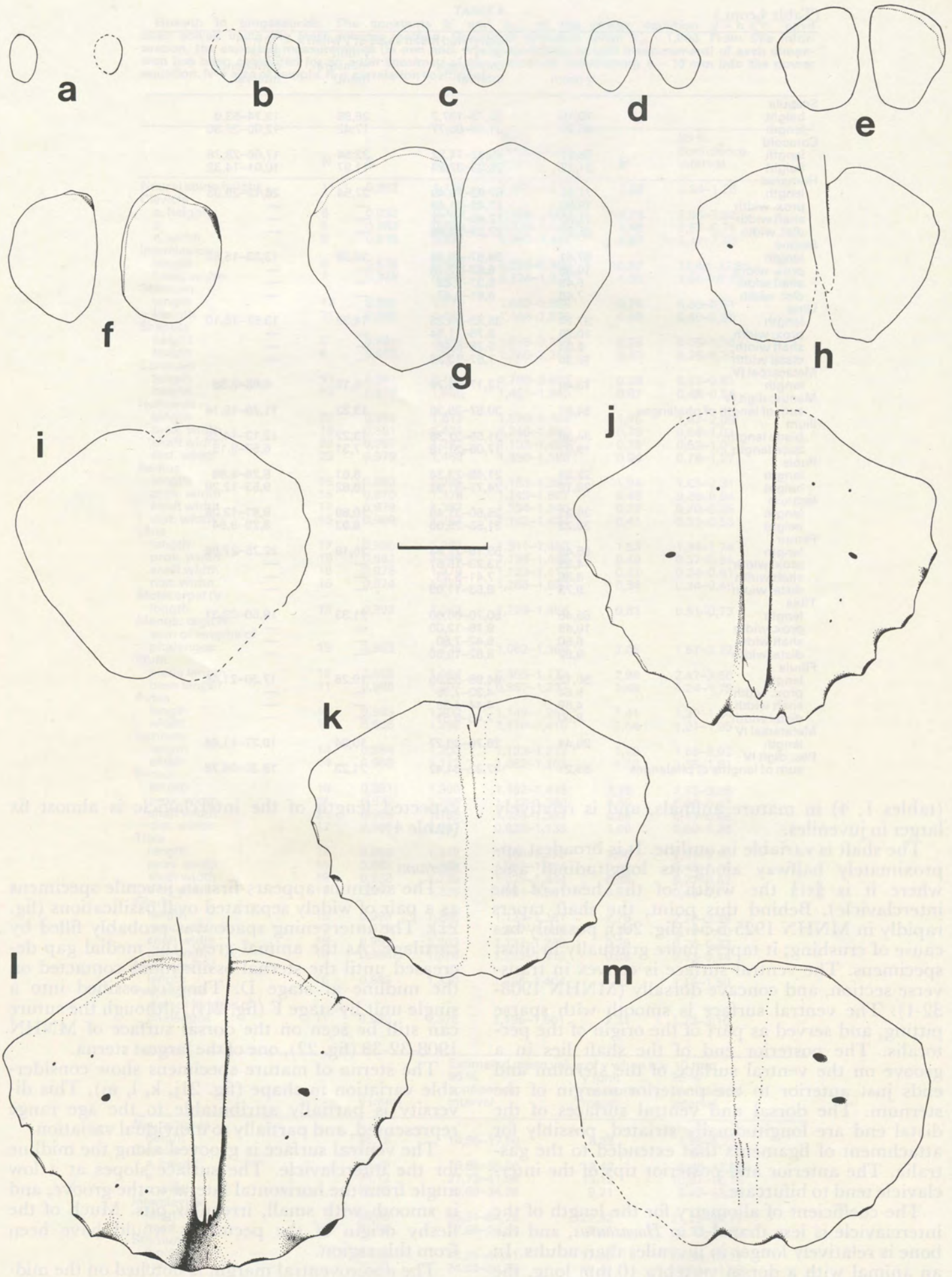

Figure 21. *Hovasasaurus boulei*, sternum, ventral view. a, MNHN 1908-21-8; b, MNHN 1908-32-29; c, MNHN 1925-5-30; d, MNHN 1908-21-7; e, MNHN 1908-32-77; f, MNHN 1908-32-23; g, MNHN 1925-5-12; h, MNHN 1925-5-29; i, MNHN 1908-32-26; j, MNHN 1908-21-24; k, MNHN R147; l, MNHN 1908-21-18; m, MNHN 1908-32-67.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

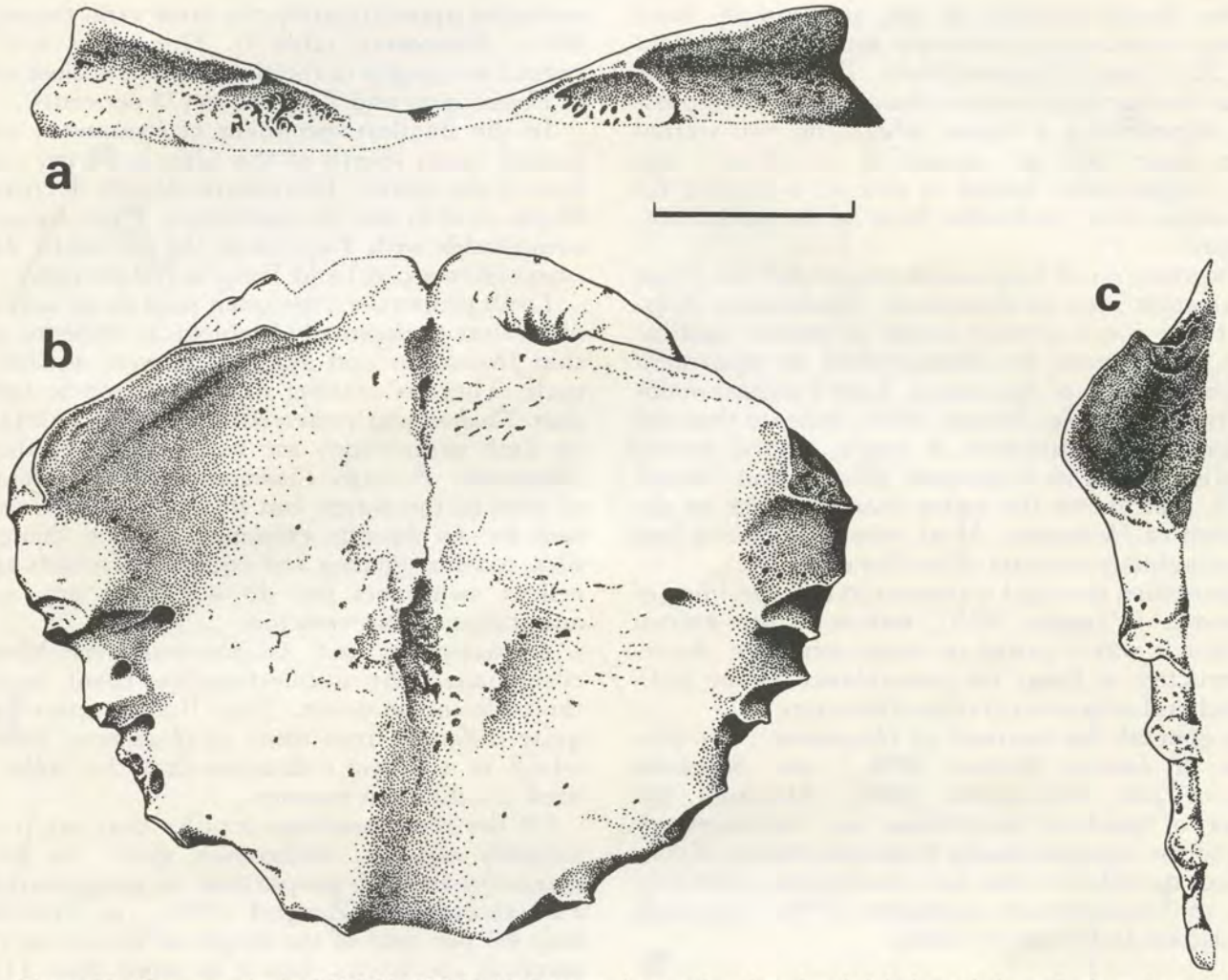

Figure 22. *Hovasaurus boulei*, MNHN 1908-32-38. Sternum in anterior, dorsal and right lateral views. Scale = 1 cm.

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

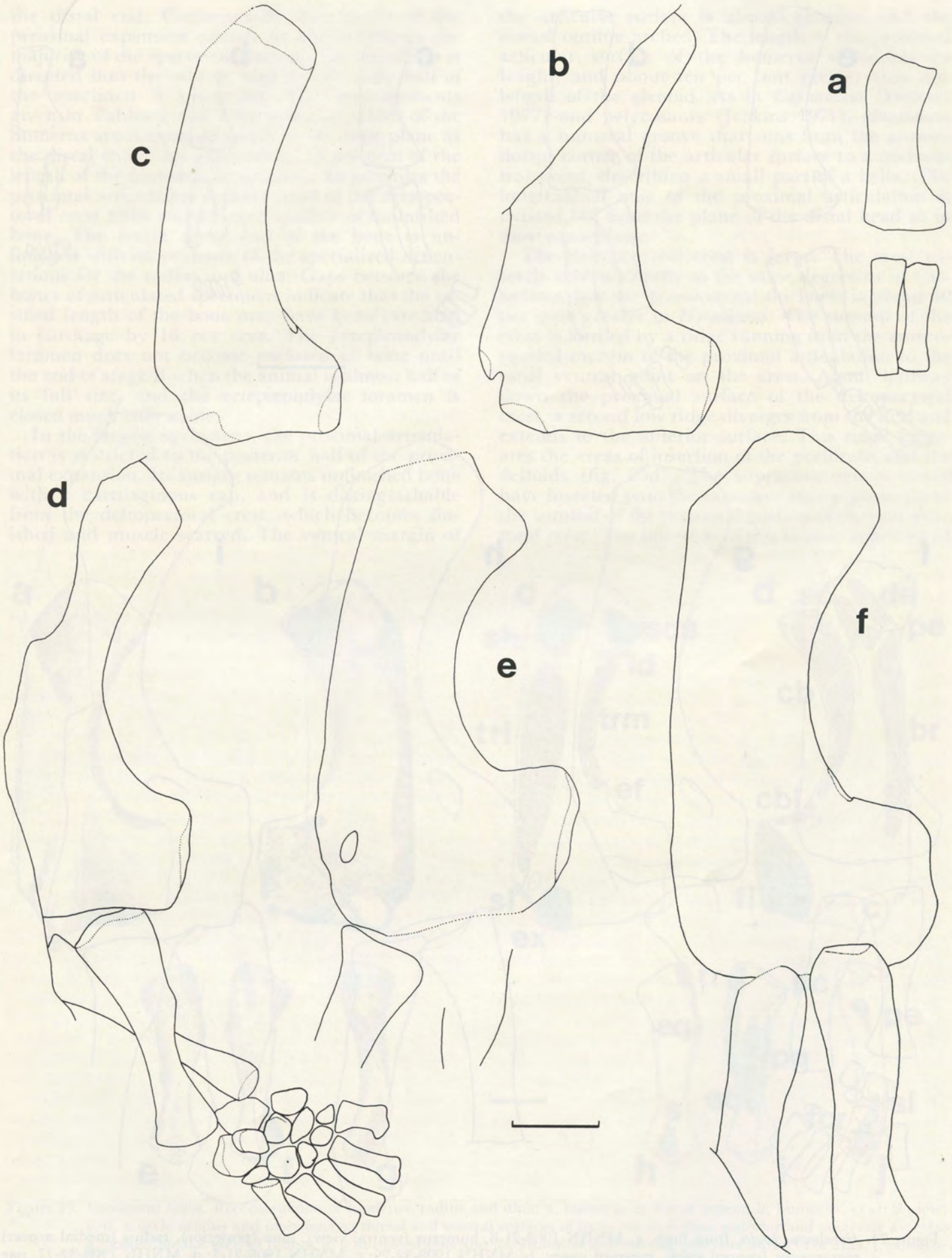

Figure 23. *Hovasaurus bolei*, front limb, a, MNHN 1908-32-1, humerus (dorsal view), radius (anterior view), ulna (anterior view); b, MNHN 1925-5-50, humerus, reversed image; c, MNHN 1908-32-24, humerus, reversed; d, MNHN 1908-32-59, humerus, radius, ulna, carpus, reversed image; e, MNHN 1925-5-46, humerus;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

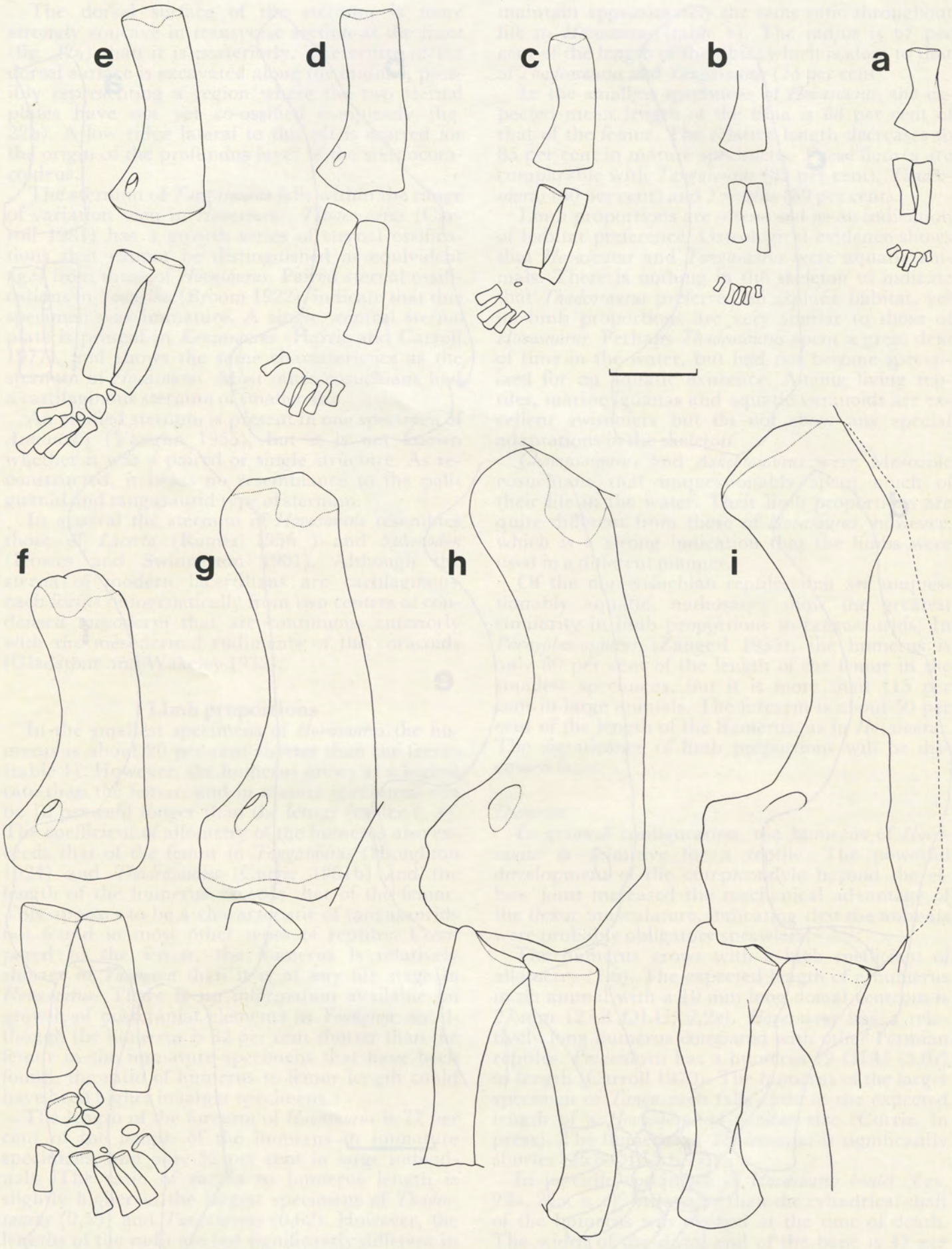

Figure 24. *Hovasaurus boulei*, front limb. a, MNHN 1908-21-8, humerus (ventral view), ulna (posterior), radius (medial aspect), metacarpus (ventral view), reversed image; b, MNHN 1908-32-29; c, MNHN 1908-21-7; d, MNHN 1908-32-77, partially restored from right side; e, MNHN 1908-32-23, reversed; f, MNHN 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

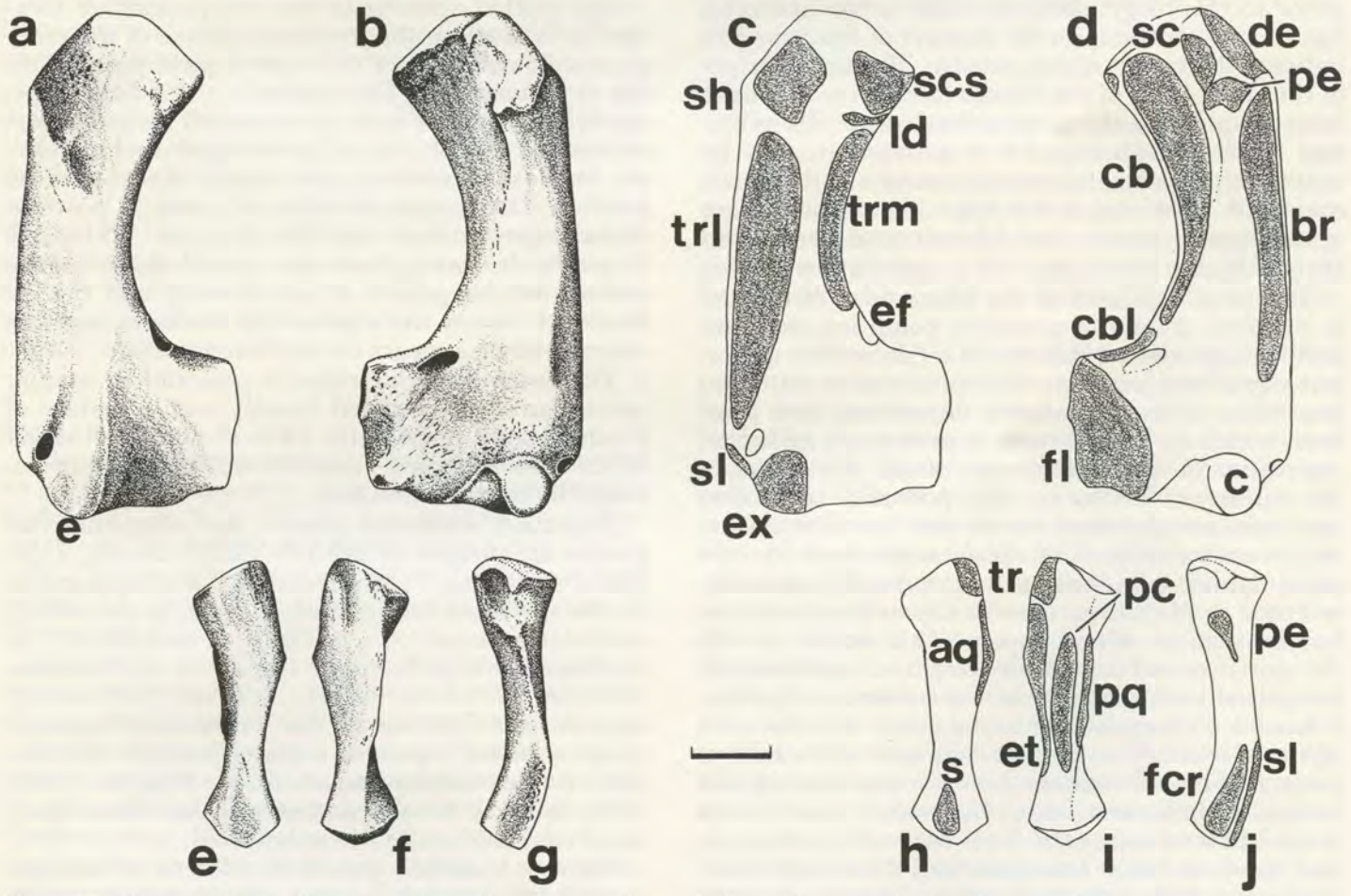

Figure 25. *Hovasaurus boulei*. Reconstruction of humerus, radius and ulna; a, humerus in dorsal aspect; b, humerus, ventral view; c, d, muscle origins and insertions on dorsal and ventral surfaces of humerus; e, f, ulna, anterior and posterior aspects; g, posteromedial view of radius; h, i, muscle origins 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 3,7x. This is not significantly different from the length in *Thadeosaurus* (15,1 OLU; 3,9x). 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-

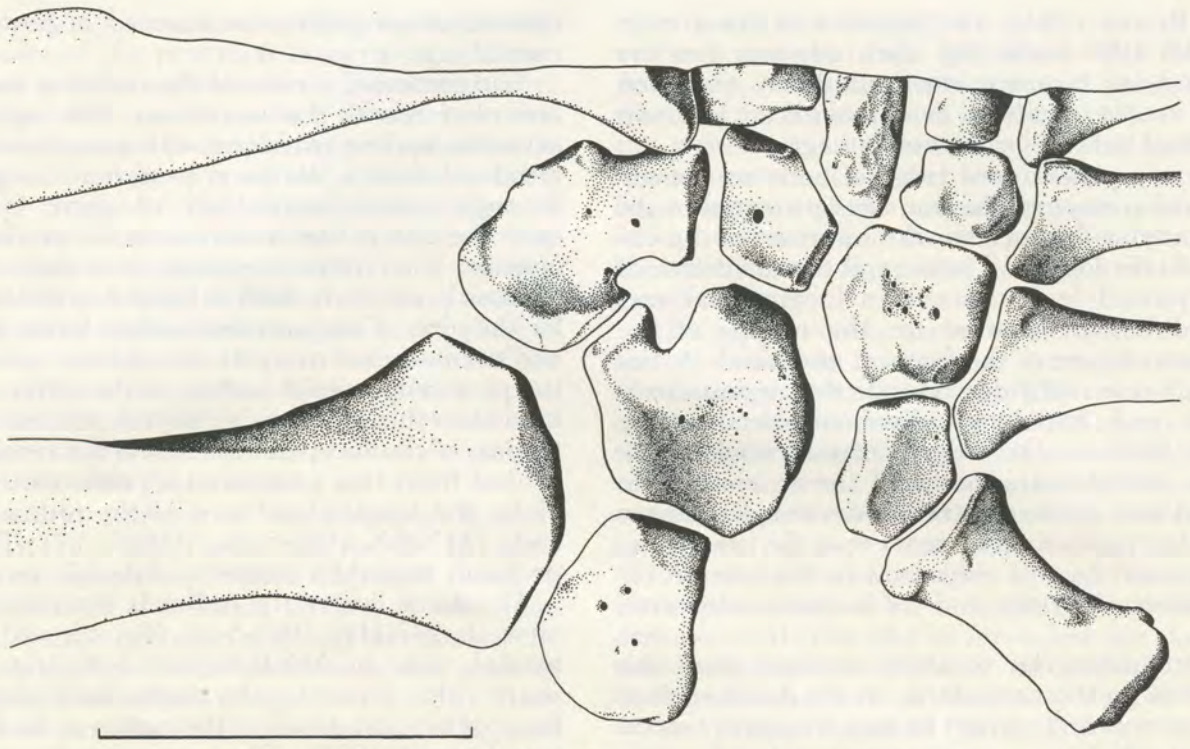

Figure 26. *Hovasaurus boulei*, SAM 9457, manus, ventral aspect. Scale = 1 cm.

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

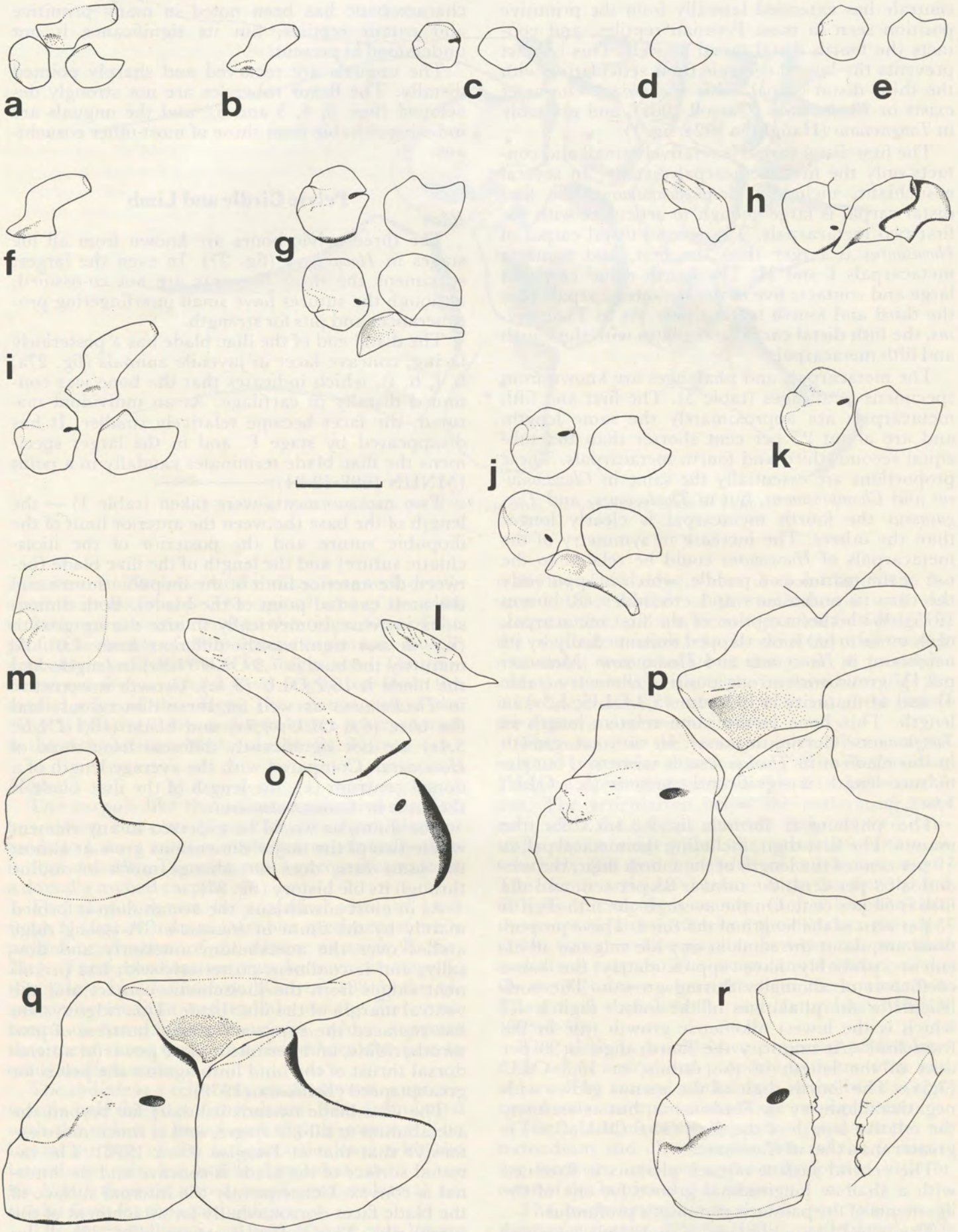

Figure 27. *Hovasaurus boulei*, pelvic girdle. a, MNHN 1925-5-10, composite drawing from right and left sides; b, MNHN 1925-5-20, reversed image; c, MNHN 1925-5-25; d, MNHN 1908-21-8, reversed; e, MNHN 1908-32-29, composite; f, MNHN 1908-32-21, reversed; g, SAM 9460; h, MNHN 1908-32-4, ilium (medial 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.

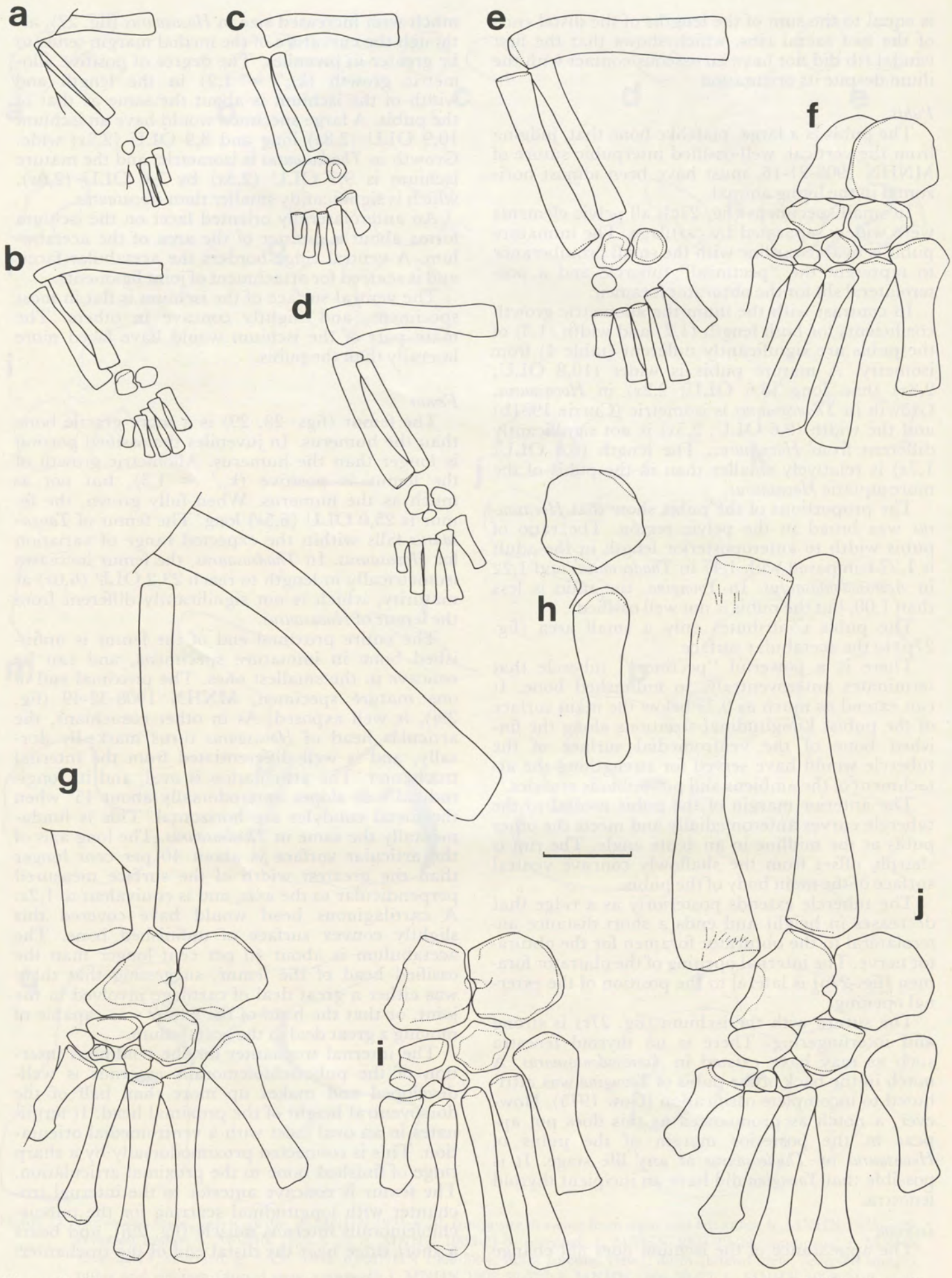

Figure 28. *Hovasaurus boulei*, femur (posterior view), tibia (posterior), fibula (anterior) and tarsus (dorsal). a, MNHN 1925-5-20, reversed image; b, MNHN 1925-5-18; c, MNHN 1908-32-21, reversed; d, MNHN 1908-21-2, reversed; e, MNHN 1925-5-41; f, MNHN 1925-8-14; g, MNHN 1908-32-24; h, MNHN 1908-21-6,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

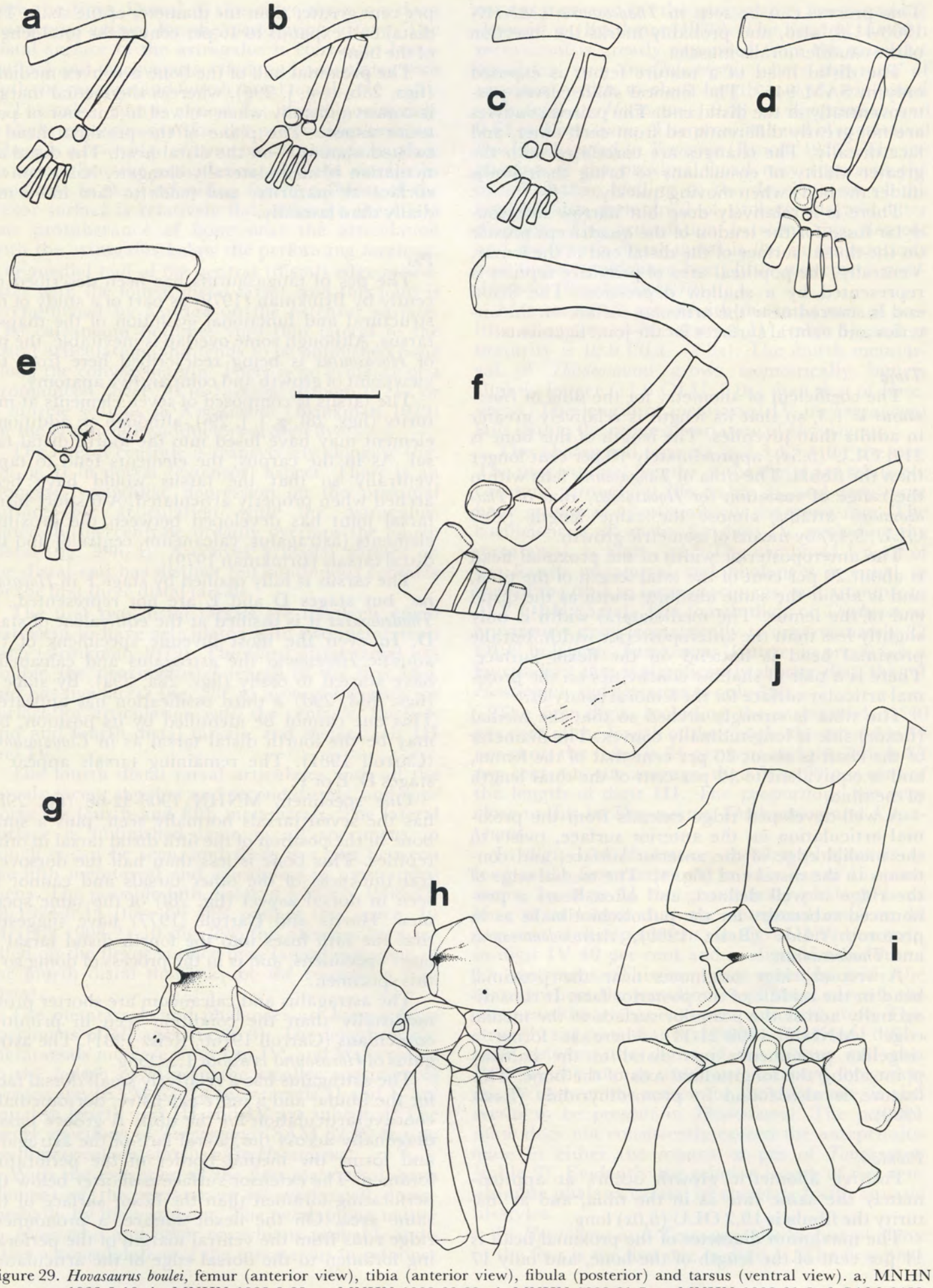

Figure 29. *Hovasaurus boulei*, femur (anterior view), tibia (anterior view), fibula (posterior) and tarsus (ventral view). a, MNHN 1925-5-10; b, MNHN 1925-5-25; c, MNHN 1908-32-29; d, MNHN 1908-21-7; e, MNHN 1908-21-5; f, SAM 9459; g, MNHN 1925-5-32; h, MNHN 1908-32-68; i, MNHN 1908-21-10, reversed;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

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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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A PROTOSUCHID CROCODILIAN FROM THE FOREST SANDSTONE FORMATION (UPPER KAROO) OF ZIMBABWE

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ABSTRACT

A protosuchid crocodilian is reported from the Forest Sandstone Formation (Upper Triassic) of the central Zambezi Valley, Zimbabwe. It is closely related to known protosuchians from terminal Karoo deposits in South Africa and it is provisionally referred to cf. *Notochampsa* sp.

INTRODUCTION

Vertebrate fossils were first reported from the vicinity of the confluence of the Angwa and Maura rivers in the central Zambezi Valley, Zimbabwe, by Raath *et al.* (1970). The local occurrence of prosauropod dinosaurs comparable with those recovered from the Forest Sandstone Formation in the Nyamandhlovu district north-west of Bulawayo (Bond 1955, Attridge 1963) suggest that the central Zambezi Valley deposits represent a local equivalent of the Forest Sandstone; thus these deposits are considered coeval with the upper part of the late Triassic Elliot Formation ("Red Beds") of South Africa (Bond 1955, Raath *et al.* 1970). Subsequent field work in the exposures of the Maura River has yielded more fossils, including the remains of several more prosauropod dinosaurs, parts of two specimens of the theropod *Syntarsus*, and the specimen which is reported here — a partial skeleton of a small crocodilian. It is registered as QG 49 in the palaeontological collections of the National Museums and Monuments of Zimbabwe, formerly stored in the Queen Victoria Museum, Salisbury, and now housed in the National Museum, Bulawayo.

Specimen QG 49 was recovered from the south bank of the Maura River, downstream of the bridge over the Maura River on the road north to Kanyemba and approximately halfway between that bridge and the confluence of the Maura and Angwa rivers (fig. 1). The locality co-ordinates to the nearest five seconds are 16°13′30″S; 30°05′30″E (Zimbabwe 1 : 50 000 Series, Mapsheet 1630 A1).

As with many of the fossils from this locality the bones of QG 49 are variably coated with the black, nodular crust of manganese-rich material reported by Raath *et al.* (1970). Its hardness and thickness hampers preparation of the fossils, and the blotchy discoloration it causes has made interpretation of the bones of QG 49 difficult.

DESCRIPTION AND PROVISIONAL IDENTIFICATION OF QG 49

The specimen consists of much of the skeleton of a protosuchid crocodilian (figs. 2, 3). The hind part of the skull is preserved, but poorly. It is so extensively eroded, fragmented, distorted and discoloured that virtually no cranial features can be recognised other than what is taken to be the right upper temporal opening and parts of the mandibular rami (fig. 2a, b). Although the postcranial skeleton is reasonably well articulated, few elements are clearly recognisable because of the nature of preservation. However, some elements are unmistakable (vertebral centra, osteoderms, coracoid) and they are sufficiently diagnostic to indicate the relationships of the fossil. Nash (1975: 232–233) notes that an elongate coracoid and a sculptured external surface of the dorsal osteoderms are among the features that are characteristic of Crocodilia. Specimen QG 49 bears these features (fig. 4a, b), and the coracoid (fig. 4a) is very similar to that of *Notochampsa* (Haughton 1924: fig. 18A) and of *Orthosuchus* (Nash 1975: fig. 12A). Other features of QG 49 that are closely similar to those described in *Orthosuchus* (Nash 1968, 1975) include the dorsal vertebrae, particularly the nature of the transverse processes, and the configuration of the dorsal ribs with their proximal expansions. Furthermore, the Zimbabwean specimen is comparable in size with the South African forms (table 1).

TABLE 1
Protosuchid crocodilians: comparison of bone measurements

Measurement (mm)	*Notochampsa istedana* *SAM 4013 (Haughton 1924)	*Orthosuchus stormbergensis* *SAM — K409 (Nash 1975)	QG 49
CORACOID:			
length	25	23	29
maximum breadth at glenoid end	—	12,8 (Nash 1968)	15
minimum width at mid shaft	3	—	6
maximum breadth at ventral end	15	11,2	11
DORSAL VERTEBRAE:			
range in length of preserved centra	?	7,4–10,5	8–11,7

*SAM: South African Museum, Cape Town.

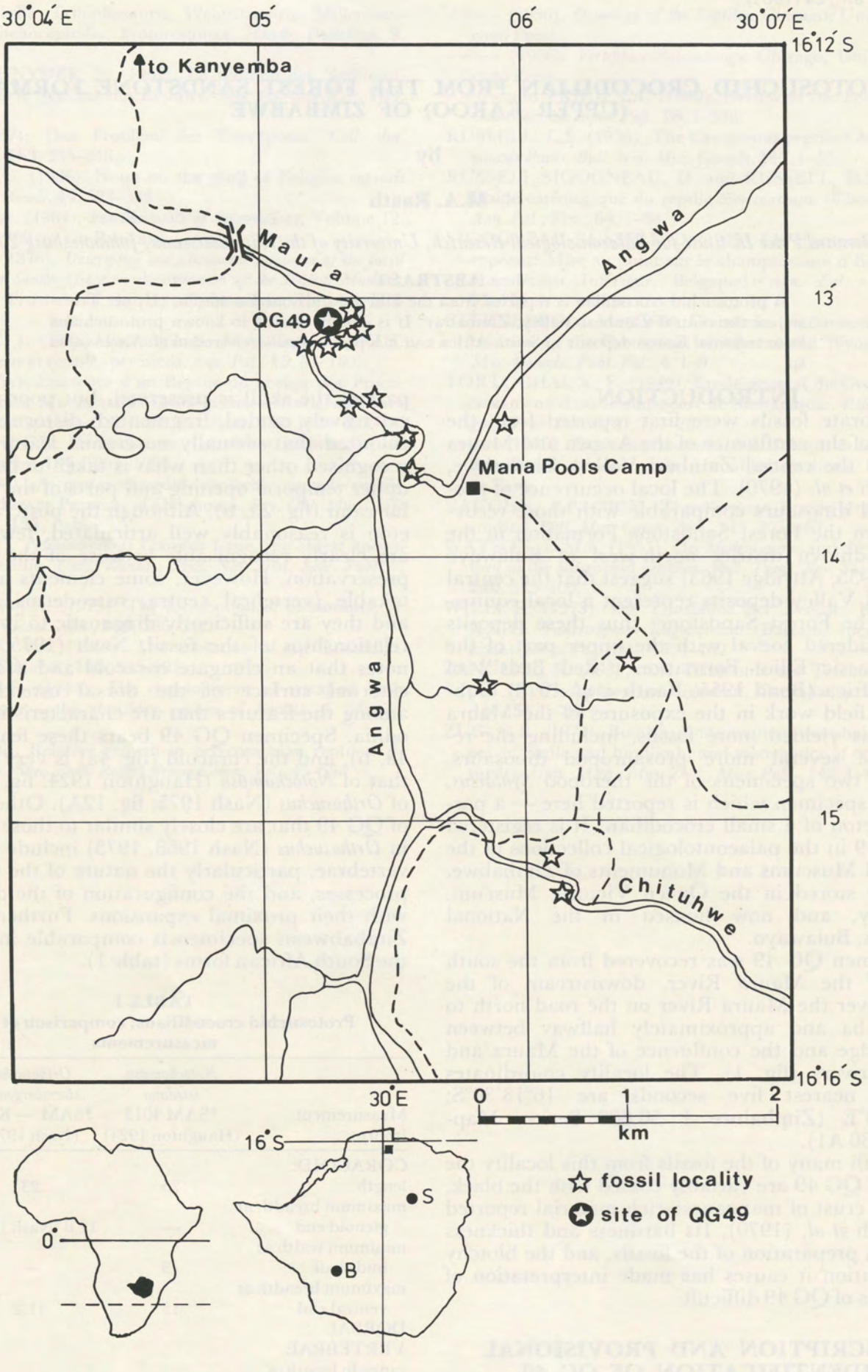
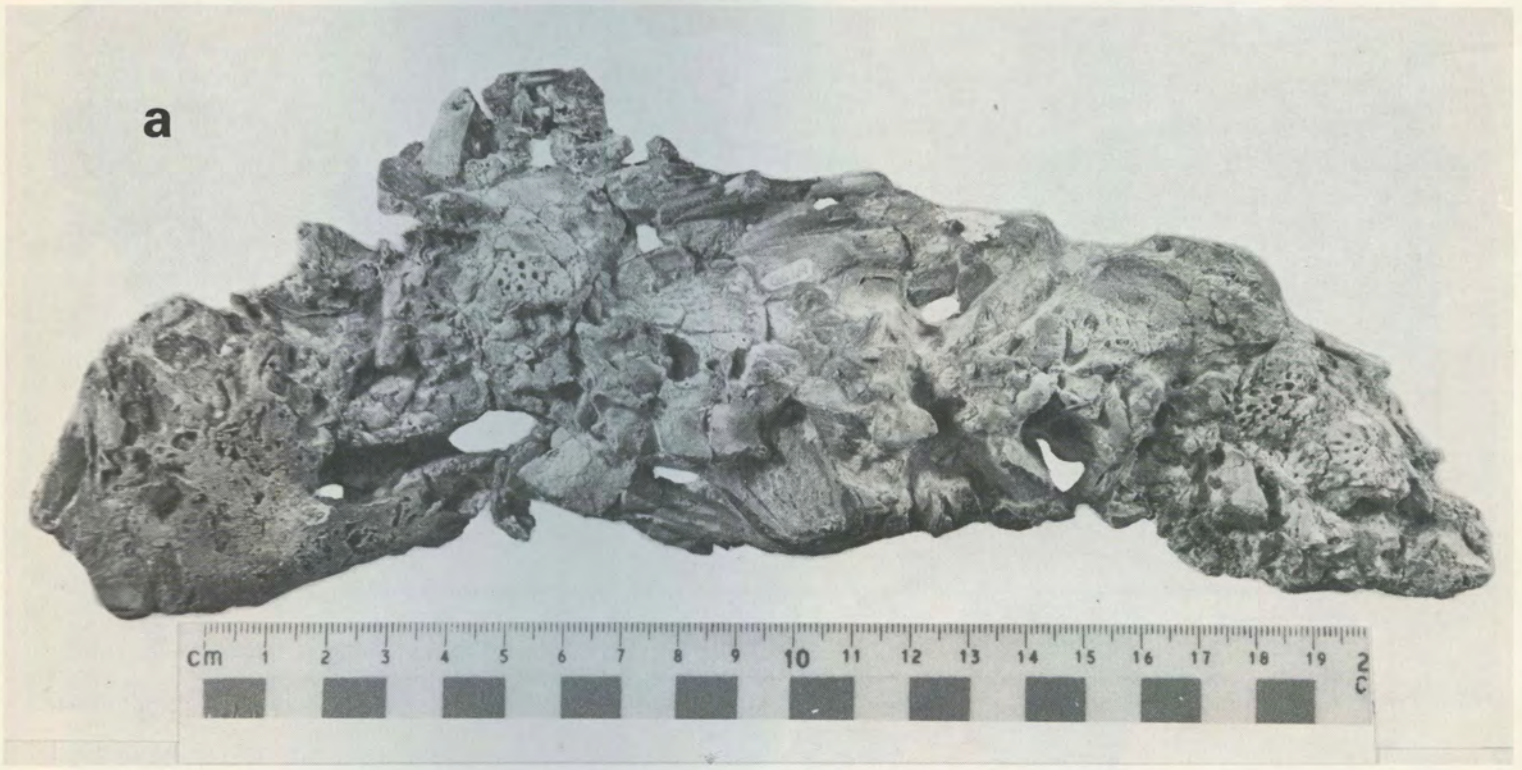


Figure 1. Map of fossil localities on the Maura River (adapted from Raath *et al.* 1970: fig. 1).



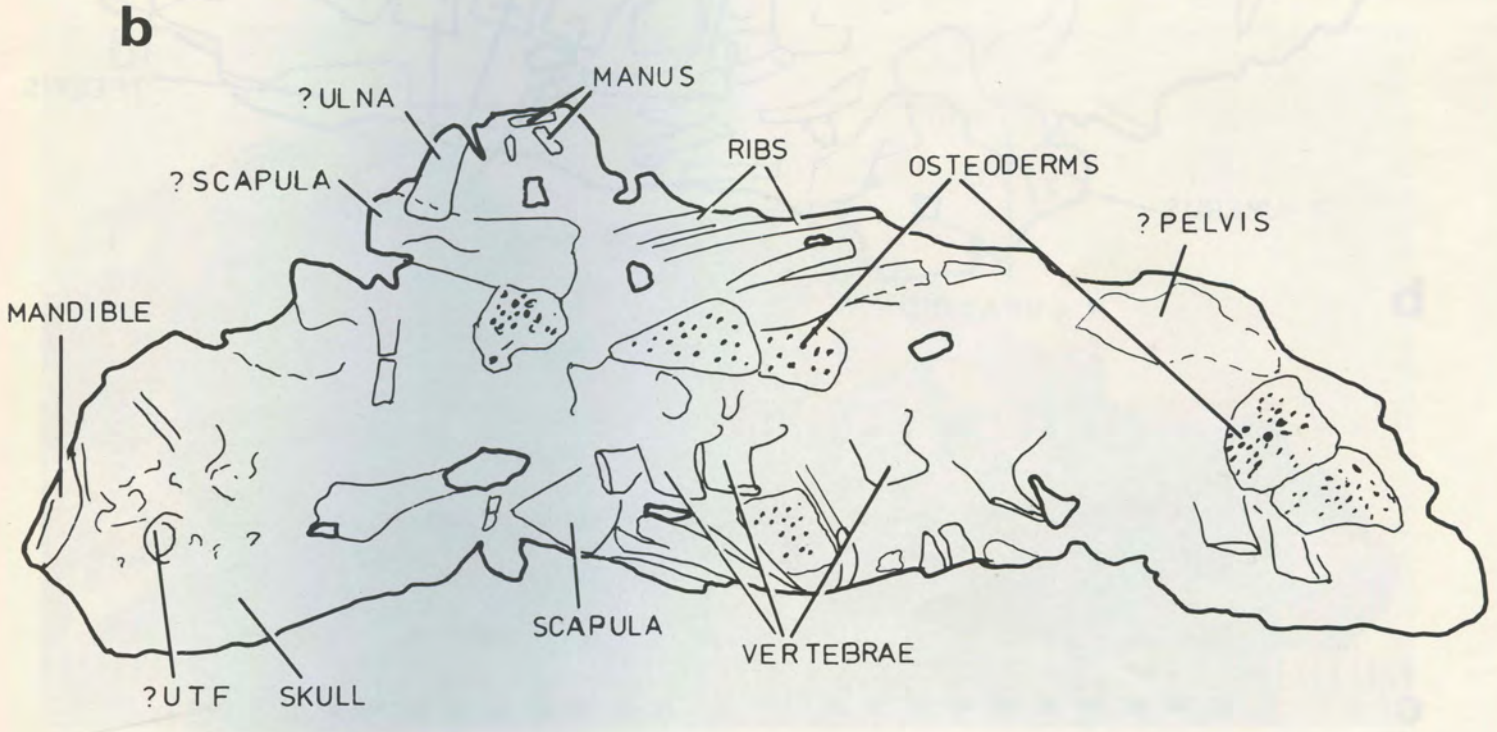
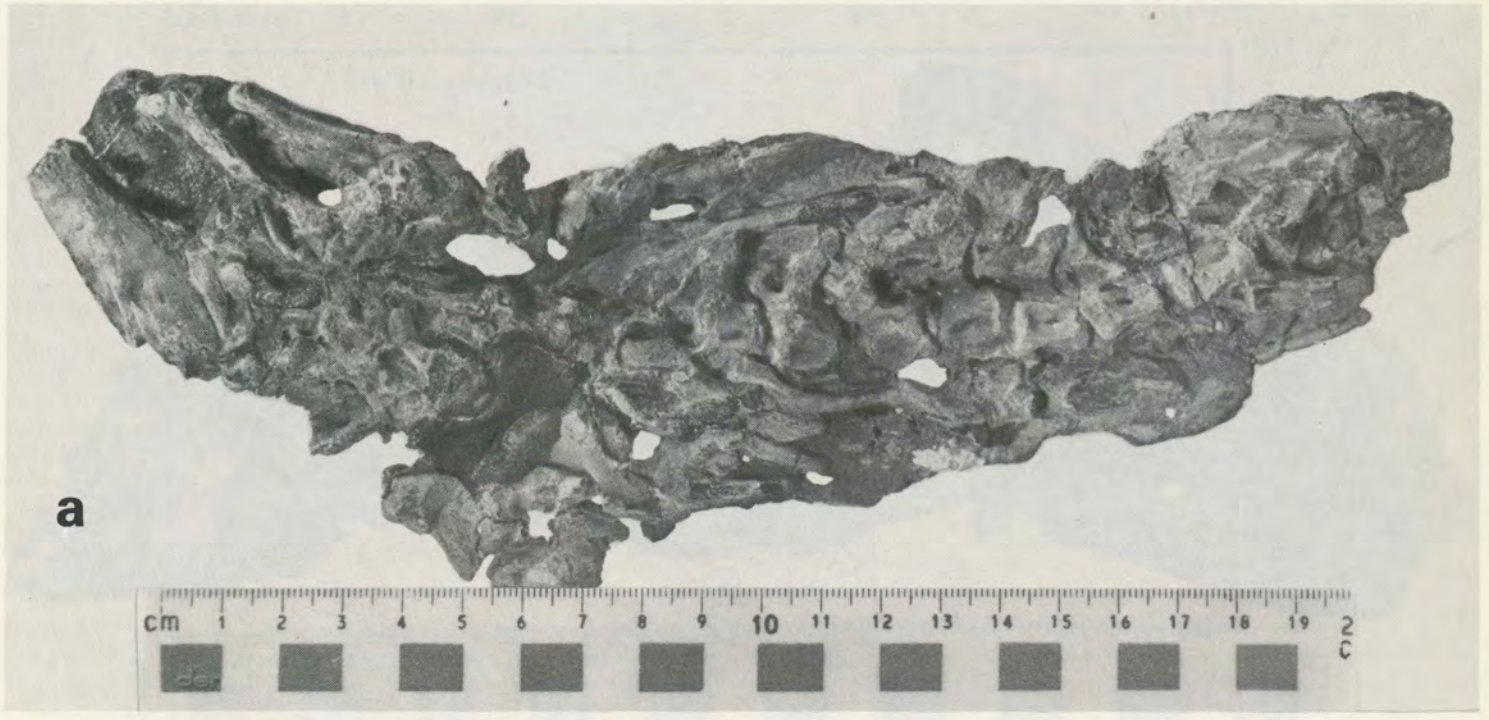


Figure 2. QG 49, cf. *Notochampsa* sp., from Zimbabwe:
(a) dorsal view
(b) graphic interpretation of (a).



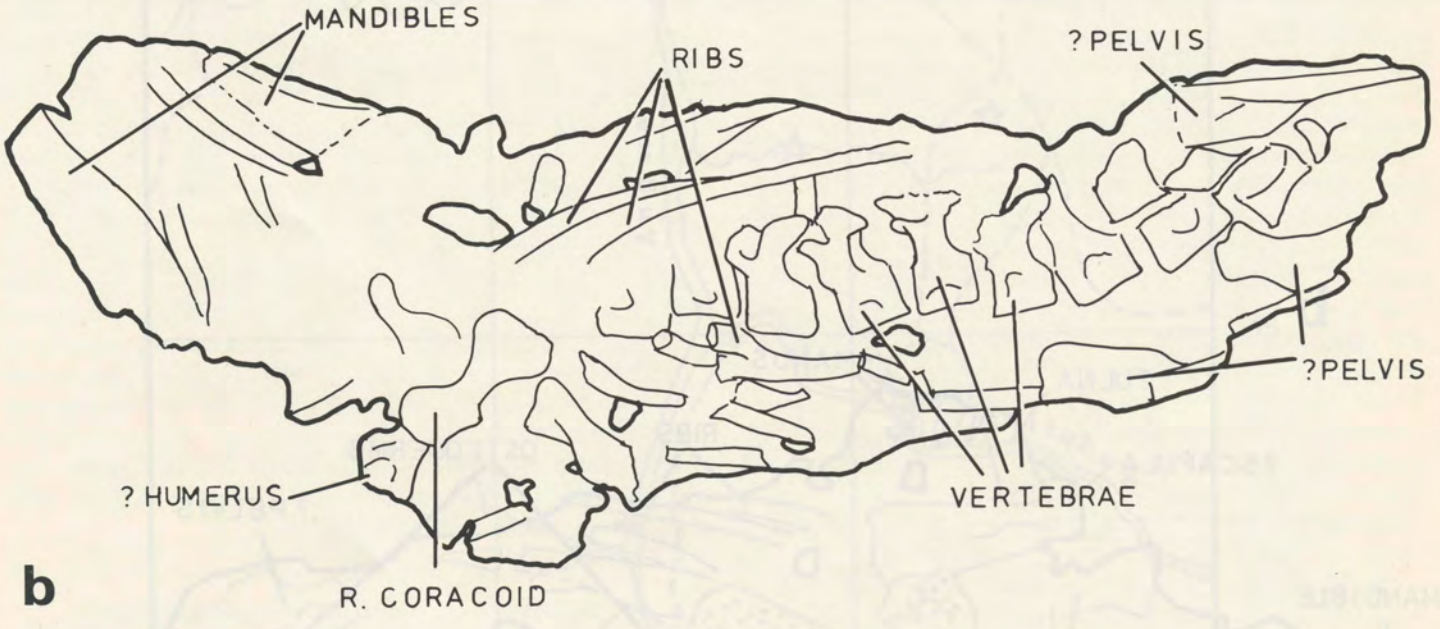




Figure 3. QG 49, cf. *Notochampsa* sp., from Zimbabwe:
(a) ventral view
(b) graphic interpretation of (a)
(c) same as (a), stereopair.

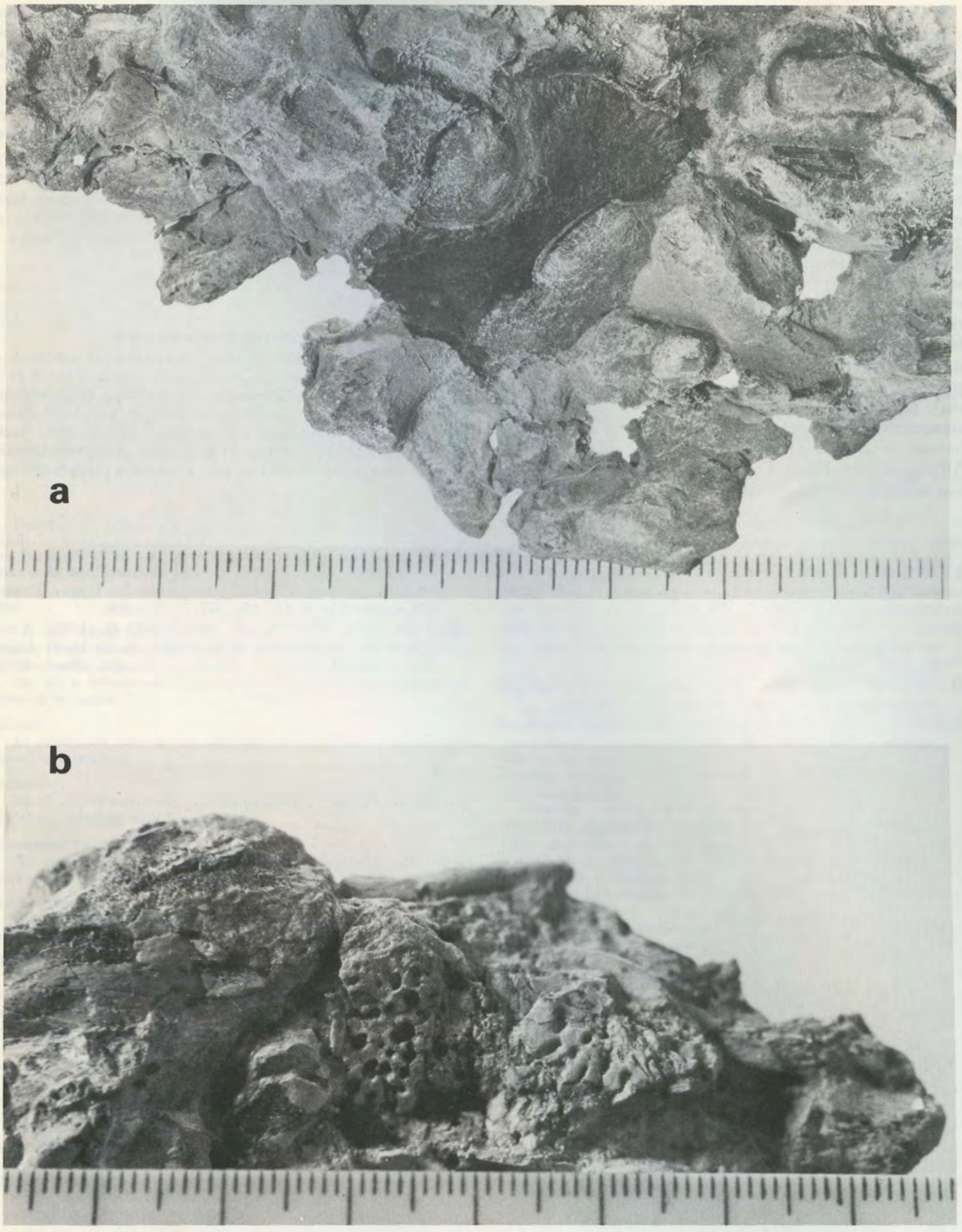


Figure 4. QG 49, cf. *Notochampsa* sp., from Zimbabwe:
(a) right coracoid (centre, darker) (scale in mm)
(b) characteristic external surface texture of dorsal osteoderms (visible at right hand end in fig. 2a) (scale in mm).

Notochampsa was collected from the lower Clarens Formation (formerly known as the Cave Sandstone) in the Barkly East District, South Africa, and *Orthosuchus* from the upper Elliot Formation (formerly known as the Red Beds) of the Qacha's Nek area in Lesotho. Other specimens of protosuchid crocodilians have subsequently been recovered from upper Elliot Formation exposures in a number of places in South Africa, and some of these specimens are currently the subject of study by Dr. C.E. Gow and A. Busbey. Wherever these crocodilians are found they are associated with a fauna consisting predominantly of medium-sized prosauropods (cf. *Massospondylus*). In a few places tritylodontid and tritheledontid cynodonts, rare morganucodontid mammals (cf. *Erythrotherium*, *Megazostrodon*) and coelurosaurian theropods (*Syntarsus*) have been recovered from a similar stratigraphic horizon. This association of protosuchids with prosauropods in both countries supports the view that the Forest Sandstone Formation of Zimbabwe is a stratigraphic equivalent of the South African upper Elliot Formation and perhaps of the lower levels of the Clarens Formation. The diversity of the South African fauna suggests that thorough examination of these exposures in Zimbabwe may yet yield a more diverse tetrapod fauna than has been recorded there hitherto.

In view of the poor preservation and absence of generically diagnostic features, it is not considered possible to identify QG 49 to generic level with confidence. However, because it bears several resemblances to *Notochampsa istedana* (Haughton 1924) (and to the very similar, possibly even congeneric, form described by Nash (1968, 1975) as *Orthosuchus stormbergensis*), it is proposed to refer it provisionally to cf. *Notochampsa* sp.

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*Full paper presented at PSSA First Conference, July 1979