

AN ANATOMICAL AND SYSTEMATIC STUDY OF THE FAMILY MESOSAURIDAE
(REPTILIA; PROGANOSAURIA) WITH SPECIAL REFERENCE TO ITS AS-
SOCIATED FAUNA AND PALAEOECOLOGICAL ENVIRONMENT IN THE WHITE-
HILL SEA.

by

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(With 84 text-figures and 7 tables)

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ABSTRACT

The anatomy and taxonomy of the southern African fossil rep-
tile Mesosaurus from the Whitehill Shale Formation, its palaeoe-
cology and associated fauna were studied.

A study of the biozonation of the Whitehill Shale has shown
that the Formation is a chronostratigraphic unit. It is postu-
lated that the almost identical Whitehill and Traty Formations
were deposited in shallow contemporaneous embayments of a cen-
tral sea arm that occupied a position between the two continents.
The water body was stratified with anoxic, toxic, bottom brines
that prevented the establishment of a benthonic fauna.

A study of the newly collected fossil material led to a new in-
terpretation of the cranial morphology of Mesosaurus and it was

found to be anapsid and closely allied to Limnoscelis. If M.tenuidens is to be regarded as typical for the Mesosauridae, all the members of the order Proganosauria will have to be transferred to the order Cotylosauria.

M.tenuidens was found to differ from M.brasiliensis and is the only species of Mesosaurus in the southern African Permian-Carboniferous Whitehill Formation. Along with it two more forms, Noteosaurus africanus Broom and a yet unidentified species, identical with or closely allied to Stereos-
sternum tumidum occur.

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INTRODUCTION

"Of contemporary tetrapod life in Gondwanaland we know almost nothing with one notable exception" (Romer 1970 p. 2). This "notable exception" is Mesosaurus which became closely associated with the theory of continental drift and affords one of the strongest arguments that can be derived from vertebrates in favour of the former union of the southern continents. This argument, used by early advocates of the theory of continental drift e.g. A.L. du Toit, was reiterated so frequently that it became entrenched in Gondwana literature to such an extent that any evidence for continental drift derived from fossil reptiles automatically becomes associated with Mesosaurus. This explains why Ager (1975) in a general textbook on Geology confuses the discovery of Lystrosaurus in Antarctica with Mesosaurus.

The axiom that the endemicity of Mesosaurus in the Whitehill and Iraty Formations of southern Africa and South America respectively is proof for the juxtaposition of the two continents during deposition of the shales in which Mesosaurus occurs, is based upon its supposed inability to "breast the waves over several thousand miles of oceans which now separate these two continents" (Romer 1970 p. 3). Had modern turtles been known to man as fossils only would any palaeontologist have dreamed that these seemingly clumsy creatures could navigate the high seas?

The axiomatic acceptance of Mesosaurus as proof of a former African-South American link weakens if we critically examine our knowledge of the Mesosaurus species from the two continents. In fact, of Romer's (1970) "notable exception" we know very little. To date a thorough comparison of Mesosaurus type material from the two continents has not been made, the cranial morphology of the South African form is virtually unknown and diffe-

rent interpretations of the girdle anatomy of the species from the two continents were made by Seeley (1892), Broom (1904) and Mc Gregor (1908).

In spite of the present, almost universal acceptance of continental drift albeit by the new theory of plate tectonics, and the wealth of new palaeontological and palaeomagnetic data that was accumulated in its support, our knowledge of Mesosaurus has remained stagnant in the more than thirty years since Du Toit's epoch making book "Our wandering continents" was published in 1937. The last major work on South African Mesosaurus material was done by Von Huene as long ago as 1925.

It should be clear that a study of the Whitehill Formation (formerly known as the White Band) its fauna and palaeoenvironment is long overdue. This study aims at providing answers to questions such as the biozonation of the Whitehill Formation the salinity, water depth and the connections between the Whitehill and Iraty Basins with each other and with the world oceans. In collecting new material of Mesosaurus and in studying the Permo-Carboniferous Formation in which this aquatic fossil reptile occurs, it was hoped that the cranial anatomy of the southern African form (or forms) and its palaeo-environment could be unravelled.

To some of these problems solutions were found, others remain to be answered conclusively but even on the latter terrains our better knowledge of the Whitehill sea and its environment will hopefully provide us with the insight to theorise with a little more confidence.

From this stem the dual nature of the present study. In the first instance a better understanding of the palaeo-environment of the Whitehill Sea was sought and in the second instance the

morphology of the southern African Mesosaurus-species was studied to clear up the taxonomy and to establish the systematic position of the family within the Reptilia.

The conclusions reached in the present study on the deposition and environment of the post glacial beds confirm to a large extent the views expressed by Du Toit (1937). It is thus fitting to quote from his book (p. 78). "They" (the Whitehill and Iraty shales) "were deposited in shallow seas, in basins like the Black Sea or Baltic or in estuaries, where the bottom muds were in places charged with sulphuretted hydrogen. Their dominantly fine grained nature is obviously due to the small relief of the ice-worn continent, the high proportion of bare rock-surface and the clayey texture of the morainic covering." The post Du Toit literature shows little sign that workers had grasped the full significance of his brilliant insight. This is perhaps not surprizing because Du Toit himself altered his views somewhat in a later work (Du Toit 1948).

This study is the first to deal with the general morphology and the affinities of Mesosaurus since the work of Von Huene (1925, 1941) and the first attempt ever, to unravel the cranial anatomy of the southern African species, Von Huene's (1941) description of the skull being based exclusively on the South American species.

My interpretation of the skull differs considerably from that of Von Huene. Apart from what are obviously species differences between M. brasiliensis and the south African M. tenuidens, there are also differences on a more fundamental level e.g. Von Huene interprets the temporal region as synapsid whereas I find it to be anapsid.

It is therefore clear that a re-examination of the South-American material is necessary and perhaps long overdue. Numerous attempts to obtain the types of the South American species, Mesosaurus brasiliensis and Stereosternum tumidum failed and only a replica of the type of Braziliosaurus sanpauloensis housed in Japan, could be obtained. A much needed comparison of the types from the two continents and a re-examination of the cranial morphology of the South American forms must therefore be given high priority in future studies in this field.

THE WHITEHILL SHALE FORMATION (WHITE BAND)

1. NOMENCLATURE AND DISTRIBUTION

The Whitehill Formation was formerly known as the White Band, a name that is well established in the literature (e.g. Schwarz, 1903; Rogers and Du Toit, 1909; Du Toit, 1937; 1954; Haughton and Frommurze, 1936; Russel, 1939; Von Huene, 1956; Schreuder and Genis 1973-74; McLachlan and Anderson 1973; Anderson and McLachlan, 1979). The name Whitehill Shale Formation, was coined by Johnson, Botha, Engelbrecht, Hugo, Keyser, Turner and Winter. (1975). According to Anderson and McLachlan (1979) this was not a formal proposal in accordance with the requirements of the South African Code of Stratigraphic Terminology and nomenclature (S. Afr, comm. Strat., 1977) and these authors still use the old name. In the present work I shall use the name Whitehill Shale Formation in preference to White Band and it will be applied to indicate the unit of white weathering fissile black shales near the base of the Karoo sequence only (see Fig. 3). The cherty beds and intercalated volcanic ash layers which are so conspicuous in the south-eastern part of the Karoo above and below the white weathering shales are therefore excluded. It therefore implies that only the third member of Russel's (1939) "White Band" is taken as the equivalent of the Whitehill Shale Formation.

The Whitehill Shale therefore occurs between the Prince Albert Shale Formation of the southern Karoo (part of old "Upper Dwyka Shales") and its equivalents elsewhere in the basins to the

north and the Collingham and Tierberg Shales in the southeast and northwest respectively. It therefore forms part of the Eccca Group the lower contact of which is taken at the top of the Dwyka Tillite and the upper contact of which is a vague border somewhere below the first purple mudstones of the Tapinocephalus zone of the Lower Beaufort and the Waterford Formation in the south. Elsewhere in the Namibian/South West African Basins the upper contact is even less well defined. The white weathering shales can be traced on both its conspicuous lithology and its fossil content over vast tracts in southern Africa. (See Figs. 1 A and 3A & B).

Like the Iraty Formation of the Parana Basin of Brazil, which the Whitehill Formation closely resembles in lithology, palaeontology and age, it is monotonously homogeneous over immense areas with only the slightest of facies changes in small nearshore areas of the sedimentary basins. The black silicious shales presently occur in four separate basins in southern Africa covering more than 300,000 Km² (Anderson and McLachlan 1979). According to these authors its original depositional area could have been close to twice its present size but on what grounds this assumption is based is not made clear.

The Iraty shales are even more extensive, covering more than three times the area of the Whitehill Formation and the Iraty and Whitehill outcrops combined, not including areas lost by erosion, are about three times that of the Black Sea (Anderson and McLachlan 1979).

(1) The major part of the Formation is preserved in the Great Karoo Basin (name from Martin, 1961 and McLachlan and Anderson 1973). The basin is separated in the north west from the more northerly basins by the Ghaap plateau and Transvaal "highlands"

(McLachlan and Anderson 1973) for most of its length. In the Orange River region between Upington and Vioolsdrift the basins are at present only separated by the erosion valley of the Orange River, a valley which is most probably a re-excavated pre-Dwyka drainage canal (Helgren 1979). It is therefore not impossible that the Great Karoo Basin was once confluent with the Namibian basins to the north.

The Whitehill Formation is recognised as far north as the Hertzogville area in the west (Cole 1978) and the southern Transkei in the east (Du Toit 1920). Tentative reports of the presence of this unit from the Port St Johns area (Rogers and Schwarz 1900; Du Toit 1920; 1946) should be treated as unconfirmed until its presence can be confirmed on palaeontological grounds. Anderson and McLachlan (1979) who followed up the tentative reports were unable to locate it. In the southern part of Namibia this Formation is present in two more basins.

(2) Firstly the Karasburg Karoo Basin (name from Schreuder and Genis 1973-74 with synonyms: Warmbad Basin; Martin, 1961; McLachlan and Anderson, 1973; Anderson A. M., 1975; and Orange River Basin; Frakes and Crowell, 1970). This basin, as has been indicated, was probably connected to the Great Karoo Basin to the south and also to the Kalahari Karoo Basin immediately to the north and east.

(3) Secondly the Kalahari Karoo Basin (name from Green 1967 and Anderson and McLachlan, 1979 with synonyms: South Kalahari Basin; Martin, 1961; 1968; 1970; 1975; Kalahari Basin; Martin, 1961; Heath, 1966; McLachlan and Anderson, 1973). This basin has a white-weathering unit at the top (Fig. 3B) whose correlation with the Whitehill Formation was in doubt

(Martin 1953). This unit is restricted to the south-western corner of the greater Kalahari Karoo Basin which extends over a large area underneath a covering of young Kalahari sands. The shales of the white-weathering unit are in general coarser and less fissile than the typical Great Karoo Basin shales but as the stratigraphical position of the palaeontological zonations of the Kalahari Karoo shales is identical with that of the unit in the main basin, the correlation is confirmed.

(4) The most northerly outcrops are in the Huab Karoo Basin (Synonyms: Huab-Ugab Basin, Reuning and Martin, 1957; Huab Basin, Martin, 1975; McLachlan and Anderson, 1973; Araujo, 1976). The name was decided on for the sake of consistency with the names of the other three basins.

The correlation of this basin and its sediments is partly based on the presence of tillites and of Mesosaurus at Doros crater. The identification of the fossils was initially done by Haughton in 1919 (Von Huene 1925) and was confirmed by Von Huene (1925) after a thorough study of the material. Recent doubts of the validity of the identification (Martin, 1975; Hodgson and Botha 1973-74) come as a surprize in view of the scientific stature of Haughton and Von Huene.

Their identification is certainly endorsed by the present study. Mesosaurus has to date been found only at Doros crater but it is clear from the lithology in the basin that the horizon is also present on the western slopes of the Brandberg and north of Doros crater, at Twyfelfontein and at the "Petri-fied forest." The typically white weathering black shales are seemingly absent from this basin. In view of the fact that the major part of the sediments has subsequently been removed

by erosion the same fate could have befallen the presumably more centrally situated, black shales. In this study a small patch of white weathering black shale was however found near the Brandberg West-Uis road south-west of the Brandberg. These shales resemble the black shales of the Whitehill Formation in outcrop and lithology but a search for fossils in the small outcrop was unsuccessful. A final correlation can therefore not be made but I am of the opinion that this may represent the lower unfossiliferous half of the Formation. The coarse grits in which Mesosaurus occur in this basin would then be a nearshore facies of the upper fossiliferous part of the Whitehill Formation.

A thorough search of the outcrops in the basin will most certainly yield more Mesosaurus material while some of the other typical Whitehill fossils might also turn up.

2. GENERAL LITHOLOGY

In the past the Formation was generally referred to as a white-weathering black carbonaceous shale (e.g. Schwarz, 1903; Rogers and Du Toit, 1909; Du Toit, 1937; 1954; Haughton and Frommurze, 1936; Engelbrecht, 1961; Potgieter, 1973; Potgieter, 1974; McLaren, 1974; McLachlan and Anderson, 1973, 1977a; 1977b; Van der Westhuizen 1979). It was also defined as such when the new name, Whitehill Shale Formation, was proposed for the old White Band by Johnson et al (1975).

According to Anderson and McLachlan (1979) the 12-14 percent organic matter quoted by Du Toit (1954) probably refers to samples from the vicinity of Hopetown where Cunningham-Craig (1914) and Botha (1940) investigated the oil-shale potential

of the Whitehill Formation. These values, reiterated by e.g. Engelbrecht (1961), as well as the values given by Haughton, Blignault, Rossouw, Spiess and Zagt, (1953) for the southern Karoo (6-12 percent) seem to be maximum values. Subsequent reports of studies on fresh samples from boreholes in areas selected for its potentially high oil shale qualities give maximum values of 10 percent fixed carbon with a mean value of only 4.3 percent (37 samples) (Cole 1978). This illustrates that the carbon content of the Formation had been grossly overestimated in the past. In outcrop, these sediments are macroscopically usually nearly devoid of any traces of recognisable carbonaceous matter. This is underscored by the fact that Botha (1940) on results obtained from analysis of weathered samples from outcrops decided that the Formation had no potential as an oil shale. In the course of the present study too, the impression was gained that the outcropping Formation, is usually poor in carbon. In a few localities the shales were found to be visibly rich in carbon in outcrop, the most notable occurrence encountered being on the farm Frisgewaagd. Samples from this locality however failed to ignite but when heated turned to the typical greyish white colour of the Formation in outcrop. This is probably caused by the oxidation of the material (carbon?) which gives the fresh shales its black colour.

The spontaneous ignition of Whitehill (Kimberley) shales west of Kimberley is reported by Schwarz (1912) and Russel (1939). Local inhabitants near Klaarstroom in the southern Karoo claim that the name of farm "Kolegat" was derived from the mining of the Whitehill shales for fuel. Nel (1977) mentions the mining of Prince Albert Formation shales on the farm Leinster

222 at about the turn of the century.

In conclusion however, it is felt that, in view of the average of 4.3 percent carbon obtained in the area most promising for a high carbon content (Cole 1978) and the general impression gained from outcrops, the shale does not merit being called a carbonaceous shale. This black shale most certainly is not "highly carbonaceous" as e.g. Anderson and McLachlan (1979 p.83) call it in the most recent work on the oil shale potential of the Formation, in spite of their eventual conclusion that the potential is very poor. X-ray diffraction analyses of samples from outcrops in the Great Karoo Basin give a high Silica oxide (SiO_2 , 72-78%) and Aluminium oxide (Al_2O_3 , 11-18%) content whilst oxides of Potassium, Sodium and Phosphorus are present in small quantities. Traces of other elements are also present (see Table 1). Potgieter (1973) reports the same range of values for samples from the area to the north of Douglas.

The shales almost exclusively occur as paper thin laminae and nodules of any size and kind are usually absent from the major part of the basin. Structures that are described as ochreous and ferruginous concretions (Engelbrecht 1961) are most probably infilled, structureless, somewhat elongated conprolites. These structures are abundant at some localities north of the Orange River and peter out southwards. Where nodules of other kinds are present they occur above dolerite sills.

None of the fossils I collected from the shales showed a veneer of, or was infilled or replaced by iron pyrite as is often the case in the Iraty shales (Araujo 1976). From the area north of the Orange River, Engelbrecht (1961) and Cole (1978)

report abundant veneers, stringers, laminae and lenses of iron pyrite from the shales but other workers do not mention its presence (Potgieter, 1973; Potgieter, 1974; Van der Westhuizen, 1979; McLaren, 1974). In the Gross Daberas outcrops of the Kalahari Karoo Basin, Heath (1966) reports limonite pseudomorphs after pyrites. The presence of limonite interpreted by Cooper (1979) as indicative of marine conditions, a view confirmed by Berner et al (1979). These workers found that in marine sediments reactive iron is depleted before H_2S and sulphate. Iron monosulphates thus react with the remaining sulphur to produce pyrite and they claim to have demonstrated that pyrite dominance over Fe_2S in sediments, as is the case in the Whitehill shales, indicates sedimentation in marine conditions. In this study the shales, in outcrop, showed very little sign of pyrite in any form and the limonite pseudomorphs at Gross Daberas seem to be atypical for the Formation as a whole. It would seem however, that the near absence of pyrite in outcrops is a result of its complete loss during weathering because Cole (1978), at least, definitely found abundant pyrite in unweathered shales. Intercalated red-weathering shale layers are sometimes met with (Russel, 1939; Engelbrecht, 1961; Potgieter, 1973; McLaren, 1974). These shales were found to be sporadically developed at inconsistent stratigraphic horizons and may occur from the bottom right through to the very top of the unit as e.g. in the Tanqua Karoo on the farm Blaauwboschkolk and in the Worcester outlier where the topmost Notocaris tapscotti bearing zone is red weathering. The relative abundance of sulphur and calcium carbonate in some areas results in the formation of gypsum

on weathering. Wherever climatic and other conditions are favourable, deposits of economic importance accumulate. Whitehill gypsum has been mined near Laingsburg. At present the mineral is mined in the Tanqua Karoo but the largest mining activity is near Baroe siding in the Eastern Cape.

A silty shale unit is intercalated in the middle of the Whitehill Formation. It is developed in the Gellap plateau of the Kalahari Karoo Basin, on the farms Aussenkjer and Kirchberg in the Karasburg Karoo Basin and also in the north west and south east of the Great Karoo Basin. In the latter basin the intercalated unit is a green silty shale in the south east and a yellow (buff)-weathering unit in the north west. In the Kalahari Karoo and Karasburg Karoo Basins the unit is also green and closely resembles the green shales immediately above and below the Whitehill Formation (see Fig. 36 B).

The buff coloured intercalated unit of the Great Karoo Basin is best developed east of Van Wyksvlei on the farm Gannavloer and seems to peter out south of Calvinia. In the extreme south and southwest this unit is absent. The green facies of the unit is best developed in the area immediately west and east of Prince Albert. It is of importance to note that a sandy shale unit is developed also in the middle of the South American Iraty Formation.

Dolomitic lenses and layers are developed in the eastern outcrops of the Whitehill Formation in the Great Karoo Basin.

Finely layered black dolomitic lenses showing stromatolite-like slump structures have been described by McLachlan and Anderson (1977a). The slumps are illustrated in figure 17A. In these dolomitic lenses a yet unidentified crustacean is present (Fig. 15).

In the upper portion of the Formation lenses of cream coloured dolomite are present. This rock which occur as far north as Calvinia, reaches a maximum thickness of more than 2m on the farm Driekoppen (Fig. 17B).

Small lenses of black dolomite are also present in the Kalahari Karoo Basin. (Fig. 17C).

3. THE SEDIMENTARY ENVIRONMENT

Historic background to the setting of the basins

Before the deposition of the Whitehill Formation in the early Permian or late Carboniferous, the southern tip of Africa had suffered a long history of marine transgressions. These transgressions are well documented starting in the upper Ordovician (Teichert 1970) or Lower Silurian (Rust 1969) with the deposition of the Table Mountain Group. This was followed by the marine sediments of the Bokkeveld Group (Theron 1972) and by that of the Witteberg Group which is also mainly marine. These sediments accumulated in epicontinental seas that, according to most reconstructions, formed part of the central block of the supercontinent of Gondwanaland.

This long period of transgression ended with the Permo-Carboniferous glaciation and finally with the formation of the Karoo Basin, the first unambiguous record of a continental environment being the presence of reptilian fossils in the Waterford Formation of the Ecca Group (Barry, 1970; B. Rubidge pers comm.). The last unambiguous marine fossils occur at the base of the Prince Albert Formation immediately on top of

the glacial tillites (Schroeder, 1908; Range, 1912; McLachlan and Anderson, 1973 and Oelofsen and McLachlan, in preparation). Between the base of the Prince Albert Formation and the Waterford Formation a slow transition from marine to fluvial conditions occurred. Exactly when and by what sediments this transition is marked is still in question. Some characteristics of Ecca sediments above the Whitehill have however been interpreted as possibly indicative of a marine environment. (Marchant 1979, Cooper 1979).

This transition can be expected to be diachronous if a model of deltaic infilling of the basin is accepted. As the deltas built up and transgressed northwards along the southern margin of the basin, the line of transition would also have moved northwards. In this simple model, other deltas would also have transgressed southwards from the northern shores until the lines of transition met, with the deltas filling in the basin and terminating marine conditions.

Another possibility is that epeirogenic movements of the crust severed the connection between the inland, partly landlocked, basin and the world oceans.

In this model, favoured by McLachlan and Anderson (1979), a relatively sharp transition would be expected, marked by fairly isochronous sediments covering large areas. The meaning of the Whitehill Formation in these models has been a point of speculation (McLachlan and Anderson 1973, 1979) and it was hoped that more information on this point would be gained with this study.

Whether marine, brackish or fresh water, the inland (epicratonic) sea in which the Prince Albert, Whitehill and Collingham Formations were deposited, covered a vast area (The Aus-

senkjer Formation in the Karasburg Karoo Basin in this study is regarded as the equivalent of the Collingham Formation of the Great Karoo Basin). That this body of water lasted well into post Whitehill times is shown by the presence of distal turbidites developed in Ecca deposits overlying the Whitehill Formation (Cole 1978, Anderson and McLachlan 1979). The absence of subaerial or shallow water emergent features reported by McLachlan and Anderson (1977a) is confirmed by the present study. The question however is, how deep was the water?

Water Depth of the Whitehill sea

Nearshore, relatively coarse, lenticularly bedded sediments could be identified in a few places suggesting the proximity of the shore, the most unambiguous being the subaerially deposited, red-weathering, coarse clastic strand grits and channel lags at Doros crater in the Huab Karoo Basin. These sediments are correlated with the Whitehill Formation on the presence of Mesosaurus notwithstanding the apparent lithological differences. The mode of preservation of Mesosaurus as disarticulated, rolled bones is duplicated in the northernmost outcrops of the Formation in the Kalahari Karoo Basin (Fig. 7). These sediments in the vicinity of Gross Daberas and Daberas Ost are much more sandy and contains a fair amount of calcium carbonate. North of Kimberley a coarser facies with lenses of siltstone and silty sandstone is developed in the Great Karoo Basin (Cole 1978). Immediately to the north of this area the Ventersdorp landscape was seemingly not submerged as the Prince Albert and Whitehill Formations thin out and disappear.

The black shales therefore accumulated not only in the "deep" central portions of the basins but also in the perhaps shallow water of the nearshore areas. This is confirmed by the presence of limulid trackways in typical white-weathering shales of the Karasburg Karoo Basin reported by Anderson (1975), modern Limulus frequenting shallow marine environments only. Stromatolites which can only exist in the photic zone are present in the interglacial sediments below the Whitehill Formation in the northern Great Karoo Basin (McLaren 1974). This likewise indicates shallow conditions.

The absence of Whitehill sediments from the Ghaap Plateau to the northwest of Douglas may further indicate that this pre-Dwyka landscape feature was not submerged by the waters of the Whitehill sea. The escarpment is embanked by Dwyka Tillite which indicates that, as a geomorphological feature the plateau predates the Dwyka glaciation (Helgren 1979). The Whitehill outcrops to the east of this escarpment at present occur on nearly the same topographic level as the eastern rim of the escarpment ($\pm 1200\text{m}$). It can be reasoned that, had the waters of the Whitehill sea, where it covered the nearby Whitehill sediments, been deep, it would also have submerged the Ghaap Plateau. If so, Whitehill sediments could have formed and remnants preserved somewhere on the 60 Km wide feature. Of course a covering of sediments could easily have been stripped off by denudation. Helgren (1979) however states that, although the presence of some Karoo rocks on the plateau (Prince Albert Formation or tillite?) is indicated by its presence in Kimberlite pipes, it is "difficult to postulate a means of removing the Karoo sediments once covering this region, while still leaving the surface only scarred by

shallow polje drainage networks" (p. 113-114). The covering could therefore not have been more than a thin veneer in which case the complete Prince Albert and Whitehill Formations could not have been present on the plateau. Consequently, the Whitehill sediments to the east of it must have accumulated in relatively shallow water. The assumption that the Ghaap Plateau was not submerged and that the Whitehill sediments adjoining it were deposited in shallow water will however be invalid unless it can be established that the elements of the present day landscape occur in their original position and attitude relative to each other. Their relations could easily have been upset by post depositional crustal movements. Let us now consider whether such factors did influence the region concerned.

The preserved Palaeoslope

Helgren (1979) in a study of the Vaal River Basin came to the following conclusions:

(1) "There seems to have been no geomorphologically significant regional tectonic deformation of the lower Vaal Basin since the deposition of the Dwyka shales" and

(2) The "bedding dips in the Dwyka shales are virtually horizontal with a slight inclination to the south" (p. 97). Nel (1977) also noted this slight inclination of about $\frac{1}{2}$ a degree in the Hopetown area. Hälbich (1958) however states that the shales near Loeriesfontein show a slight dip to the north, an observation which was confirmed by the present study. Helgren (1979) furthermore states that "the Pre-Karoo photo-lineaments usually have not been translated upwards through

the Dwyka shales" (p. 97) and he concludes that the modern surface in the lower Vaal Basin "not only preserves the hills and valleys of a Paleozoic landscape, but exhibits them "at essentially their original attitude" (p. 97). A parallel situation exists west of Loeriesfontein where the Krom River has exhumed and reutilized a preglacial river valley (Hälbich 1958) and from the authors observations it is clear that in this area the pre-glacial landscape is likewise preserved in essentially its original attitude.

Matthews (1970) in a study of preglacial landscapes in Natal found them preserved in essentially their original attitude and refer to the present slope of the pre-Dwyka palaeoplain he studied as "essentially a paleoslope" (p.3). Martin (1953, 1975) describes a large number of modern topographic features in Namibia which have been inherited from exhumed pre-Dwyka landscapes. Thus, in Namibia a picture similar to that in the Vaal Basin emerges. Palaeoslopes of ancient rivers once more funnel sediments towards the still, nearly horizontally preserved Dwyka sediments that were originally deposited from sediments transported by ice along the same ancient outlets. Such a river drains the valley west of Garis into the Kalahari Karoo Basin (Martin 1953). The sediments of this Basin were derived from the Windhoek Highlands (Martin 1953) and at present retain a gradient of $\pm 1\text{m}$ in 63 Km which should approximate the palaeoslope of the floor of the original sedimentary basin very closely.

In the Kaokoveld most of the large valleys draining westward into the Atlantic contain remnants of Karoo tillites which prove these structures to be exhumed pre-Dwyka features. It is also clear that the Joubert mountains served as a major

watershed even in pre-Dwyka times. Because of these features Martin (1953) concludes that "the pre-Karoo topography consists of a great number of geomorphological elements and it seems that over wide areas the present day topography diverges only slightly from that of the old pre-Karoo landscape" (p. 41).

In spite of the Graben type uplift and subsequent sinking of the west coast area of Namibia, proposed by Martin (1975), the valleys nevertheless seem to have either returned to or retained their original attitude.

The fact that the pre-Dwyka, Palaeozoic landscape which is at present being re-excavated by erosion, has retained its original attitude over wide areas, makes it tempting to speculate that the overlying Dwyka sediments (at least in some selected areas) preserved the original bottom slope of the sedimentary basins. If this line of argument is followed and is applied in the section of the Great Karoo Basin between Calvinia and Kimberley an estimate of the water depth in the basin can be made.

Calculated water depth

The southward dip of the shales near Kimberley and the northward dip at Loeriesfontein-Calvinia suggest that the deepest part of the basin lay somewhere in between. This assumption is supported by the presence of halite crystals in this middle region for, as heavy brines are funnelled into the deepest portion of basins halite will precipitate after the more soluble Calcium salts have precipitated in the shallower facies. The outcrops near Loeriesfontein at present lie topo-

graphically below those of the Carnavon district where the deepest part of the basin is postulated to be. This negative tectonism becomes more pronounced southwards towards the Tanqua Karoo and further on towards the Cape Fold Belt with which the downwarping can at least partly be associated. The fact that the pre-glacial landscape itself had a north-south downslope is illustrated by the downslope movement of the glaciers during the preceding glaciation (Theron and Blignault 1975, Du Toit 1954). During this period the lowest point in the basin was in the Loeriesfontein area as is proved by the general convergence of the ice towards the west. (Theron and Blignault, 1975; Visser, 1978).

If it is accepted that the superimposed downwarping of the Cape orogenic movements on this palaeoslope waned northwards, away from the orogenic centre, the present difference in altitude between the outcrops of Whitehill shale in the Carnavon and Kimberley districts can be regarded as a maximum value. The original difference between these two areas on the basin floor could only have been less.

It can be reasoned that, by using the present difference in altitude between the nearshore Kimberley outcrops and those from the postulated deeper part of the basin, between Carnavon and Loeriesfontein, an estimate of the maximum water depth in the basin can be made. The difference in altitude obtained from topographic maps is 150m over a distance of 300 Km which gives a maximum bottom slope of 1:2000 for the basin and a maximum water depth of less than 150m for the Whitehill sea. This rather unconventional calculation of the water depth finds unexpected support from the calculations of Visser and

Loock (1978) who, following a totally different line of approach, postulate water depths of $\pm 30\text{m}$. As the 150m of the present calculations is a maximum value for the deepest part of the basin, depths of about 30m could have prevailed over large areas. In general then, shallow rather than deep water conditions seem to have prevailed in the basin and it is useful to remember that Du Toit (1937) expressed the view that the White Band and Iraty were deposited in shallow seas. Other researchers, e.g. McLachlan and Anderson (1977a) however, regarded the Whitehill shale as a deep water deposit and sought alternative explanations for the presence of apparently shallow water laminated carbonates in the basin. These authors refer to their deep water model as being "in accordance with the established ideas on the palaeoenvironment of the White Band" (p. 92). Their interpretation of the slumping and deformation of the dolomitic layers as indicative of the instability of the sediments in a steep slope environment must also be questioned in view of the near absence of bottom slope in the basin.

Evaporite minerals in the formation

An exciting new aspect of the character of the Whitehill Formation came to light with the discovery of evaporite minerals albeit in small amounts and mostly only as casts of crystals of gypsum, halite and layers and lenses of dolomite.

The dolomite was first described by McLachlan and Anderson (1977a) who also pointed out the presence of casts of primary gypsum crystals in the dolomite. The author has recovered casts of gypsum rosettes which grew in the shales, (Fig. 39)

south of Calvinia. The presence of halite crystals was first noticed by Van der Westhuizen (1979) on the farm Buffelbout, Carnavon district. It is important to note the distribution of the evaporitic minerals in the basin. The dolomite occurs in the extreme south and east of the basin while the gypsum rosettes occupy an intermediate position between the dolomites (with gypsum) and the halite in the northwest. The presence of these minerals undoubtedly indicate a high salinity environment.

The distribution of sediments in the basins

The striking, near absence of coarse clastic sediments from the formation even in nearshore, shallow water environments, leaves the impression of an extremely sediment starved shallow water basin. This impression was strengthened by the failure to identify any major river systems that fed into the basins. The only exception is the presence of grits and channel lags in the remnants of the Huab Karoo Basin. Even these sediments, in spite of the grit sized grains indicate very low energy environments of transport and deposition for the grains are poorly sorted and highly angular.

The absence of major drainage systems feeding the Whitehill Basins is compatible with the post-glacial topography that dominated the scenery around the shores of the basins. This landscape is referred to as "of moderate relief" (King 1962 p.246) and "very smooth and almost flat" Visser and Loock (1978 p. 189). Contrary to conditions in the Black sea today where the Black reducing sediments first started to accumu-

late in the deepest parts of the basin (Degens and Stoffers, 1976) the fine sediments of the Whitehill Formation seemingly started to accumulate almost simultaneously over the entire basin floor. This can be inferred from the consistency in the thicknesses of the biozones in the basins. Evidence for the means by which the sediments were distributed so evenly over such vast areas is totally lacking in the sediments. No primary structures such as sole markings, asymmetrical ripples or any other features reminiscent of flowing water in the basins, break the monotony of the paper-thin flat laminations of the shales; the sole exception being three records of low amplitude (1mm) oscillation ripples (Fig. 8). One of the records is from the Hopetown district (Nel 1977) the other two were found by the author near Loeriesfontein and Calvinia. Both the latter sets were found associated with the intercalated silty shale member. The origin of these ripples in the deep offshore part of the Great Karoo Basin is puzzling. A slow oscillating movement of the bottom waters is about the only possible explanation. Such a (tidal?) oscillatory movement of the bottom waters of the basin is probably also the cause of the type of orientation found in the fossils. All fossils measured show a general preferential orientation (Figs. 9, 10). That the orientation was caused by an oscillatory rather than a streaming movement of the bottom waters is illustrated by the absence of a consistent head-tail positioning of the fossils. Therefore vectorial agents like unidirectional bottom currents can be ruled out. Both ripples and fossil orientation therefore point to an oscillatory movement of the bottom waters. It is therefore not fortuitous that the orientation of the fossils is perpendicular to the

strike of the ripples. A surprising factor is the general consistency shown in the orientation of the fossils over great distances in the Great Karoo and Karasburg Karoo Basins (Figs. 9, 10). Besides emphasising the uniformity in conditions that prevailed over great distances on the Whitehill sea floor it becomes tempting to speculate that the oscillation was caused by an omnipresent factor like a tidal surge. The slight local deviation from the general pattern recorded in the Kalahari Karoo Basin (Fig 10 - Klein Spitskop) most probably indicate a deflection of the tidal movement by bottom irregularities in this nearshore area of the basin.

Other examples of epicontinental sediment deposition

The model most frequently used as comparison for the sedimentation of the Whitehill shales is the Black Sea (Du Toit 1937, 1954; McLachlan and Anderson, 1973; Anderson and McLachlan 1979). The Whitehill and Iraty Basins can also be compared with some other epicontinental seas in which black shales form or have formed. Two such basins which have been studied well is the Catskill Delta sea of Devonian age in North America and a modern basin in the Gulf of Carpentaria-Arafura area between Australia and New Guinea (Heckel 1972).

In these basins black shales accumulate in central sediment-starved areas of no deposition and the shales phase out into dolomitic, carbonate facies in areas where little or no sediments are (or were) delivered into the basins (Heckel 1972). Where sediments do reach the basins the black shales change into a green-shale-sandy-shale-sandstone facies. In the mo-

dern, bay of Carpentaria Basin proto green shales and sandstones are present as soft sediments along a wide marshy border on the northern edge of the basin.

The Whitehill Formation closely resembles the sediments in the aforementioned models. The black shales of the Whitehill also phase out into green shales and sandy shales and also show dolomite precipitation elsewhere on the margins of the basins. In contrast to the basins mentioned above the relative proportion of the black shale developed in the Whitehill Formation seems to be much larger. The more extensive development of the coarse clastic facies in the Catskill and Bay of Carpentaria basins is directly related to the steep gradient between the basins and adjacent mountainlands.

In the Bay of Carpentaria the sediments are shed into the basin from the \pm 3000m high mountains which form the backbone of New Guinea and have extended the island up to 200 miles (\pm 320 Km) into the sea as a swampy deltaic plain. On this plain recent alluvial, paludal and lacustrine deposits have accumulated to a thickness of perhaps 2,000 feet (600m). Sediments range from conglomerates to mud and generally become finer grained seawards. (David 1950, in Heckel 1972). The marshland act as a sediment trap and causes sediment starvation in the central region of the basin where black muds consequently develop.

Towards the Australian coast, in shallow conditions where very little sediment is derived from the adjacent low lying country, dolomite is precipitated.

With these examples in mind an attempt is now made to set up a model for the sedimentation of the Whitehill Formation.

Models for the precipitation of the Whitehill Shale Formation

The deposition of the Whitehill sediments may be interpreted in three ways:

(1) The basin may have been much larger than is indicated by the present day remnants, extending landward with a wide rim of bordering marshland which trapped incoming sediments and caused the starvation of the central areas. The Great Karoo Basin Whitehill sea would have received most of its influx from the north (as has been indicated by Du Toit, 1954; Ryan, 1967 and Stratten, 1978). The equivalent of the marshland sediments of green shales and sandy shales (with the development of vegetation luxurious enough to produce coal?) is represented by parts of the northern Ecca. This correlation has already been proposed by various authors, e.g. Van Eeden (1973) and Anderson and McLachlan (1979).

The dolomites in the southern and southeastern sections of the basin would then indicate shallow, sediment-free areas.

(2) The second model calls for the near absence of topography between the basins and the immediately adjacent country. This is the view Du Toit (1937) probably had in mind when he referred to the post glacial landscape as a "worn down continent" (p. 78). This "fairly smooth" (Visser and Loock 1978 p. 189) landscape was probably drained by a few sluggish rivers only. Such rivers could deliver little sediment into the basins. After the loose morainic material was redistributed and some of it deposited as part of the Prince Albert Shale Formation and its counterparts in the other basins (Fig.2) the rivers would have been clear, carrying their sediments in fine

suspension and mainly in solution. These sediments derived from the clayey morainic remnants could then account for some of the Whitehill material. (This corresponds with the "Black Sea model of other authors)

(3) The third model is a combination of features from the previous two and is in my opinion closest to the original circumstances of deposition.

This model also postulates the final pediplanation of the landscape by the post glacial erosion cycle and the redistribution of the morainic material into the shale units above the tillites, e.g. the Prince Albert Shale, Auob and Nossob sandstones and associated shales in the Kalahari Karoo Basin and Zones 1 and 11 of Hodgson and Botha (1973-74) of their Twyfelfontein Formation in the Huab Basin (Fig.2). These shales therefore could represent the outwash of morainic material left behind by the retreating glaciers as part of the first post glacial erosion cycle. Reworked morainic material is well documented (Visser et al 1979). As has been reasoned in the other models, this erosion cycle created a smooth and featureless countryside which led to a drastic reduction in sediments delivered into the basins. Minor marshlands developed along the shores to the north. Even before the onset of the sediment starvation of the central parts of the basins the adjacent post glacial countryside was covered by vegetation (Visser et al 1979). During this pre-Whitehill period ample evidence exists for such a flora because wood and tree trunks were washed into the basins and became fossilised in the shales and sandstone deposits between the glacial beds and the Whitehill Formation. Wood and tree trunks are well documented and were reported by various authors in all the

basins (Martin, 1953; Van Eeden, 1973; McLachlan and Anderson, 1973; Schreuder and Genis, 1973-74). With the presence of abundant wood in the sediments the local development of coal swamps should be expected and it is therefore not surprising that coal seams are present below the Whitehill Formation in the Namibian basins and locally also in the Great Karoo Basin (Visser et al 1979). These coal seams led to the correlation of the Whitehill Formation with the middle, coal bearing Ecca (Van Eeden 1973, McLachlan and Anderson 1979). These embryonic coal swamps probably only later developed into the extensive growths which formed the main Ecca coal seams. The development of the coal swamps probably saw the contemporaneous development of black shales in the basins to the south and west. These black shales, which we see today as the Whitehill Formation, were probably fringed by transitional green muds, today represented by interdigitating green shales which occupy a position between the black shales in the south and the coal-seams to the north.

THE CONNECTIONS OF THE BASINS WITH THE WORLD OCEANS

In spite of the enormous size and relative shallowness of the Whitehill water body no indication of large scale fluctuations of the water level were recorded by emergent features such as e.g. mud cracks along the shores of the basins. The effect of evaporation on such large, shallow basins, even in high latitudes must have produced severe fluctuations of the water level. To explain the constant water level by a precisely compensating influx of fresh river water is ridiculous. The only alternative explanation is that the basins were connected to a body of water large enough for evaporation to have little or no effect, in fact, the world oceans. Can evidence for such a connection be advanced, what was the nature of the connection(s) and where was it situated?

In the zone where South America and Africa abut against each other in most reconstructions of Gondwanaland a (narrow?) stretch of water (an intracratonic arm of the sea) must have been present from as far back as the Silurian (Rust 1967) or even the Precambrian (Germs 1974). Transgressions of this sea onto the western and southern parts of southern Africa and the eastern part of South America is documented by the presence of marine fossils.

Marine faunas that document these transgressions are known from large areas of central Gondwanaland. Silurian age transgressions are known in South Africa (Rust 1967) and in northern Brazil (De Loczy 1971), from marine deposits in the Cape and Maranhao Basins respectively. Marine sediments of Devonian age are present in the abovementioned basins as well as in

Angola (De Loczy, 1971). In North Africa too, thick successions of Ordovician-Silurian age marine strata are present (De Loczy, 1971).

All these transgressions, as well as those in which the marine tillites of the Dwyka (Frakes and Crowell, 1975) and the Prince Albert shales (Oelofsen and McLachlan in preparation) were deposited, can best be linked with this epicratonic incursion of the ocean. It is proposed here that this sea served as a central arm of which the Whitehill and Paraná seas were embayments onto the continents of Africa and South America respectively (see Fig. 1C).

This proposed sea itself must have been to a large extent, epicontinental and landlocked. Epicontinental basins connected to it both to the east and the west were bound to be euxinic in nature and being transgressive onto landmasses with a similar glaciated immediate prehistory could not be anything else but almost identical in nature.

The black shales, the distribution of evaporitic dolomites, the common endemic faunas, in short the fact that the Whitehill and Iraty Formations are almost mirror images of each other can only be explained satisfactorily in this way. This amazing similarity, first noticed by Du Toit (1927) was confirmed by the observations of Martin (1961).

In the present study additional instances of similarity were found (see Figs 11 and 12).

The existence of a Whitehill-Iraty connection accounts for the facts much better than does an alternate theory suggested by e.g. Araujo (1976) and Anderson and McLachlan (1979) who suggested that the Whitehill and Iraty Basins were separated by a continuous "highland" barrier.

A problem that arises from the presence of such a connecting sea is that the sediments which must have accumulated in it, can not be demonstrated. This interesting problem "the case of the missing sediments" have been explained in two ways.

The first explanation can be referred to a statement of De Loczy (1971 p. 383) that "during the orogenesis the oceanic crust may have been resorbed in the marginal trench systems," and with it the sediments would have gone.

An alternative and very ingenious explanation was offered by Martin (1975) which involve post Ecca graben type rifting, uplifting and erosion of the sea bottom, with an eventual sinking and burial of the material below younger sediments on the continental platform off the coast. (Martin offers this explanation for the coast of Namibia near the Huab Karoo Basin).

The problem of the connections of the Whitehill and Iraty Basins reduces to that of an intra-continental arm of the sea that invaded along a N-S extending zone of (-) epeirogenesis in early Permian times. This may have been the forerunner of the suture, which more than 100 m.j. later separated the two continents to form the early Atlantic ocean (see Fig. 1C).

Position and nature of the connections of the Whitehill Basins with the intra-cratonic arm of the sea (see Fig. 1C)

The nature and position of the proposed connections between the Whitehill Basins and the intra-cratonic sea was probably inherited from the preceding glaciation and Prince Albert transgressions. The Windhoek highlands that shed its sediments into the Kalahari Karoo Basin (Martin 1961) formed a

highland between the Huab Karoo Basin and the more southerly basins (Fig. 1C). These basins were therefore interconnected only via the more westerly situated sea arm with the Huab Basin which thus formed a separate embayment north of the Windhoek highlands. These highlands also formed the northern shore of the Kalahari, Karasburg and Great Karoo Basins which were all part of one large southern embayment. (see Fig. 1C).

The position and nature of the southern shore of the connection is poorly known. The position and presence of a southern highland can only be inferred from the ice-flow directions during the preceding glaciation. Information on ice-flow directions from the south western part of the Great Karoo Basin however is scant and conflicting. Reconstructions of the direction of the iceflow has been made. Traditionally (e.g. Du Toit, 1954; Stratten, 1968 ; 1970; Rust, 1975) a vector towards the east was accepted. Palaeontological evidence from glacial erratics (Cooper and Oosthuizen, 1974) however cast some doubt on the validity of the eastwardly directed flow. Subsequent reinvestigations of the ice-flow directions led to a reversal of the direction of flow (Theron and Blignault, 1975) and consequently a westward flow is now accepted by workers in this field (Visser, 1978; Anderson and McLachlan, 1979; Oosthuizen, in press; Oelofsen and McLachlan, in preparation). The northwest projecting prong of a proposed southern highland, as visualised by Stratten (1970) therefore probably never existed. The presence of an outlier of Whitehill, showing biozonation identical to that of the Great Karoo Basin, on the downthrust side of the Worcester fault, may indicate that the basin extended even further south. The connection with the sea there-

fore could have been wide and it is likely that remnants of Whitehill shale will someday be discovered in Antarctica. A wide connection with the sea arm may furthermore explain why a full scale evaporitic succession never developed in the Whitehill sea as is usually the case in proper euxinic basins (Hite 1970). Can the presence and the distribution of the evaporitic minerals which are present however be satisfactorily explained within the framework of this model?

The Whitehill sea as a potential evaporitic, euxinic basin

The finely layered, slumped, black dolomites present as layers in the south-eastern section of the basin gradually diminish and eventually virtually disappear to the north of Loeriesfontein. Casts of syngenetic gypsum crystals are present in the dolomites from as far east as Damascus farm (McLachlan and Anderson 1977c) to as far west as Patatsfontein between Laingsburg and Ceres.

In the area to the south of Calvinia casts of small gypsum rosettes are present in the shales, the best examples were found on the farm Groote Brak north of De Bos in the Tanqua Karoo. The rosettes are associated with individual casts of blade-like single gypsum crystals (Fig. 39). In the northern part of the basin, on the farm Buffelbout in the Carnarvon district, Van der Westhuizen (1979) found casts of halite crystals. Subsequent finds were made by Strydom (1979). This isolated occurrence of halite and the absence of evaporitic minerals such as carbonates and gypsum which by nature of the chemistry of evaporite precipitation,

should precede the precipitation of halite, is puzzling. The presence of dolomite and gypsum elsewhere in the basin rules out the possibility that the chemistry of the water was of such a nature that halite could have precipitated from it without carbonates and gypsum having precipitated out first for "in marine evaporites gypsum-anhydrite is never found without underlying or interbedded limestone or dolomite; halite does not occur without gypsum-anhydrite" (Borchert and Muir 1964 p. 76).

Seemingly isolated occurrences of gypsum and halite crystal casts in sediments are generally interpreted as indications of greatly increased salinity (brines) and should occur in the same range of environments in which evaporites can form (Heckel 1972).

Modern gypsum rosettes growing in sediments are known from subsurface clays and sands and precipitate from highly saline seawater which sinks into the underlying sediments (Masson 1955). Such brines, having lost their load of insoluble salts (carbonates and anhydrite-gypsum), will tend to be funnelled downslope and collect in the deeper parts of the basin, or be funnelled out of the basin.

Reflux of the Whitehill sea seems to have been good enough to prevent substantial precipitation of evaporites and it was only in or on the sediments itself that the brines could be trapped long enough for the rosettes and halite crystals to grow.

The physical and chemical properties of brines are discussed by Hite (1970) who states that,

- (1) Brines can have a salt content of ten times that of sea water with very low pH values.

(2) Brines are usually anoxic because of the depletion of oxygen by the decay of organic material and the depressed solubility of oxygen in concentrated salt solutions.

(3) Toxic concentrations of hydrogen sulfide are also characteristic of these waters and

(4) High brine temperatures are common owing to a greenhouse effect caused by solar radiation passing through the influx layer of fresh sea water into denser reflux layers.

The presence of such toxic, anoxic brines in the bottom layers of the Whitehill sea could account for the accumulation of the black shale. The Whitehill Formation can perhaps be compared with the Paradox Basin of Pennsylvanian age in Utah and Colorado where the evaporite succession of the Hermosa Formation is underlain and capped by black shales (Hite 1970). These Paradox black shales were deposited when reflux of the basin was great enough to prevent the precipitation of evaporites. The Whitehill, with its minor evaporite development could possibly be compared to the lower black shale unit of the Paradox Basin. In contrast to the Paradox Basin however, the Whitehill Basins, possibly because of the absence both of depressions in the floor and of a geographical barrier to the world oceans, never developed into a proper evaporitic basin. This model would also help to explain the impoverished benthic fauna of the Whitehill sea: The toxic brines in the basins, and escaping through the connection with the sea, prevented bottom faunas from entering and establishing themselves in the basin. It was only when oxic conditions returned and the green intercalated silty shale was deposited that the layering of the water was upset and benthic and fossorial orga-

nisms entered the basin (see the distribution of trace fossils in the sediments p.75). In this respect the Whitehill differs from the Black sea where benthic macrofauna flourishes in the shallow waters along the shores (Shimkus and Trimonis 1974). As Van der Westhuizen (1977) reports halite crystals from the base of the formation it is unlikely that the evaporitic minerals can be explained by the Whitehill sea starting off as an isolated body of fresh water which gradually salted up through evaporation. The possibility that the brines in a totally landlocked basin would remain on the threshold of halite precipitation without forming evaporites in any quantity, seems to be infinitely small. Stratified waters and bottom, anoxic brines would also explain the formation of the pyrite present in the shales. Stable stratified conditions lead to the anoxic-bacterial decay of organic matter (Heckel 1972). The organic matter in the shales was probably largely produced in the oxygenated, less saline surface waters as is the case in the Black sea today (Shimkus and Trimonis 1974).

Very little organic matter was probably derived from the adjacent lowlands. Had the carbon been derived from plant debris washed into the basin, more fossil plant material would have been present for wood can drift for long distances and can withstand mechanical and biological attrition very well. The author certainly can not confirm the claims of Van Eeden (1973) of the abundant presence of vegetable matter in the shales nor that of Cooper (1974) of silicified wood in a number of outcrops. My own collecting turned up numerous specimens of fossil material usually considered to be rare but only a single piece of silicified wood (in the Worcester outlier)

was found. Recognisable vegetable matter was likewise found to be rare with the possible exception of "furoid straps" that may not be of vegetable origin at all. Other records of single pieces of wood is a trunk in the collection of R.D.F. Oosthuizen of Zwartskraal, Prince Albert and a trunk reported by Nel (1977).

THE TRANSPORT OF SEDIMENTS INTO THE BASIN

From the extremely fine nature of its sediments it can be inferred that the material that was carried into the basin by water was in solution and suspension. Any such fresh water that entered the basin would have flowed over the denser bottom brines.

An important fraction of the Whitehill shale was however blown into the basin as is at present the case in the Black sea (Shimkus and Trimonis 1974). At least part of the material is known to be derived from distant volcanic sources (McLachlan and Anderson 1977a). With this airborne dust small light objects like insect wings also reached the basin. It is only through aeolian transport that the random distribution of insect wings in both nearshore and central sediments can possibly be explained (Fig. 5). Even stratified waters and surface currents could not have facilitated the transport of such frail objects over such long distances.

Stratification of the water would explain why primary sedimentary structures are absent from the sediments in the basin in spite of the fact that relatively shallow conditions over wide areas are postulated. In shallow water wave action is registered up to 50m deep (Shimkus and Trimonis 1974) and the fetch of the waves bases must surely have reached the bottom and should have produced ripples. If strong, sediment distributing currents were operative, stream ripples and sole marks should have been present. None of the dampening effects proposed by Heckel (1972) other than stratification of the water can explain this universal absence of vectorial primary structures in the Whitehill sediments.

To sum up, the Whitehill sea is visualised as a relatively shallow, sediment starved, euxinic embayment surrounded by low lying almost flat, marshlands. The stratified waters with highly toxic bottom brines and relatively fresh upper layers prevented the development of a bottom fauna but sustained pelagic organisms (e.g. fish and mesosaur reptiles). Surplus organic material from the less saline upper layers reached the bottom brines where it was decayed by anoxic bacteria, which resulted in the formation of the highly sulphuretted black muds. Very little material was shed into the basin from the adjacent land and the bulk of the sediments were transported as windblown dust or in solution and fine suspension. The single most striking impression gained however is that the sediments were deposited in an almost energyless environment.

THE FOSSIL FAUNA OF THE WHITEHILL SHALE FORMATION

The foregoing section on the lithology of the Whitehill Formation will have prepared the reader for an impoverished and peculiar fauna in the Whitehill shales. This is indeed the case, the fauna consisting of but two vertebrates, two crustaceans, a few problematic forms and scrappy pieces of vegetable matter. The vertebrates comprise the fossil reptile Mesosaurus and a number of species of palaeoniscid fish of which only one (Palaeoniscus capensis Broom 1903) has been formally described. A single crustacean Notocaris tapscotti (Broom 1931) has been formally described with junior synonyms listed by Kensley (1975). At least one new crustacean was recovered from the thinly banded, black dolomites of the Formation.

Two insect wings with mecopteran and plecopteran affinities were recently discovered in the black dolomites (McLachlan and Anderson 1977b) and three more were subsequently recovered. One from the Carnavon district (Strydom 1979), one from Loriesfontein and another from the Worcester outlier.

An exciting discovery of a fossil which could be interpreted as a cephalochordate was made in the eastern outcrops of the Formation. The only ichnofossils that were recovered from typically white weathering shales are arthropod-trails and body impressions from the Karasburg Karoo Basin.

Ichnofossils from the intercalated silty shale member include Zoophycos and Scolicia type feeding trails, Bifungites-like impressions and star-like traces of the Asterichnus type which are also known from the Iraty (Mezzalana 1971). A new

ichnogenus and species of the feeding trail type is described. A number of problematica were encountered. These include pentaradiate echinoderm-like hollow spheroids which show ambulacral and food groove-like structures; an impression reminiscent of a brachiopod valve and spicula-like impressions possibly of a glass sponge.

The distribution and stratigraphic occurrence of the ichnofossils, body fossils and problematica were studied.

THE DISTRIBUTION OF FOSSIL FORMS IN THE WHITEHILL BASINS

(1) Mesosaurus

The genus Mesosaurus in southern Africa is confined to the shales of the Whitehill Formation which outcrops in four at present separated basins. Whereas the fossil is usually present in the white weathering black shales in the Great Karoo-, Karasburg Karoo- and Kalahari Karoo Basins, the occurrence in the small northernmost Huab Karoo Basin is atypical for the material, is preserved in the coarse sediments of the so-called Doros bone bed.

The Great Karoo Basin

Prior to this study Mesosaurus was known from the western part of this basin only. Du Toit (1927) in his account of the distribution of Mesosaurus implies that it is present also east of Laingsburg and in the Worcester outlier but no specimens collected from these areas are documented. During the deposition of the underlying Prince Albert Formation (formerly part of the Upper Dwyka Shale) the Great Karoo Basin was subdivided into two sub-basins, a western and an eastern. The

conspicuous absence of fossils from the outcrops east of Laingsburg were thought to indicate that conditions in the eastern sub-basin was such that Mesosaurus was not present or did not fossilise or that fossils if present were obscured by the metamorphic effects of the Cape Folding (McLachlan and Anderson 1973).

In the present study it was established that during Whitehill Formation times the Prince Albert sub-basins were no longer in existence. Different conditions in the eastern section can thus no longer account for the absence of fossils and a careful search of the outcrops to the east of Laingsburg duly yielded Mesosaurus in fair abundance. It was confirmed that an obscuring cleavage is present in the shales as a result of the Cape Folding: the shale tends to split along the new cleavage planes and no longer along the original bedding planes. This may explain why the fossils were never noticed in the long, albeit often poorly exposed outcrops to the east of Laingsburg. The most easterly record of this study is from near Kommadagga where pieces of rib, unmistakably that of Mesosaurus were recovered from a quarry in the Whitehill Formation on the farm Grasfontein. Mesosaurus was also discovered in the small outlier of Karoo rocks on the downthrow side of the Worcester fault. Although the outcrops in this outlier are rather poor, the complete Whitehill Formation is present and a surprisingly large number of specimens have been recovered from it. This is the most southerly record for Mesosaurus.

Mesosaurus remains are usually found as hollow moulds of the bones from which the original material had been leached out, but a variety of less common modes of preservation were also

encountered. In some of the less weathered specimens, bone material which was shown by chemical tests to be surprisingly unaltered, was still present. In a few specimens the bone material was found to be extensively carbonised (e.g. specimen no U.S.S. 2/8/1). No specific pattern in the distribution of the carbonised specimens seems to be present. Carbonised specimens from the Whitehill shales often occur in shale with a low carbon content which differ radically from the mode of preservation of carbonised Iraty specimens that the author has seen. The latter specimens seem to occur exclusively in a very dark soft oily shale. Only one South African specimen vaguely resembles the South American material in this respect. This specimen is no U.S.S. 1/2/12, a poorly preserved carbonised skull from the farm Blouputs near Loeriesfontein.

The Kommadagga specimen is replaced by iron oxide and some of the specimens from the Worcester outlier are infilled with silica. Only one specimen from the main Great Karoo Basin, collected by S.H. Haughton at Elandsdraai in the Tanqua Karoo (SH 1414, S.A.M. 10672) also show this positive, silica replacement mode of preservation.

The Karasburg Karoo Basin

The first reference to Mesosaurus in this basin is of a specimen, recovered from Kanibeam (Haughton and Frommurze 1927). Excellent specimens, now in the possession of G. Genis of the Geological survey in Windhoek was recovered from the farm Kirchberg. (Schreuder and Genis 1973-4). In general the specimens from this basin are preserved in much the same way as

that of the Great Karoo Basin.

The Kalahari Karoo Basin

Specimens of Mesosaurus were first recovered from the Gellap Ost plateau (Martin 1961) north west of Keetmanshoop. In this area I collected 23 excellently preserved specimens with very fine details of the bones preserved in the hollow moulds.

On the Gellap plateau the Whitehill Formation, not only because of its fossil content but also by its lithology can easily be recognised. The preservation of the fossils is also similar to that in the two southern basins. The Whitehill Formation however becomes less silicious and more carbonate rich northwards and some specimens are preserved as silicified bone in limestone. In some of these specimens (e.g. U.S.S. 6/1/8 Fig. 21) the relatively harder silicified bone had weathered out of the limestone matrix producing beautiful, three dimensionally preserved, vertebrae. On the edge of a low escarpment \pm 5 Km due west of the homestead on the farm Gross Daberas on the road to the Vingerklip (Mukorob), specimens, preserved in a greenish, thinly bedded marl, occur. Slightly white weathering finely laminated units reminiscent of Whitehill shale are also present. Martin (1961) first reported the presence of Mesosaurus from this part of the Kalahari Karoo Basin and specimen P.C. 37 (State Museum, Windhoek) is figured by Heath (1966) who however, incorrectly referred to it as Noteosaurus.

The Huab Karoo Basin

Fossilised reptilian remains, discovered in the coarse grit at Doros crater (20°45'S 14°15'E) was first identified as Mesosaurus by Haughton in 1919 and was later fully figured and described by Von Huene (1925). According to Von Huene (1925) the material was discovered by Reuning. Hardly any material from Doros is available in museum collections, the material presented to the State Museum by Martin (Martin oral comm.) was apparently never catalogued and is lost. As a result the presence and identification of the material has been in doubt (Hodgson and Botha, 1973-4; Martin, 1975) and the correlation of these sediments with the Whitehill Formation abandoned. A special and successful effort to collect new material from this isolated locality was made and its stratigraphic occurrence was restudied.

The bones occur in two thin (\pm 30 cm) layers of coarse grit, two thirds up the northwestern slope of Doros crater (see Figs 4 and 14A). The grit consists of angular, poorly sorted clear quartz grains in a red, iron rich matrix, in which the bones are set. The bones are usually weathered out leaving only hollow moulds but in fresh samples the relatively unaltered white bone is present.

In spite of the doubts voiced about the identification of the bones this study has shown beyond doubt that the identification of the bones as Mesosaurus made by Haughton and by Von Huene (1925) is correct. On the assumption that the identification was wrong, Hodgson and Botha (1973-4) renamed these sediments the Twyfelfontein Formation. This new unit in view of the excellent description and detailed illustrations of the material by Von Huene (1925) and the results of the

present study confirming the earlier identifications, is clearly the chronostratigraphic equivalent of part of the Prince Albert and Whitehill Formations.

Problematic records

Some localities for Mesosaurus entered in the catalogue of the Albany Museum and the State Museum I found to be suspect for they are stratigraphically incompatible with the known records of Mesosaurus.

The specimen in the Albany Museum (no 240) is mentioned by Seeley (1892) as coming from the town of Burgersdorp. This obvious error was pointed out by McLachlan and Anderson (1973) (Burgersdorp lies on Beaufort sediments nearly 320 Km from the nearest Dwyka outcrops). I traced this record in the catalogue of the Albany Museum and found a double entry. One, stating that the specimen originated from Burgersdorp, proved to be an incorrect copy of the original entry. The older entry gives the locality as Kimberley (Whitehill)shales and the donor as a resident of Burgersdorp. The nature of the matrix of the specimen itself leaves no doubt that it is in fact Whitehill shale as are the other specimens from Kimberley (now in the British Museum) described by Seeley in 1892. I was also able to correct the locality records of two specimens in the State Museum, Windhoek. When examining specimens PC. 38 and PC. 40 (a third specimen under the same entry, PC. 39, could not be traced in the collection) it became clear that their locality record, given as Rehoboth, was in all probability an error, because the stratigraphy of this district makes the occurrence of Mesosaurus unlikely.

The donor of these specimens, F. Steyn, was traced who stated (oral comm.) that all the specimens were collected by a Mr Du Preez in the Gellap Ost area. The greenish silty shale matrix of specimen no PC.40 points to its probable origin from the intercalated shale developed in the Whitehill Formation of this area

(2) Crustacea

The Crustacea in the basins are represented by the prawn-like Notocaris tapscotti Broom. Notocaris tapscotti is the senior synonym for Anthropalaemon and Pygaspis ginsburgi Fabre (McLellan and Anderson 1973; Kensley 1975).

To date the following works refer to pygocephalomorphic crustaceans in the Whitehill shales: Rogers and Du Toit (1909) refer to "probably Anthropalaemon" (p. 193), Haughton (1919) mentions Anthropalaemon from the White Band near the Orange River station and Woods (1922) figures and refers to pygocephalid crustaceans from the White Band at Kimberley. A short description of what is obviously N. tapscotti is given but a name was not formally proposed. Wood's material was re-examined by Broom (1931) who named it Notocaris tapscotti.

The first worker since Broom (1931) to study the form was Fabré (1967) who collected material from the Whitehill outcrops near Laingsburg and because (the author suspects) he never realised that one species could be so widely distributed, created a new species; Pygaspis ginsburgi. I found Notocaris tapscotti to be universally present throughout the Great Karoo Basin (see Fig. 6) and extended its eastward distribution from Laingsburg to Willowmore. Further to the east it could not be traced, but this must be because of the poor outcrops rather than its absence. The author also found it in the Worcester

outlier. The first record of N. tapscotti from the Karasburg Karoo Basin is by Schreuder and Genis (1973-4). In the present study its universal presence in this basin also, was established.

Prior to this study, N. tapscotti was not known from the Kalahari Karoo Basin. However the author found it on the Gellap Plateau and in abundance on the farm Spitskop to the north-east of Keetmanshoop.

Another, yet indeterminate crustacean was found in the black, thinly layered dolomite of the eastern part of the basin. It was first discovered by Mr R.D.F. Oosthuizen who has some beautifully preserved specimens in his collection (Fig 15). Of this form the carapaces only, are usually preserved. I traced its distribution from west of Laingsburg to Lake Mentz in the east. In general appearance, mode of preservation and stratigraphic position, this crustacean strongly resembles Paulocaris clarki from the Iraty.

(3) Fossil Fish

Prior to this study the fossil fish from the Whitehill Formation were represented by a single species, Palaeoniscus capensis Broom (1913). Considerable confusion exists about the precise locality of the type specimens although Broom (1913) in the original description of the material states that it is from 12 miles (+ 19 Km) west of Calvinia. The type material is housed in the South African Museum, (S.A.M. 1061) and Broom (1913) in his description refers to three specimens but only figures and describes the type specimen. The only other reference Broom (1913)p. 1) gives to the other two specimens is that "in the other two the tail halves" are present. These specimens were re-examined by Gardiner (1962) who contrary to

Aldinger (1937) believes that the identification by Broom (1913) of the material as Palaeoniscus is correct. McLachlan and Anderson (1973) state that Jubb identified fish they collected from the Whitehill Formation on the farm Ezelsfontein near Loeriesfontein as identical with the incomplete specimens in the South African Museum (S.A.M. 1066) which Broom (1913) by implication saw as paratypes of Palaeoniscus capensis.

The Cape Town material (S.A.M. 1061, 1062 and 1066) was re-examined by Jubb and Gardiner in 1975. Specimens S.A.M. 1062 and 1066 were consequently removed from Palaeoniscus capensis and tentatively referred to Watsonichthyes lotzi. (The material of Anderson and McLachlan (1973) from Loeriesfontein will now also be referred to W. lotzi as is the fragmentary material (S.A.M. K1162) collected from the same locality by Cluver and Kensley);

To date Palaeoniscus capensis was therefore represented by the type specimen (S.A.M. 1061) only but I collected additional specimens from the Loeriesfontein area. As has been pointed out (McLachlan and Anderson, 1973; Jubb and Gardiner; 1975) the original record in the catalogue of the South African Museum gives the locality of this specimen as "Waterval farm, Prince Albert district, Cape Province". This original entry was crossed out and a new locality stating "Hantam mountains 19 miles west of Calvinia" was made. As the farm Waterval in Prince Albert district lies entirely on lower Beaufort sediments, the specimens, which undoubtedly is of Whitehill origin by virtue of its matrix, could not have come from this locality. Upon examining the fossil fish collection of the South African Museum I found two specimens with the same number S.A.M. 1061. One of these is the type of Palaeoniscus capensis Broom and

the other is a fragment which seems to be lower Beaufort rock with Atherstonia-type scales. On this specimen an inscription reads "Waterval, Prince Albert". As the type specimen of P.capensis bears an inscription "Hantam mountains, 12 miles west of Calvinia" there can be little doubt that this must be the correct locality.

Jubb and Gardiner (1975) pointed out that Palaeoniscum Agassiz has priority over Palaeoniscus as Broom (1913) used it. Consequently the valid name for this fish is Palaeoniscum capensis.

The first report of fish from the White Band (Whitehill) is by Rogers and Du Toit (1909) who refer to Elonichthyes sp. from Calvinia. In the present study the distribution of fish in the Whitehill Formation was traced by systematic collection and a number of new localities were discovered (Fig. 13).

Prior to this study fish were known from the farm Ezelsfontein (McLachlan and Anderson 1973) and Langberg (Hälbich 1958) near Loeriesfontein as well as from the vicinity of Prince Albert (Haugton, Blignault, Rossouw, Spies and Zagt, 1953) and the farm, Vlakte onder Hangklip (Rossouw, Meyer, Mulder and Stocken 1964) from the same district.

The easternmost record is now from the farm Zwartskraal near Klaarstroom and the northermost record is from the farm Jachtscherm northwest of Vosburg where fish were found by Mr J.C. Look (pers comm.). The author also recovered fish scales from the Worcester outlier, which makes this the southernmost record. The presence of fish in the form of fish trails was recorded on the farm Gannavloer near Van Wyksvlei in the Carnavon district (Fig. 18).

In the Whitehill outcrops from De Bos in the Tanqua Karoo in

the south to the farm Narosies north west of Loeriesfontein I found the fish to occur in dense concentrations in a thin zone in the middle of the formation. From the description of Hälbich (1958) it is likely that only the lower half of the formation is present in the Langberg area for the fish acme zone seems to be present near the top of the outcrop in this area. The upper few feet of Whitehill sediments on the Langberg according to Hälbich (1958) together with the fish also contain abundant "plant impressions" (p. 124). From the general biostratigraphy in this area it is possible that the "plant impressions" are the worm trails present in the intercalated shale in the middle of the Formation.

The presence of fossil fish material in the Karasburg Karoo Basin is documented by Anderson (1975) from Goeie Hoop.

I have collected good impressions of palaeoniscid fish scales from the farm Kirchberg and a single bony plate probably also of a palaeoniscid fish from Aussenkjer. Schreuder and Genis (1973-4) mention fish from shale above the tillite but do not mention fish in the Whitehill Formation. The Kalahari Karoo Basin, like the Karasburg Karoo Basin, has yielded abundant fish from the shale between the tillite and the Whitehill Formation (the equivalent of the Prince Albert shale in the Great Karoo Basin) (Gürich, 1923; Gardiner, 1962; McLachlan and Anderson, 1973). From the Whitehill Formation no fish had been recovered to date. In the present study, with the exception of a single impression, probably of a bony plate of a palaeoniscid fish, no fish was found. The single record is from a loose block of silty shale found on the farm Gross Daberas (Fig. 19).

(4) Insect Wings

The first record of insect wings from the Whitehill Formation was from Modderdrift and Krantzpoort, farms in the eastern section of the Great Karoo Basin (McLachlan and Anderson 1977b). Both specimens were recovered from the black, slumped dolomite. From the north western part of the Great Karoo Basin another wing was found by J.C. Terblanche (Strydom 1979). This specimen, now in the collection of the Zoology Department University of Stellenbosch was identified by E van Dyk (pers. comm.) as a coleopterid wing. The wing is preserved in the typical white weathering shale. From the Worcester outlier, C. Potgieter recovered a wing in a calcareous concretion. The incomplete, folded wing (Fig, 20) is difficult to identify and to evaluate systematically.

A fifth wing was found in white weathering shale on the farm Kaffersdam in the Kubiskou range near Loeriesfontein. The paucity but nevertheless wide distribution of the insect remains could be important in evaluating the transport systems that were operative in the basins. According to Anderson and McLachlan (1977b) two possible transport mechanisms could have been involved, (wind and water currents), and they come to the conclusion that wind was the most probable agent responsible. Flying insects are known to be carried for vast distances over the ocean and light objects floating on the surface are also commonly carried along by the wind. There is therefore no necessity to invoke water currents from e.g. incoming rivers as a transport mechanism. In any case, if currents were involved, driftwood and leaves emanating from the natural habitat of the insects might have been expected at least in some abundance, in the sediments. In fact, plant material, other than the odd

(possibly windborne?) leaf or two is virtually absent (see next section). The role of wind as a transport agent is confirmed by the presence of volcanoclastics such as glass shards and lapilli (McLachlan and Anderson 1977a).

(5) Plant Material

Fossil wood is exceedingly rare in the Formation. A few records of wood from the Formation are all from the Prince Albert area of the Great Karoo Basin (Haughton *et al.*, 1953, Rossouw *et al.* 1964, and Oosthuizen pers, comm.) Cooper (1975 p. 377) mentions the presence of silicified wood in "a number of outcrops" and Van Eeden (1973) postulates that the carbon in the northern White Band outcrops was derived from forest areas to the north. Nel (1977) found a silicified trunk in the north-western outcrops. Notwithstanding the claims of some of these authors I never came across any fossilized wood in the course of my field work with the sole exception of one record from the Worcester outlier. I have certainly gained the impression that the shales are for all practical purposes devoid of driftwood. Of a number of other workers who studied and mapped areas in the north-western section of the Great Karoo Basin (e.g. Potgieter, 1973; McLaren, 1974; Potgieter, 1974; Lemmer 1976) none mentions the occurrence of plant material.

The record of leaves in the formation is likewise restricted to a few specimens. Schwartz (1912) and Du Toit (1954) refer to Glossopteris material from the White Band but the original specimens could not be traced (Anderson and McLachlan, 1976). The latter authors documented the presence of a single leaf fragment from the dolomitic layers. The specimen was referred to the fern-like Condwanidium rather than to Glossopteris.

An impression of a somewhat enigmatic plant was found by R.D.F. Oosthuizen on a joint field trip in the Calvinia district. (specimen G 38, collection of Oosthuizen). The specimen was described and illustrated by Anderson and McLachlan (1976) who could not reach a definite identification on the specimen. A number of flat leaf-like structures were collected by me from the shales. Some of the specimens (U.S.S. 1/10/4 and 1/7/4) were described and illustrated by Anderson and McLachlan (1976). These authors point out that some of the strap-like structures are smooth while others show a blocky surface resembling "Vertebraria roots" (p 34). Where the ends are preserved it can be seen to be smooth and bluntly rounded. Some of the straps are preserved in a serpentine manner and they vary in width from one to almost 10 cm. One particularly well preserved specimen is 4.75 cm wide and 45 cm long. These "fucoid straps" are problematic and Anderson and McLachlan (1976) even doubt whether the structures are of vegetable origin. I am of the opinion that these structures could either be impressions of the blades of large kelp-like algae or flattened fleshy stems.

A record of Cyclodendron lesliei is the only reference to fossil wood in the Karasburg Basin (Schreuder and Genis 1973-4). It is however not clear whether the record is from the Whitehill Formation itself.

A specimen from Aussenkjer, collected by the author, was also described and figured by Anderson and McLachlan (1976, Fig. 15). The leaf-like impression is bilaterally symmetrical with a longitudinal median ridge but shows no sign of secondary venation. Regular rows of small bumps arranged obliquely across the structure are uninterrupted by the median ridge. The re-

gularly spaced individual bumps in the rows as well as the rows themselves, are about 5 mm apart. Neither end of the impression is intact and the interpretation of the specimen is problematic (Anderson and McLachlan 1976). The authors decide that it could possibly be either the impression of a fern leaf with the bumps representing the fern sori or the flattened fleshy stem of a reproductive cone.

From the Kalahari Karoo Basin outcrops capping the Gellap Plateau Haughton and Frommurze (1927) mention fossilised wood which I could not confirm. The only plant material I found is an impression of a single Glossopteris leaf. (This specimen was also described and figured by Anderson and McLachlan, 1976; Fig. 14). It shows a well developed midrib and secondary venation running nearly perpendicular to the midrib. In personal communication to Anderson and McLachlan (1976) Kovács-Endrody described these features as indicative of an advanced form of Glossopteris. Heath (1966) reports abundant fossilised wood from the Whitehill Formation at Gross Daberas and Daberas Ost but in this case too I was unable to verify the claim.

(6) Cephalochordate

In October 1976, a member of a student group under the guidance of J.C. Loock, senior lecturer in Geology at the University of the Orange Free State found a fossil imprint on the farm Zwartskraal in the Prince Albert district. The fossil was found in the Notocaris tapscotti acme-zone about one meter from the top of the Formation. The specimen was donated to the University of Stellenbosch and is now housed in the collection of Whitehill fossils in the department of Zoology. A detailed description of the fossil is being prepared

for publication.

Both sides of the 11 mm long organism are present as imprints (Fig. 22) on the bedding plane. The spindle shaped body imprint is clearly visible but details of its anatomy can only be studied with the aid of a stereomicroscope. A study of the specimen with a scanning electron microscope was attempted but the results were very poor because of virtual absence of relief.

Along one of the long edges there is a conspicuous series of spine-like structures and this is interpreted as being the dorsal side. Near this edge both imprints show clear impressions of a longitudinal rod-like structure that stretches along the whole length of the body. This rod occupies the position of the notochord in chordates. The anterior tip of the rod tapers to a fine point which reaches the extreme anterior tip of the spindle shaped body and thus resembles the notochord of the Cephalochordata rather than that of vertebrates. (For a diagrammatic comparison of the fossil and a modern cephalochordate see Figs 23 and 24). Dorsally to this notochord-like rod a second impression, also that of a rod-like structure is present. Relative to the first and judging from its position in the dorsal region of the spindle shaped body, this structure occupies the position of the dorsal nerve cord in chordates. This rod-like impression, like the first, tapers off smoothly at both ends without any sign of a bulge indicating the presence of even a rudimentary brain. If this impression was left by the connective tissue sheath of a nerve cord, the absence of a brain again points to a cephalochordate, rather than a vertebrate affinity. Even a brain as small as the lamprey's, however poorly preserved,

would still have shown up.

On the ventral side of the one end of the body a cup-shaped structure which resembles the oral hood of modern cephalochordates, is present. Behind this cup-shaped oral hood is a series of slanting striations (34+). The series of striations by analogy to the anatomy of modern cephalochordates is interpreted as a series of pharyngeal branchial arches. In number, arrangement and shape these correspond more closely (even remarkably so) to cephalochordates than to any known vertebrate although a filter feeding agnathostome of some kind cannot, on the branchial region alone, be entirely excluded.

The wide branchial region of the alimentary canal tapers off into a thin tube running immediately below the notochord. In the region of the posterior fin-like extension of the body, the tube shows a distinct ventrally directed flexure which could indicate the position of the anus (Fig. 23). The anus in modern cephalochordates is similarly situated (Fig. 24). No trace of a possible atrioporal opening can be expected. The spindle shaped body bears dorsal, ventral and caudal fin-like structures. The large size of the fin-like structures is of interest in that it indicates a free swimming mode of life. This assumption is supported by the absence of a bottom fauna in inter alia, the Notocaris tapscotti zone in the Great Karoo Basin, caused by the reducing nature of the sediments, the complete absence of bioturbation in the sediments and indications of the presence of toxic bottom brines. These conditions would rule out any possibility that the organism under discussion could have pursued the largely semi-fossorial mode of life found in living cephalochordates.

The most striking feature of the fossil is the impressions of 14 chevron shaped objects in the free edge of the dorsal fin (Fig. 22). These structures each serve as a base for a single curved barb. The depth of the impressions indicate that these structures consisted of material considerably more resistant than the rest of the body and they obviously represent some kind of skeletal skin (dermal or epidermal) structure. Nothing similar occurs in cephalochordates but the structures are strongly reminiscent of the spines and hook shaped ornamentation seen in some primitive anaspids e.g.

Birkenia and Pterygolepis. A common agnathostome-cephalochordate ancestor could very well have borne similar structures.

The anterior part of the dorsal fin shows short striations with a slant rather similar to those of the branchial region. Superficially they may thus seem to be dorsal extensions of the striations of the branchial region. The branchial striations however are more horizontally inclined anteriorly, gradually changing to a more vertical position in the posteriormost region. The change in slant is absent in the striations of the dorsal fin and this rules out the possibility that they are mere extensions of those in the branchial region. The striations in the dorsal fin, by analogy to the anatomy of the dorsal fin in modern cephalochordates, could represent fin rays (fin boxes).

Should the identification of the organism, tentatively arrived at above (i.e. that it represents a descendant of an early cephalochordate with possible agnathostomate-vertebrate affinities), be correct then it is obviously a discovery of

of the greatest importance. It is thus highly desirable that attempts be made to collect further material to reach a better understanding of the form.

PROBLEMATICA

A. The "Echinoderms"

In the Loeriesfontein, Calvinia area of the Great Karoo Basin, coinciding roughly with the area of maximum thickness of the shales, two horizons containing problematic hollow moulds in great numbers, were found.

The spherical, slightly dorso-ventrally flattened objects vary in size from about three to 30 mm in diameter (Fig. 25). A pentaradiate system of branching ridges are present in all specimens with the upper and lower surfaces of the spheres differing in the configuration of the ridges. One of the two sides superficially resemble the ambulacral grooves of the edrioasteroid Timeischytes as figured by Ehlers and Kesling (1958). The centre of each ambulacral-like groove shows a superimposed groove resembling the food groove in some Echinodermata. In some specimens an area that seems to contain impressions of a few plates arranged around a central opening is visible. The latter could possibly be an anal opening. By injecting silicone rubber into the moulds and splitting the shale along the bedding planes, three dimensional casts of the moulds were made. In these casts the relationship of the ambulacral-like ridges of the two sides of a sphere could be studied. It was established that the ridges on the two semi-flattened sides join to form a complete pentaradiate structure with the ambulacra forming a less regular pattern than in the common sea urchin. The spheres seem to have constant upper and lower sides as they are usually all found with the same side uppermost (usually the "anal" side). The constancy in form and configuration of the grooves point

to the organic nature of the objects. Amongst multicellular animals it is only the Echinodermata which possess a pentaradial symmetry. Elsewhere a pentaradial symmetry is found only in the fructifications of some of the higher plants. As these plants are all terrestrial it is most unlikely that its fructifications would have assembled in this part of the basin without any trace of the rest of it. Therefore it seems unlikely that we are dealing with casts of fructifications. The only other possible explanation is that the imprints are indeed those of echinoderms. However, Nichols (pers comm.) rejects this affinity on the grounds that there is no evidence of the presence of skeletal plates. The reason for the absence of fine detail could be ascribed to their mode of preservation as hollows, and to the nature of the weathered sediment: a soft poorly binding, powdery silt. All objections to the contrary, the author is still inclined to believe that these objects represent moulds of organisms of echinoderm affinity. A final decision on their nature will however have to be postponed until such time as unweathered specimens can be obtained.

B. A problematic fossil object, superficially resembling the impression of a brachiopod valve was collected by Nel (1977) from Whitehill outcrops in a quarry on the farm Devondale near Witput station, north of Hopetown. The specimen was figured by the latter author but not described and was identified by him as a brachiopod valve.

The specimen, which is now housed in the collection of Whitehill fossils of the department of Zoology, University of Stellenbosch, was subsequently examined by Dr. N. Hiller who is of the opinion that it is not a brachiopod. No explanation

other than that it could possibly be a feeding trail can be advanced at this stage. The impression (Fig. 26) is three mm wide at the base with 12 mm long branching rays fanning out to a maximum cross diameter of 15 mm. About eight of these rays form the base of the structure with the first bifurcation occurring 3.5 mm from the base.

A second series of bifurcations are present in all the first order branches about 8 mm from the base and indications of a third zone of bifurcations about 11 mm from the base can be recognised along the top of the object.

Individual rays are bilaterally symmetrical, a single median ridge being present in the floor of individual ray impressions.

C. One specimen showing bundles of spicules was collected from the Loeriesfontein area (Fig. 16). McLachlan and Anderson (1977) have found sponge spicules in the dolomites of the formation and as the structures I figure here closely resemble spicules of a large sponge this seems to be the most likely identification.

TRACE FOSSILS

Although a variety of widely distributed trace fossils were collected from the Formation their occurrence is sporadic and restricted to the intercalated silty shale member. It seems that it was only during the deposition of this member that bottom conditions were favourable for fossorial organisms. The following different types of ichnofossils were found.

(1) Arthropod trails

Four different types of arthropod trails were collected. In the Great Karoo Basin trackways were collected on the farm Kafferdam near Loeriesfontein and in the "Skimmelkoppe" north of De Bos in the Tanqua Karoo. The specimen from Kafferdam (Fig. 27) superficially resembles the trails described by Anderson (1977) from the Prince Albert Shale south of Loeriesfontein. The track consists of a double row of transverse, somewhat oblong dots grouped into sets of three of which three pairs are wholly or partly preserved. The tracks in each set are evenly spaced at intervals of about 2 mm with each individual track about 5 mm wide and strongly crescentic in outline. Each set of three tracks is displaced sideways (to the right?) in relation to the previous set as the animal moved forwards. No grooves or dots other than the crescentic tracks are visible and the tracks suggest an arthropod that moved, raised well above the substratum, on three pairs of functional walking legs. The sideways displacement of the tracks suggest a skew crab-like movement (Fig. 28).

As far as can be gathered from the ichnofossil literature this particular type of trail has not been described before. The rest of the arthropod-trails are of the "Diplichnites" group of trace fossils, like Umfolosia sinuosa, Savage (1971) from the Natal Ecca or Machulichna varia Anderson (1977) from the Prince Albert shale near Loeriesfontein.

The only trail of this kind from the Great Karoo Basin was found in the "Skimmelkoppe" in the Tanqua Karoo. This trail is nearly 13 mm long, 10 mm wide (outside diameter) with each individual crescentic track measuring ± 3.5 mm. The weathered, pitted nature of the bedding plain surface on which the trail is preserved hamper detailed observations and comparisons, but the trail can in all probability be referred to Umfolosia sinuosa Savage (1971).

The second record of this type of arthropod trail is from near Haib mission station in the Karasburg Karoo Basin. The trackways, collected by D. Scott, are preserved in the typical white-weathering silicious shales of the Whitehill Formation and is the only record of trace fossils outside the intercalated silty shale member of the Formation. The only other records of trace fossils from this basin are those mentioned by Schreuder and Genis (1973-4) from the boulder shale on Aussenkjer and the Limulus trackways described by Anderson (1975). Schreuder and Genis (1973-4) claim that the tracks in the boulder shale are those of Notocaris tapscottii but the restricted stratigraphic occurrence of N. tapscottii casts doubt on this identification.

Some of the Haib trackways (Fig. 29) and associated body imprints (Fig. 30 A and B) were compared with measurements of specimens of N. tapscottii of comparable size. Parameters such

as the distances between the walking legs, the length of the sternal width between the bases of the walking legs were found to coincide very closely. It can therefore, with a fair degree of confidence be speculated that the Haib, Umfolosia-type trails, were made by Notocaris tapscotti, known to be present in the basin, or by a closely related form. The precise stratigraphic position of the trails are unfortunately not known and it is thus not possible to know whether the trails are from the N. tapscotti zone.

The body imprints show the walking legs in the typical bent posture in which they are usually preserved in the actual fossils of N. tapscotti and as some of the imprints have trackways leading up to them no doubt about the association of the body imprints and the Umfolosia-type trails can exist.

On one of the Haib slabs a sinuous groove-like trail showing a central ridge is preserved (Fig. 31). This small 1 mm wide trail shows no detail of scratch marks of appendages but from the regular pattern in which the sediment on the borders of the trail is disturbed it is clear that the trail was made by an arthropod.

(2) Star-shaped trace fossils

Specimens of star-shaped trace fossils from two localities in the Whitehill Formation have been collected. One locality is on the farm Maritzdam in the Carnarvon district (Srydom 1979).

The other specimens were collected by me on the farm Brandhoek near Calvinia.

Similar structures have been described from the Pennsylvanian of the United States as the ichnogenus Astericnus (Bandel 1967).

Similar traces are also known from the Iraty of Brazil (Mez-
zalira, 1971) and from modern deep sea environments (Häntzschel
1970).

The star-like trace fossils, approximately circular in cross
section with a diameter of ± 5 cm, consist of 4-5 bundles of
unbranching rays. These groove-like rays radiate from a
round knob like centre ± 1 cm in diameter with rays of ad-
jacent "stars" tending to meet (Fig. 32).

According to Bandel (1967) these are subsurface trails made
within the sediments along the bedding planes in the same way
as other recent and fossil starlike traces and are produced
by a large organism of unknown systematic position. These
fossils have practically no stratigraphic significance (Grubic
1970).

(3) Zoophycos trails

The author has collected Zoophycos trails from the intercala-
ted silty-shale member of the Whitehill Formation in the Great
Karoo Basin on the farms Brandhoek near Calvinia and Vlake
onder Hangklip near Prince Albert.

The traces (Fig. 33) are ± 28 mm wide and are of the antler-
type planar variety of Zoophycos comparable to the specimens
illustrated by Roderiquez and Gutschick (1970, Fig. a plate 7),
Häntzschel (1975, Fig. 75) and Crimes (1976, Fig. 39).

This type of trace is one of the most discussed problematic
fossils and it has been interpreted in various ways e.g. as
marine algae, body fossils of sponges or corals and lately
as the feeding burrows of soft bodied worm-like animals. They

are said to have produced the traces by systematic mining and foraging through the sediments. According to Taylor (1967 p. 11) "Much remains to be discovered about these trails" and "no single interpretation has yet found general acceptance". The work of Plicka (1969), Stevens (1968) and Bischoff (1968) have however convincingly shown that the helical types of Zoophycos are the fossilised prostomia of sedentary marine polychaete worms of the family Sabellidae. If this interpretation is accepted the antler-like planar variety of Zoophycos which certainly does not fit this interpretation should be separated from the helical forms. In this respect I am in full agreement with Simpson's (1970) distinction between the planar antler-like Zoophycos and the helical Spirophyton.

(4) Feeding trail

From the farm Kafferdam in the Kubiskou mountains near Loriesfontein a rose-like feeding trail, convex in hyporelief, was collected from the silty shale member of the Whitehill Formation. This trail superficially resembles the trace fossils Spirorhabe and Helminthoidea as figured and described by Häntzschel (1962) but is in fact distinctly different from both these ichnogenera in the arrangement of the spirals. It is clear from the trail (Fig. 34) that the feeding organism removed only the most superficial veneer of sediment on the bedding plane. The thickness of the sediment removed, vary and the depth of an excavation is related to its width, the deepest trails being also the widest.

It can be inferred from the bordering ridges of the trails that feeding commenced on the perimeters of the trace and

continued inwards in ever decreasing circles until a final central scoop was removed. As there is no indication that the trail was formed by mining or burrowing into the sediment and as no infill of any kind is present it is fundamentally different from Spirorhabe and Helminthoidea. The trails vary in width from one to four millimeter and show no sign of turning and looping back in the centre as is typical of Spirorhabe (Häntzschel 1962).

I am consequently convinced that this is a hitherto unknown trace fossil and because of its very distinct nature it may perhaps be appropriate to name it formally.

The name proposed for this trace is derived from its rose-like form and the original Afrikaans name of the Whitehill Formation. It was named in accordance with the proposed "code for trace fossil nomenclature" of Basan (1979).

Ichnogenus Rosaichnus gen. nov.

Characteristics:

A rose-like feeding trail formed by the removal of a thin veneer of sediment on a bedding plane with feeding commencing on the perimeter of the trace and continuing inwards in ever decreasing circles with a final central scoop removed. The central excavation is not connected with the outside trails. Diameter of individual trails vary from one to four millimeters, depth \pm one millimeter.

Ichnospecies Rosaichnus witbandicus gen. et. sp. nov.

Characteristics:

As for genus; formed by an animal of uncertain systematic position; probably a soft bodied worm-like organism.

Holotype; U.S.S. 1/3/5 kept in the collection of the Department of Zoology, University of Stellenbosch (Fig. 34).

(5) Scolicia-type trails

These trails were found in abundance, in the intercalated silty shale member of the Whitehill Formation. They can be classified into two types which will be referred to as types A and B.

Type A trails are larger than type B and measure up to 15 mm in width. It is a composite trail and consists of a number of parallel or sub-parallel smaller subtrails with a diameter of ± 1 mm. About nine to eleven of these small trails may be present across the diameter of the composite main trail (Fig. 35).

The smaller type B trail has a diameter of ± 5 mm and seems to differ in origin from the larger type A trail. It normally shows no sign of the smaller subtrails and the areas of undisturbed sediment present between the adjacent subtrails in type A are absent from type B. In section however, and in some specimens also in hyporelief, there are indications that type B might also be a composite structure. Where types A and B trails intersect it can sometimes be seen (Fig. 35) that the smaller subtrails are associated with both types with the effect that no sharp corners are formed at points of intersection.

At some localities only type B trails seem to be present e.g. in the Kalahari Karoo Basin (Fig. 36B) and in the eastern section of the Great Karoo Basin on the farm Josias de Kocks Kloof near Prince Albert. At the latter locality the three meter thick intercalated silty-shale member is extensively tunnelled.

The type B trails seem to be identical with the trails de-

scribed by Hobday and Taverner-Smith (1975) from the middle Ecca of northern Natal (see Figs. 5 and 6 of these authors). Identical trails are also present in the green mottled siltstone that underlies the Whitehill shale over very large areas in the north western section of the Great Karoo Basin and in the Karasburg and Kalahari Karoo Basins. Similar trails are also present below the Whitehill Formation near the Brandberg, Huab Karoo Basin (Fig. 36C). As Potgieter (1973) has justly pointed out this green mottled, tunnelled shale can serve as a valuable marker horizon over large areas and where the Whitehill Formation has been removed by denudation its position may be pinpointed by the presence of this marker horizon. Identical trails were also found to be present in the green shales of the Collingham Formation above the Whitehill shales in the Great Karoo Basin.

In correlative work these trails therefore could prove to be of value in establishing the relative position of the Whitehill Formation beyond its cut off point in the northern Ecca. In this respect the identical trails described by Hobday and Taverner-Smith (1975) in the middle Ecca point to a correlation of this section of the northern Ecca with the Whitehill Formation in the south.

It is of interest to note that the presence of these trails in the shallow water Ecca deposits is seen by Hobday and Taverner-Smith (1975 p. 50) as "possibly unusual" for it is usually associated with deep water deposits as part of the Zoophycos ichnofacies of Zeilacher (Visser and Loock 1978). Fossils of the shallow water Cruziana and Skolithos ichnofacies of Zeilacher (1967) is however present in some abundance only in the Karasburg and Kalahari Karoo Basins.

In deciding upon the validity of ichnofacies as water depth indicators it should be kept in mind that animals are usually able to survive at varying water depths and that the right substratum rather than a specific depth of water will determine the inhabitant spectrum.

(6) Bifungites-like traces

A most promising trace fossil for correlative purposes is the dumb-bell-shaped surface impressions of which some superficially resemble Bifungites. These traces occur in vast numbers (Fig. 37) on the cherty layers in the Collingham Formation immediately on top of the Whitehill shales, over vast areas in the Great Karoo Basin. It occurs from Lake Mentz in the east to the Worcester outlier in the south and as far north as the Van Wyksvlei area. This trace fossil is not known to occur in either the Prince Albert or Whitehill Formations. Hobday and Taverner-Smith (1975) however describe it from the middle Ecca in Natal. Together with the Scolicia type trails it could thus prove to be very useful in determining the relative stratigraphic position of the Whitehill Formation in the northern Ecca in which case the Whitehill shales seem to correlate with the middle Ecca in the north.

THE BIOSTRATIGRAPHY OF THE WHITEHILL FORMATION

Although the vertebrate fauna of the Whitehill Formation has been known for a long time (e.g. Mesosaurus was described in 1864 and Palaeoniscus in 1913) very little was previously known of the biostratigraphy of the unit. No systematic collection of fossils from this Formation, on a local or basin wide basis was ever attempted in spite of pioneering work on biozonation done in the Beaufort sediments as early as 1905 by Broom (Keyser and Smith 1979). The hiatus in our knowledge on the biozonation of the Whitehill Formation veiled the fact that the Formation is a chronostratigraphic unit. Its wide use in correlations as a chronostrat unit by various authors (e.g. Martin, 1961; Van Eeden, 1973; Heath, 1966; Schreuder and Genis, 1973-4) was based on intuition rather than proven fact. So few facts were available that the validity of the assumption was actually questioned by McLachlan and Anderson (1976).

The present work is the first to provide proof based on the biozonation of the Formation, for its validity. The consistency in the biozones throughout the different basins prove that the shales themselves or any of their endemic fossils can, with great confidence be used for correlations between the different basins. A determined search for the extensions of the biozones in the sediments beyond the cut off point of the Whitehill Formation might in future provide final answers as to whether the middle Ecca coals are older or younger than the Whitehill shales.

Du Toit (1918) proposed that the coal measures of the northern Ecca are isochronous with the southern Ecca (this is the "old"

Ecca excluding the White Band and the rest of the "Upper Dwyka" shales). This correlation was subsequently followed by most authors (e.g. Du Toit, 1926; Haughton, 1969; Rust, 1973; Cooper, 1974; and Anderson 1975 b). According to Anderson and McLachlan (1976 p. 37) the "currently more fashionable" theory is however that the coal measures are isochronous, not with the Ecca sediments above the Whitehill Formation, but with the Whitehill and Prince Albert Formations themselves. The latter correlation was advocated by Kent (1938) Van Eeden (1961, 1973), Plumstead (1961), McLachlan and Anderson (1973) and J.M. Anderson (1973).

The most obvious place to search for the biozones will be the Port St Johns area following up reports of earlier observers that the Whitehill shales are present there (Rogers and Schwarz, 1901; Du Toit 1920; 1946) directly overlying the massive tillites. A search for these sediments might reveal the presence of the biozones of the Whitehill Formation, a find which will certainly be of much value.

As has been explained in the section on trace fossils, the Bifungites and Scolicia type trails may also be of value in the correlation.

It is finally not only for the benefit of long distance north-south correlations that the new knowledge on the biozonations of the Whitehill Formation is important but also for correlations over short distances in the basins. One example to illustrate this point will be quoted.

In a project, investigating the oil shale potential of the Whitehill shales by Cole (1978), boreholes were sunk in the area north of the Orange River. In some boreholes the Formation was unexpectedly found to be missing. Explanations given

for the absence are uplift and subsequent erosion in one case and an erroneous map in the other. In the present study the biozonations in this area revealed the existence of a hiatus in some outcrops (see profile 5 Fig. 11) where the top of the unit is absent and was probably removed by a post Whitehill, Pre-Tierberg erosion cycle. In some places the shales have been completely removed thus accounting for their absence in the boreholes. In places the Whitehill is thus unconformably overlain by the Tierberg shale along the northern limit of the Formation. Such relationships should however not necessarily be seen as an indication that the Whitehill Formation lies stratigraphically below the northern Ecca as was implied by Anderson and McLachlan (1979).

RANGE ZONES IN THE WHITEHILL FORMATION

Four range zones can be recognised in the Formation. These are, going upward, the trace fossil zone, the fish and Mesosaur zones and the N. tapscotti range zone. Of the four only the trace fossil zone (=intercalated silty shale) was not originally universally present in the basins (see Fig. 11). The different zones will now be discussed in more detail.

(1) Trace fossil range zone

This zone coincides almost without exception with the intercalated silty shale unit in the middle of the formation (Fig. 11). As is explained in the section on trace fossils this ichnozone is characterised by the presence of especially Scolicia-type trails and Zoophycos feeding trails. Umfolosia-

type trails of the "Diplichnites" group and other ichnofossils may be sporadically present in this zone which also marks the lower borders of the fish and Mesosaurus range zones (Fig. 11).

(2) The fish range zone

This zone starts near the middle of the Formation either in the upper unit of the intercalated silty shale member (where developed) or in the middle of the black shales and goes up all the way to the top of the Formation (Fig. 11). An acme zone in the lowermost portion of the range zone is very conspicuous in the western outcrops between De Bos in the Tanqua Karoo and the farm Narosies north-west of Loeriesfontein. In some places the very thin acme zone can be in the order of only ten centimeters but contains fair concentrations of fish. In spite of the numerous impressions, the fish are hardly ever superimposed. This indicates that the individual fish occurs on different bedding planes of the paper thin laminae which is the result of a slow accumulation of dead individuals from a large population. It is certainly not the result of a catastrophic event which would have resulted in all the fish accumulating on the same bedding plane. Some of the fish are beautifully preserved but in some cases the bodies are twisted and show signs of slow decomposition. This mode of preservation could be indicative of shallow to intermediate water depths if the reasoning of Ziegler (1972) is followed. No sign of a "scale rain" indicative of a very dense fish population (Wilson 1978) was found.

(3) The Notocaris tapscotti range zone

N. tapscotti occurs in vast numbers (Fig. 31) in a very restricted range zone, about 1 m thick and ending about 1 m from the top of the Formation. In view of the vast numbers of fossils and the extremely restricted range the entire range zone could be referred to as an acme zone.

The thickness and distance from the top of the Formation of this zone are remarkably constant and remain constant over the vast outcrop area of the basins. An extremely interesting and important aspect of this zone (it is also a feature of the other zones) is that its thickness and distance from the top of the Formation is directly proportionate to the total thickness of the Formation itself. In those areas where the Formation reaches its maximum thickness of ± 65 m the range zone increases (Fig. 11) from ± 1 m to ± 2.5 m and lies an equal distance below the top of the Formation.

In some localities north of the Orange River between Hoptown and Kimberley (e.g. in the quarry next to the road from Witput station to Luckhoff on the farm Devondale) this zone is absent and typical green siltstone of the overlying Tierberg Formation directly overlies the Mesosaurus range zone. In other outcrops in the same area however the complete succession is present, e.g. on the town commonage of Jacobsdal and on the farms Kolkop, Hopefield and Roschcommon in the Herbert district.

In this area the Whitehill Formation seems to be preserved as loose patches, associated in outcrop and preserved by the presence of dolerite sills in the Formation. (It is of interest to note that almost without exception the lowermost

sills are present in this Formation). The patchy nature of the Formation can therefore be interpreted as the result of modern denudation (Engelbrecht 1961). The fact that the topmost fossil range zones are absent in some outcrops whilst present in others nearby where both outcrop-types are overlain by green Tierberg shales indicates a local post-Whitehill-pre-Tierberg erosion cycle. This could account for the total absence of the Formation or the topmost sections in some outcrops. This postulated erosion cycle finds support in the presence of a coarse grained, white sandstone immediately on top of a thin remnant of Whitehill shale in a borehole in the Welkom area (J.C. Looek, pers. comm.).

The presence of this zone in the Karasburg and Kalahari Karoo Basins was established by the recovery of specimens from the same stratigraphic horizon as in the Great Karoo Basin. A single specimen found on the Gellap Plateau (U.S.S. 6/4/26) proves that the zone was also present in this area. The specimen from the highest point on the plateau illustrates the value of the recognition of the biozones, for from this single specimen it is clear that the top of the Formation (the N. tapscotti zone) is now almost completely removed by denudation. The presence of this zone in the basin was established beyond doubt by the discovery of the complete sequence on the farm Klein Spitskop north-west of Keetmanshoop. The absence of this zone and the fact that the Mesosaurus zone is exposed at the top of the Gross Daberas-Daberas Ost Plateau is most likely also the result of denudation.

The distribution of the hitherto unnamed crustacean (Fig.15) which is associated with the black dolomitic layers naturally coincides with the position of these rocks in the lower

half of the Formation.

(4) The Mesosaurus range zone

This zone starts off in the intercalated silty shale member of the Formation and terminates in the lower portion of the N.tapscotti range zone. It shows no acme zone. Mesosaurus sometimes occurs in some concentrations while other areas seem to be almost devoid of fossils. No explanation for this phenomenon can be offered. In terms of the range zones it should be stressed that the lower half of the Whitehill Formation has to date proved to be unfossiliferous with the exception of the presence of the unidentified crustacean in the black dolomitic layers.

BIOSTRATIGRAPHIC CORRELATION BETWEEN THE WHITEHILL AND IRATY FORMATIONS

Although, as far as could be established from the literature, the biostratigraphy of the Iraty shales has not been studied in detail on a basin wide scale, some information from single localities is available. The need for such a basin-wide study was stressed by Mezzalira (1971).

Araújo (1976) gives a section from an experimental mine in São Mateus do Sul in the Paraná basin (Fig. 1b) where the majority of specimens she studied were collected. Araújo's (1976 Fig. 2) is used in Fig. 11 for comparison with an idealised composite section of the Formation of the São Paulo area after Mezzalira (1971). The intercalated shale which, according to Mezzalira (1971), is developed over large areas in the middle of the Formation (Fig. 11) in the state of São Paulo is not present in Araújo's section at São Mateus which lies about in the centre of the outcrop in the states of Paraná and Santa Catarina (\pm on the border between the two states). The Iraty at this locality consists of two layers of black oily shale intercalated with a more calcareous middle zone (Fig. 12).

According to Araújo, Mesosaurus brasiliensis appears about half way up in the Formation and increases in abundance to form an acme zone, 30 cm thick about 1 m from the top of the Formation. Fossil fish were found in the lower half of the intercalated limestone-rich layer below the first Mesosaurus. The fish have unfortunately not yet been studied. Of all species, the fish from the two basins might be expected to show the closest relationship provided that the two basins

were indeed linked by a sea connection as is postulated in this work (see Fig. 1C).

Araújo (1976) finally points out that the lower half of the Formation is unfossiliferous at her study locality. In the Sao Paulo area however Mezzalira (1971) found the crustacean Clarkecaris brazilicus preserved in dolomite over vast areas always between 1 and 3 m above the base of the Formation (Fig. 12). This closely parallels the position occupied by the unidentified crustacean in the black dolomite lenses in the southeastern section of the Great Karoo Basin.

In conclusion it should be stressed that the Iraty and Whitehill Formations are not only similar in their lithology and fossil fauna but also show an almost unbelievable similarity in biozonation as shown in Figs. 11 and 12.

THE MORPHOLOGY AND TAXONOMY OF MESOSAURUS

INTRODUCTION

Apart from casual references the skull of the southern African M. tenuidens has never been described. All comparisons with other work in the following account therefore refer to genera or species other than M. tenuidens; chiefly to Mesosaurus brasiliensis. Although the species of a genus are not expected to differ in important aspects, such as the presence or absence of bones or fenestrae any such comparisons must be treated with caution. However, the aim of any description, of cranial material as poorly preserved as are even the best specimens (compare Von Huene's, 1941 Figs 1 - 16 of M. brasiliensis with Figs 40 - 51 in this work), must be to arrive at the best possible interpretation of the mesosaurid skull as opposed to a description, accurate in all details, of any one species.

Almost all mesosaurid fossils occur as moulds in the matrix with the bone either partly or completely leached out; actual bones where present are misleading. Skulls are crushed flat and, with one notable exception (Fig. 76), disarticulated and the bones disturbed, often broken and superimposed. Outlines of individual bones are thus difficult to determine and in reassembly the correct amount of overlap has to be guessed at. The crucial question that needs to be cleared up is the presence or absence of temporal fenestra(e), as the systematic position of any reptile is still fundamentally dependent on this character.

Although M. tenuidens was described by Gervais as early as

1864 no definite conclusion could be reached on its systematic position as the morphology of the skull was not then known. The first attempt to unravel the cranial anatomy of M. brasiliensis was by Mc Gregor (1908 p. 311) who mentions the presence of "both supra and infra temporal arcades" in the gelatine casts of the skulls he studied. As the material available to him was rather poor, his interpretation was not generally accepted. The next attempt was by Wiman 1925 (on the Stockholm collection of M. brasiliensis) but again no interpretation of the temporal region was possible because of the poorly preserved material. The most successful attempt was that of Von Huene (1941) whose reconstructions of M. brasiliensis are still, after 40 years regarded as definitive (e.g. Romer 1956, Ginsburg 1967, Kuhn 1969). He showed the skull with a single synapsid-like temporal fenestra. A re-examination of part of Von Huene's material (housed in Uppsala) led N.J. Mateer (pers. comm.) to the same conclusion. In another unpublished study of the collection of Brazilian material housed at Harvard, no temporal fenestra was found (N.J. Mateer pers. comm.).

The most recent study of South American material (Araújo 1976) unfortunately does not cover cranial morphology but the author states that one of the skulls of M. brasiliensis examined shows the possible presence of a temporal fenestra. The skull of Braziliosaurus sanpauloensis was however figured by Sikama and Ozaki (1966) as anapsid.

Broom (1904) expressed the hope that a good skull would turn up to settle the systematic position of Mesosaurus beyond dispute. In contrast to Osborn (1903) who placed Mesosaurus in the superorder Diaptosauria and Boulenger and Von

Huene (1941) who opted for a close relationship with the pleiososaurs, Broom turned to the postcranial skeleton for clues. He noted similarities with Procolophon and Palaeohatteria in the pubis and ischium and in the pectoral arch he saw a modification of the Procolophon type. He concluded that Mesosaurus is descended from a terrestrial animal which might be found "among the Microsauria, Cotylosauria or Diaptosauria" (p. 109). He finally agreed with the views expressed by Osborn (1903) that Mesosaurus is descended from a primitive "Rhynchocephalian or Diaptosaurian" (p. 109) although not completely discarding the Cotylosauria as potential ancestors. Carroll (1969) and Carroll and Baird (1972) have lately advocated the idea that Romeriids take a central position in reptile ancestry. As are most reptile groups, the mesosaurs are also derived from Romeriids in their scheme of classification.

In addition it should be mentioned that although not refuting the presence of temporal fenestrae, Araújo (1976) also sees the Cotylosauria as the ancestral group of mesosaurids. (For a complete review of the literature see Araújo 1976).

The main goal of the present study was to attempt a reinterpretation of the skull anatomy, and considerable time was spent in collecting new material. The following interpretation is based on a study of this newly collected material.

THE SKULL

Broom's (1904) remark that the enigmatic relationship and phylogenetic position of Mesosaurus will only be solved if a good skull turns up, has proved to be prophetic. Such a

skull has indeed turned up and I am grateful to Mr Koos O' Kennedy of the farm Blouputs near Loeriesfontein who took considerable trouble in delivering the material to me. This skull (U.S.S. 1/11/13) had been isolated from the post-cranial skeleton before fossilisation with the advantage that no cranial bones are obscured by disarticulated vertebrae as is almost invariably the case. In splitting, the slab of shale containing the skull, the palate and skull base were exposed in both dorsal and ventral views (Figs 41 and 42). In addition the left lateral wall of the skull had become detached and had settled some 12 cm away. It was partly exposed and could be developed (Fig. 76). Unfortunately a partial break through the middle of the orbit had dislodged the ventro-lateral section of the temporal area containing amongst other bones the major part of the jugal, the quadratojugal and the squamosal (Fig. 40 B). Through a happy coincidence, however, this section was almost intact and had come to rest a centimeter or two from the main part of the skull; the missing central portion of the jugal had floated some distance away before it too had settled. These three pieces are located on the same bedding plane as the main part of the skull. Together the three detached portions make up the only complete and articulated lateral skull wall present in any collection, certainly as far as southern African material is concerned (see Figs 76 and 77).

This skull (U.S.S. 1/11/13) conclusively proves that the temporal area of M.tenuidens, at least, is completely roofed over and it has also enabled me to interpret the other often badly crushed skulls, with much more confidence. The individual elements of the skull could therefore be determined with more ac-

curacy than was previously possible.

Temporal and occipital dermal bones

The jugal is a forked element as was indicated by Von Huene (1941), one prong forming the lower rim of the orbit and the other the lower half of the posterior rim (Figs. 40 and 53). The latter meets the ventral lower edge of the postorbital element in the manner of the primitive captorhinomorph Paleothyris, the advanced anthracosaur Gephyrostegus and the microsaur, semouriamorphs and solenodonsaurids.

Below the jugal a long splint-like extension of the quadratejugal forms an extensive sloping border with a long caudal extension of the maxillary. The presence of the maxillary bone in this region is confirmed by the presence of tooth "sockets" (Fig. 40). The postorbital is a large element that forms the upper half of the posterior border of the orbit; anterodorsally it borders on an elongated postfrontal (see e.g. Figs. 40 and 43 where the postfrontals are excellently preserved). The upper edge of the postorbital meets the lateral edge of the parietal while the postfrontal borders on the frontal as well as on the anterolateral corner of the parietal.

The area of the temporal fenestra in Von Huene's (1941) reconstruction is shown by my material to be occupied by sections of the squamosal, jugal and supratemporal. The latter element was not seen by Von Huene (1941) in M. brasiliensis and the area it occupies coincides more or less with the area which in his dorsal reconstruction of the skull is indicated as the squamosal. It should be pointed out that Von Huene's reconstruction which shows the parietals meeting the squa-

mosals low down on the temporal area in fact implies that steeply sloping parietals must have met in a rather sharp dorsomedial ridge (see Figs 17 and 19 of Von Huene). Nothing would thus be retained of the flat skull table so characteristic of the early stem reptiles. My material however shows that in this respect M.tenuidens differs from M.brasiliensis in that the skull was not quite as aberrant as reconstructed by Von Huene (1941). The lateral border of the parietal is in fact a more or less straight line that meets the upper border of the supratemporal behind the postorbital, the parietals thus forming the central part of a slightly domed skull table as shown in Figs 44, 54 and 55.

The supratemporals can be observed best in specimens 6/4/23 (Fig. 46) where the right hand element is excellently preserved. This skull clearly shows that the supratemporal possesses a posterolateral lappet that wedges in between the upper posterior border of the squamosal and the tabular (Figs 53, 54 and 55).

The squamosal seems to have been a very thin and fragile element for it is usually squashed severely in dorso-ventrally flattened skulls. The area it occupies may therefore be mistaken for a temporal fenestra. This is illustrated well by the left hand squamosal in specimen U.S.S. 6/4/23 (Fig. 46). The pattern of crushing and indentation of the squamosal seems to be controlled by the form of the elements present below it, usually the well ossified quadrate.

In specimen U.S.S. 1/11/13 (Fig. 40) where the bones had not suffered a dorso-ventral compression, a distinct groove runs between the squamosal ventrally and the supratemporal and tabular dorsally and posterodorsally. This groove could well

be a relict of the obliterated otic notch of the amphibian ancestors of the reptiles which is sometimes preserved in primitive forms e.g. Limnoscelis (see Romer 1946 Fig. 3 for comparison on the skull table border). The fact that the break through the lateral wall of this skull did not follow the line of the "otic notch" indicates that a firm connection had been established between the elements involved. It also again accentuates the fragility of the squamosal and the body of the jugal.

As in Limnoscelis the relatively large tabulars of M.tenuidens are almost totally restricted to the occipital face of the skull (see Figs 40 and 46). These elements also were not seen by Von Huene (1941) in M.brasiliensis. They are beautifully preserved in specimen U.S.S. 2/4/6 (Fig. 51). The tabulars are dorso-medially and dorso-laterally bordered by paired post-parietals and dorso-laterally by the supratemporals, Contrary to the condition in Limnoscelis the tabulars therefore do not meet the parietals in a common border (Fig. 55). The tabulars reach far down ventrolaterally almost excluding the squamosals from meeting the occipital bones although the squamosal does seem to have abutted against the paroccipital process (see Figs 46 and 55).

Orbital and nasal regions

My interpretation of the circumorbital elements of M.tenuidens differs quite widely from Von Huene's (1941) reconstruction of M.brasiliensis. In M.tenuidens the jugal and postorbital together account for the whole of the lower and posterior orbital rim (Fig. 53). A relatively large postfrontal, lies dorsally to the eye and excludes the frontal from the

orbital rim. This corresponds closely to the condition in e.g. Limnoscelis (Romer 1946). In Von Huene's reconstruction the postfrontal is shown as a narrow bone behind the eye and the dorsal orbital rim is formed mainly by the frontal.

Rather surprisingly the articulated sidewall of skull U.S.S. 1/11/13 (Fig. 40) shows the lacrima to be excluded from the orbital rim, whereas in Von Huene's reconstruction it occupies a segment of the rim equal in length to that of the prefrontal. However, both sides of the Oosthuizen specimen (Fig. 44) as well as the right side of U.S.S. 2/4/6 (Fig. 51) show that the lacrimal must have had the normal reptilian relations. In many lizards for instance, the jugal meets the prefrontal medial to the lacrimal and it is quite possible that in U.S.S. 1/11/13 the posterior section of the lacrimal had been stripped away with the break through the orbit or during preparation.

The foramen nariale obturatum clearly visible in all the specimens Von Huene (1941) studied is less clear in my material. Only a few specimens (e.g. S.A.M. 9327 Fig. 45) show traces of it. The presence and margins of the septomaxillary bone are likewise not as clear in my specimens as in those studied by Von Huene (1941). What can be seen of both these structures tend to confirm Von Huene's reconstruction. Of the relative proportions, size and interrelationships of the nasals maxillae and premaxillae we have, in addition to Von Huene's interpretation, a second earlier one by Wiman (1925) the latter based on the Stockholm material. My observations confirm those of Von Huene. For illustrations of these elements see Figs 44, 53, 54 and 56. The premaxilla and maxilla of each

side bear about 48 - 52 tooth "sockets" with slightly more than half the total number on the premaxilla.

Dermal bones of the palate

The largest elements in the palate are the pterygoids each exhibiting the characteristic well developed, tooth bearing, transverse flange of early reptiles (e.g. U.S.S. 1/11/13; Fig. 41, and 1/11/10 Fig. 48). Von Huene (1941) also features this flange but without teeth. The quadrate ramus of the pterygoid is well developed and extends posteriorly to overlap the quadrate medially over an extensive area (Fig. 52). Judging from the height of the posterodorsal part of the quadrate ramus it seems possible that it could have reached up to meet with the squamosal.

The cranio-quadrate passage running medially to the quadrate ramus of the pterygoid and laterally to the sidewall of the braincase is excellently preserved in specimen U.S.S. 1/11/10 (Fig. 48, left side). For the relations of the pterygoid with the epipterygoid and basipterygoid process see p. 92 - 93.

The long interpterygoid vacuity separating the posterior third of the vomers as reconstructed by Von Huene is absent in my material. Specimen U.S.S. 2/7/1 (Fig. 50), and especially 1/11/10 (Fig. 48), clearly show that in M.tenuidens the interpterygoid vacuity is in fact short and terminates on a level with the posterior ends of the vomers. Specimen U.S.S. 2/7/1 (Fig. 50), an impression of the dorsal surface of the palate of a very large individual, shows the relations of the premaxilla, maxilla, pterygoid and vomer. In this specimen and also those shown in Figs 42 and 48 the pterygoids are seen to send extreme-

ly long and slender prongs anteriorly, extending in between the two almost equally long, tooth bearing, vomers, all four elements meeting the premaxillae. The tooth bearing vomer forms the median border of the internal naris in front of which it forms a short border with the maxilla and premaxilla. Both the tooth bearing palatine and ectopterygoid are small elements, in contact with each other and intercalated between maxilla and pterygoid, the latter elements meeting behind the ectopterygoids as they do in e.g. Limnoscelis (Romer 1946 p. Fig. 3).

A narrow, lateral anterior extension of the pterygoid separates the vomer from the palatine. M.tenuidens is exceptional in that the pterygoid as well as the palatinum enter the border of the internal naris. Von Huene (1941) shows M.brasiliensis with a large palatine entering the border of the internal naris and no ectopterygoid.

The relations of the ectopterygoids, palatines and hinder aspects of the pterygoids resemble the pattern found in most primitive reptiles e.g. Limnoscelis (Romer 1946), Paleothyris and Brouffia (Carroll and Baird 1972) and also Protocaptorhinus and Romeria (Clarke and Carroll 1973). A rather unique feature of M.tenuidens seems to be the long anteriorly directed prongs of the pterygoid which respectively reach up to the premaxilla (thus separating the vomers) and the border of the internal naris between vomer and palatine. These features can tenably be explained as resulting from the extreme elongation of the snout and could easily have been derived from a short snouted ancestral form with a palate of the morphological type found in e.g. Protothyris where the vomers are separated by the pterygoids for more than half their length. I am of the

opinion that the palate of the short snouted Braziliosarus will prove to be of the Protothyris type.

The elements of the palatoquadrate

A reconstruction of the palatoquadrate and its associated elements have been attempted in Figure 52.

The quadrate is a large, well ossified triangular element.

This robust bone usually withstands the crushing so frequently shown by the rest of the skull but is seldom preserved in situ. In specimen U.S.S. 1/11/10 (Fig. 42) the undamaged left element can be observed and the double nature of the lower condyle is shown in both left and right elements of U.S.S. 1/10/12 (not figured).

The posterior border of the quadrate is gently concave and may thus have carried a tympanic membrane. The pterygoid ramus of the quadrate is quite extensive and from the general size and shape of the bone it is clear that the ramus must have reached far forward along the quadrate ramus of the pterygoid up to or almost up to the posterolateral edge of the epipterygoid. When the quadrate is placed in this position the lower articular condyle faces downwards and slightly posterolaterally (Fig. 52). Dorsally, contact with the tabular, the squamosal and the paroccipital process would have been possible (Figs 52, 53 and 55). The nature of the connection between the posterior concave edge of the quadrate, the squamosal and quadratojugal is unknown. In side view both the latter bones would seem to project back beyond the quadrate. The usual quadrate foramen in primitive reptiles between the quadrate and the quadratojugal (Romer 1956) seems

to be present also in Mesosaurus (Fig. 55).

The epipterygoid, an element which has not been observed in any mesosaurid to date, is excellently preserved in a number of my specimens. In U.S.S. 1/11/13 (Fig. 41) the right epipterygoid is preserved next to the right clinoid process and in U.S.S. 1/11/10 (Fig. 48) the left epipterygoid which has been displaced over to the left in a dorsoventral crushing of the skull, covers the anterior part of the subtemporal fossa. Through the orbit of specimen U.S.S. 2/4/6 (Fig. 51) the element is visible, preserved in an upright position.

The epipterygoid of M. tenuidens closely resembles that of Captorhinus (Romer 1956 Fig. 36, Fox and Bowman 1966). An epipterygoid of this shape is apparently a primitive feature.

The bone has a broad base from which a slender ascending process projects, curving slightly posteromedially. In specimen 1/11/13 (Fig. 41) the epipterygoid is separated from the quadrate ramus of the left pterygoid and from the nature of the exposed surface of contact on the pterygoid it seems likely that the epipterygoid was synchondrotically bound to the pterygoid. In the abovementioned specimen a socket-like hollow is present on the pterygoid below the plane of separation with the epipterygoid. These two elements seem to have shared the basal articulation as they do in e.g. Captorhinus (Romer 1956).

The braincase

The occipital aspect of the braincase (Fig. 55) is dominated by a large plate-like supraoccipital bone, to be seen in specimens U.S.S. 6/4/23 (Fig. 46) and S.A.M. 9327 (Fig. 45). The exoccipitals are small discrete elements extending upwards

along the lateral margin of the foramen magnum and terminating against the supraoccipital plate. They are preserved in situ in specimen U.S.S. 1/11/10 (Fig. 48). As they are quite narrow their contribution to the formation of the paroccipital process is very limited (Fig. 55). The occipital condyle has a deep central pit and is exclusively formed by the basioccipital; see e.g. specimens U.S.S. 2/4/6 in Fig. 51 and U.S.S. 1/11/10 (Fig. 48) where this structure is preserved in situ. Lateral to the condyle, sutures of the basioccipital with the exoccipitals are sometimes discernible (Fig. 45). The paroccipital process (opisthotic bones) are plate-like extensions of the occipital area rather than the perhaps more usual rod-like processes. Because of the invariably severely crushed state of preservation of the occipital area none of the foramina in this region could be located.

On the undersurface of the braincase the dermal sheath of the parasphenoid extends into an extremely elongated and slender cultriform process anteriorly (see Figs 49 and 52). In the absence of a long interpterygoid vacuity the anteriormost tip of this process occupies a position dorsal to the point where the pterygoid bones diverge from each other (Fig. 56). Posteriorly the body of the parasphenoid extends onto the basisphenoid. I am of the opinion that the break in the floor of the braincase in U.S.S. 1/11/13 (Fig. 41) could be an indication of the position of the posterior margin of the parasphenoid. Of the basal tubera reported present by Von Huene (1941) very little could be detected in my material and their existence cannot be confirmed in M. tenuidens. The parasphenoid has a prominent keel on its anteroventral surface anterior to

the basipterygoid processes. The latter structures (illustrated in Fig. 42) are postero-laterally directed. This differs from the reconstruction of M. brasiliensis by Von Huene (1941) which shows the structures to be antero-laterally directed. The parasphenoid seems to contribute at least the ventral parts of the basipterygoid processes. The rather extra-ordinary orientation of the basipterygoid processes is reminiscent of the laterally projecting structures in Limnoscelis but differs from the typically antero-laterally projecting structures of the Romeriid captorinomorphs e.g. Paleothyris, Cephalerpeton (Carroll and Baird 1972) Protothyris, Romeria and Protocaptorinus (Clark and Carroll 1973).

The dorsal surface of the basisphenoid and parasphenoid region can be seen in three specimens, U.S.S. 1/11/13 (Fig. 41), 2/4/8 (Fig. 47) and 6/4/3 (Fig. 49). The sella turcica (pituitary fossa) forms a deep and prominent depression in front of the relatively high dorsum sellae. The entrance of the carotid arteries seems to have been through a single foramen in the floor of the depression (Fig. 52). The lateral walls of the sella turcica are absent or unossified and the antero-lateral edges of the dorsum sellae extend upward on either side to form pronounced wings. These clinoid processes (ossification of the pilae antoticae) seem to be more extensive in large than in small skulls. They are e.g. well developed in U.S.S. 1/11/13 (Figs 41 and 52) a large skull while almost absent in U.S.S. 2/4/8 (Fig. 47) and 6/4/3 (Fig. 49) which are both small skulls.

In spite of the extensive development of the dorsum sellae no trace of foramina for the passage of the abducent nerve

could be detected. The basioccipital bone forms the central hindermost part of the braincase floor. This element is anterolaterally flanked by the opisthotic elements which lie behind the stumps of the usually broken exoccipital elements above the occipital condyle. Anteriorly the basioccipital seems to border on the basisphenoid and parasphenoid on the level of the junction of the opisthotic and proötic elements (Fig. 42 and 41, U.S.S. 1/11/13). Neither pleuro- or orbitosphenoid ossifications were found. Such bones, if present, would be isolated elements and would probably not be recognised as such.

Of the elements which surround the inner ear cavity only some detail could be observed. In specimens 6/4/3 (Fig. 49) and 1/11/13 (Fig. 41) dorsal views of the otic capsules are exposed while U.S.S. 1/11/10 (Fig. 48) and in 1/11/13 (Fig. 42) ventral aspects are preserved. In specimens U.S.S. 1/11/13 (Fig. 41) and 2/4/8 (Fig. 47) the otic capsule shows an unossified gap that leads from the inner ear area mediad into the braincase. In this respect Mesosaurus conforms with other primitive reptiles in which the sidewall of the cranial cavity between the braincase and the inner ear cavity is unossified (Romer 1956). In specimen U.S.S. 2/4/8 (Fig. 47) a large gap that could possibly be a fenestra ovalis is present on the posterior aspect of the otic capsule, and the stapes is preserved with its wide footplate in position near this fenestra. As the fenestra ovalis lies in the suture between the proötic and opisthotic the latter element of the right hand side of specimen 2/4/8 (Fig. 47) is probably covered by the neural arch of the atlas. The areas posterolateral to the dorsum sellae probably are the proötic elements.

The distal point of the stapes (Fig. 47) curves slightly anteriorly confirming the shape and general position of the element as described in M. brasiliensis by Von Huene (1941). A stapodial foramen is absent but a small process, which could be the dorsal process for the attachment of the stapes to the paroccipital process, was noticed in two specimens, U.S.S.

1/11/10 (Fig. 48) and 2/4/8 (Fig. 47)

LOWER JAW (MANDIBLE)

General

Like the snout the mandible in Mesosaurus is a very much elongated and slender structure equal in length to the skull. The articulation of the mandible with the quadrate is slightly posterior to the cranial condyle. In only one jaw ramus in my material does the adductor fossa show. It is present as a much elongated groove in the prearticular bone on the inside of the righthand ramus in specimen U.S.S. 1/11/13 (Fig. 42). The fossa reaches anteriorly almost up to the splenial. A coronoid process is absent. The lower jaw symphysis is beautifully preserved in S.A.M. specimen K 4630 (not figured) and it is clear that the splenial enters the symphysis along with the dentary as was pointed out by Von Huene (1941). In this specimen the symphysis stretches over 18 mm of the total jaw length of 65 mm. The participation of the splenials in the symphysis is common among long-jawed and primitive forms (Romer 1956).

As has been noticed in M. brasiliensis by Von Huene (1941) the rami in the lower jaw of the southern African material fre-

quently separate along the symphysis which probably indicate that the symphysis was syndesmotic. A slightly medially directed retroarticular process formed by an extension of the articular bone is preserved on both rami of the lower jaw in S.A.M. specimen K 4630 (not figured). The lower jaw elements seem to have been only loosely bound as disarticulated lower jaw elements are frequently encountered (e.g. in specimens U.S.S. 2/4/12 and 6/4/11).

Individual elements of the mandible

Articular

This element occupies most of the central portion of the posterior ends of the rami of the lower jaw (Fig. 53). The glenoid fossa of the lower jaw articulation occupies the transversely widened upper surface of the bone. The fossa is divided into a posteromedian and an anterolateral depression by a low longitudinal ridge (see e.g. U.S.S. 2/4/1 Fig. 43). The two depressions are for the accommodation of the double condyle on the quadrate bone.

The dermal elements do not seem to contribute substantially to the small retroarticular process with the exception of the angular (Fig. 53). The articular bone is laterally bordered by the surangular and angular. The angular extends ventrally to cover the articular bone (see Fig. 55).

Surangular

The surangular is relatively small and occupies the upper pos-

terior part of the outer surface of the jaw. It occupies the area between the angular ventrally and the dentary and coronoid dorsally and wraps around the anterolateral margin of the articular.

Angular

This is a large element forming the lower lateral and the ventral surface of the posterior half of the mandible. Its anterior tip is wedged between the splenial and dentary bones (see Fig. 53 and specimen U.S.S. 2/4/6 Fig. 51). Here the angular covers an extension of the splenial which juts in between the angular and the surangular ventrally.

Coronoid (Complementary of Von Huene 1941)

A single small coronoid bone extends backwards from between the dentary above and the surangular below on the outer surface of the mandible (see e.g. specimen U.S.S. 2/4/6 Fig. 51 and 53). The coronoid seems not to have borne teeth.

Prearticular

This medial element is visible on both sides of U.S.S. 1/11/13 (Fig. 42) where the long and deep adductor fossa can also be observed. The lateral wall and floor of the fossa is formed by the coronoid and surangular elements. The dorsal edge of the prearticular is capped by the coronoid and a long ventral border is formed with the angular. From the size and general

position of the lower jaw elements it is likely that the prearticular anteriorly borders on the dentary and the splenial for a short distance (see Fig. 55).

Dentary

As is generally the case in reptiles (Romer 1956) the dentary in Mesosaurus is the largest and most prominent of all the elements of the lower jaw. The 48+ tooth sockets in the dentary are most frequently recognisable. The bone extends posteriorly for a considerable distance terminating about half way along the coronoid. The posterior margin of the bone below the orbit is usually indicated by the presence of very small teeth. This element occupies most of the outer anterior surface of the mandible and it is bordered below by the splenial. Posteriorly it borders on to the angular, prearticular, coronoid and surangular when followed from the median side up over the dorsal edge of the ramus and down the labial side. The anteriormost portion of the symphysis is formed by a median extension of the anterior tips of these elements (Fig. 55).

Splenial

The splenials partake in the formation of the major portion of the lower jaw symphysis and extend posteriorly ending in two prongs (Von Huene 1941). The material in my collection shows that in the southern African form this element is a simple splint-like bone which covers the dentary medioven-

trally posterior to the symphysis. It meets the prearticular and angular posteriorly. As in Von Huene's material the splenial in M.tenuidens is visible in lateral views of the lower jaw (Fig. 53). Along its ventral margin between the point where it loses contact with the dentary until it meets the prearticular it makes contact with the angular.

THE TEETH

The teeth are extremely long, slightly recurved, conical and slightly oval in cross section. Striations which extend along the length of the teeth were found in cross section to be infoldings of the surface enamel layer. Equivalent structures have been noticed in M.brasiliensis (Araújo 1976). These infoldings resemble the primary labyrinthodontine infoldings retained in the early reptile Limnoscélis (Romer 1956) and again illustrates the mosaic evolution Mesosaurus has undergone. In spite of having extensively specialised in the lengthening of the jaws and teeth the primitive labyrinthodont condition was partly retained.

Both upper and lower jaws have about 48 - 52 very regularly spaced and equally sized tooth "sockets" (Fig. 50). At the back of the jaw they are somewhat smaller and closer together (Fig. 40). The "sockets" have the appearance of being at best subthecodont or even pleurodont, no sign of even a low lingual wall for the tooth groove being present. One or two teeth were found that show the manner of attachment in the "sockets" (see e.g. Fig. 50, U.S.S. 2/7/1, righthand tooth) and it is not certain that the teeth were actually implanted in definite sockets as Von Huene (1941) has claimed for M.brasiliensis.

The teeth themselves are impossible to count; they are clearly very easily lost and, when preserved in any numbers, upper and lower teeth are inextricably mixed. The teeth vary in length and my material appears to confirm Von Huene's (1941) regular grouping into long teeth interspersed with two or three smaller ones. I have tentatively reconstructed them in this fashion in figure 53 in which the teeth correspond in number to the number of sockets. Whether the smaller teeth are replacement teeth is not clear at this stage.

The palatal teeth appear to be short and straight and occur in small clumps. The teeth are implanted in shallow circular grooves ("sockets"). The marginal teeth undoubtedly interdigitated and probably prevented the occlusion of the jaws.

THE POST CRANIAL SKELETON

THE AXIAL SKELETON

One of the features discriminating between the three genera of the Mesosauridae from South America is the difference in presacral vertebral count. For Stereosternum and Braziliosaurus it is stated as 34, with the latter genus having 15 cervicals and 19 dorsals while Stereosternum has 12 cervicals and 22 dorsals (Araújo 1976). This confirms the count for Stereosternum given by Osborn (1903) but differs from that given by Cope (1886) who mentions 11 cervicals and 23 dorsals. Sikama and Osaki (1966) also found 15 cervicals and 19 dorsals in Braziliosaurus.

Conflicting counts have been given for Mesosaurus brasiliensis. In the original description, McGregor mentions 11 cervicals and 18 dorsals for a total of 29 presacrals but Von Huene (1941) in a study of material from Paraná in Brazil, counted 34 presacrals. This count, according to the study of Araújo (1976) could either be that of Stereosternum or Braziliosaurus. As the cervical count is given as 12 by Von Huene (1941) Braziliosaurus is excluded and according to Araújo (1976) Stereosternum does not occur in the state of Paraná. The South African Museum in 1926 obtained a specimen of M. brasiliensis from Von Huene in exchange for southern African material. This specimen (S.A.M. 7377) has 29 presacrals. Araújo (1976) accepts 29 presacrals (12 cervicals and 17 dorsals) as the correct count for M. brasiliensis.

Prior to this study the correct presacral count for M. tenui-

dens was not known. Gervais (1864, 1865) counted 9 cervicals in the Paris type of M.tenuidens. From a cast of the type specimen it was possible to establish that Gervais erred in his count. His mistake apparently resulted from the fact that he based his count on the shape of the cervical vertebrae. Because the last three cervicals resemble the dorsal vertebrae in ventral view, Gervais did not include them in his count.

Seeley (1892) noticed this change in shape of the last cervicals in his description of the so called Cape Town specimen (S.A.M. 709). Having failed to count the atlas, Seeley erroneously refers to the change as being "beyond the eighth centrum" (p. 539). For the same reason he gives the cervical vertebral count as 11 instead of 12. Seeley's mistake could be established from the fact that he refers to the articular facets on the centra visible between the twenty second and twenty third vertebrae. As the facets are visible in only one spot in the specimen it could be established that his count of 22 vertebrae up to this point, does not include the atlas. The abovementioned counts of Gervais (1864, 1865) and Seeley (1892) are the only ones on M.tenuidens to date. The study of new material has established the presacral vertebral count at 29 with 12 cervicals and 17 dorsals which equals the count for M.brasiliensis.

The two sacral vertebrae reported present by Broom (1904) was confirmed by my observations and at least 60 caudals were counted.

THE MORPHOLOGY OF THE VERTEBRAE.

The Atlas - Axis complex

The atlas-axis complex is incompletely known in Mesosaurus (Romer 1956). In my collection the complex, or parts thereof is preserved in a number of specimens including the type specimen. In all specimens, however, it is preserved in different stages of dislocation (see e.g. specimens U.S.S. 2/4/6 Fig. 51 and 1/11/13 Fig. 42).

The centrum and intercentrum of the atlas are fused into a single unit (see U.S.S. 2/4/6 and 1/11/13 Figs 51 and 42, and S.A.M. 1327 and 709, Fig. 57) but a definite line of fusion between the two elements is still discernible. In specimens 2/4/6 (Fig. 51) and 1/11/13 (Fig. 42), the atlantal neural arches are well preserved. The two arches were apparently only weakly attached to each other and to the centrum. In none of my material could I detect a pre-atlas which must presumably have been present. The atlantal intercentrum is expanded transversely anteriorly and although the material studied shows no anterior view of this element it is safe to assume that it was procoelous for it had to articulate with the convex occipital condyle. Both centrum and intercentrum are open dorsally and form only a half ring.

The cervical vertebrae

In dorsal view the cervical and dorsal vertebrae are superficially almost indistinguishable but in ventral view the se-

cond to the ninth cervicals are very similar in form and differ from the rest of the cervicals and dorsals. From the tenth cervical onwards the transverse processes (neurapophyses) that carry the articulation facets for the cervical ribs enlarge considerably (Fig. 57) resulting in the change in shape. This causes the width of the last two vertebrae to exceed the length; and the articular facets for the cervical ribs in this region become exceptionally large.

The cervical vertebrae are frequently seen in dorsal or ventral view (see Fig. 57) and only one specimen U.S.S. 6/4/11 (not figured) shows a ventrolateral view of these elements. Specimen U.S.S. 6/4/9 (Fig. 58) shows a cervical vertebra in posterior view. In this particular specimen the articular facets on the transverse processes seem to be less well rounded than in e.g. S.A.M. 709 (Fig. 57). Both these specimens show the dorsal process to be low.

The prezygapophyses lean forward with the articular facets horizontally inclined and the postzygapophyses fit over these facets. This creates the illusion that the postzygapophyses also lean out backwards. If the centra of the successive vertebrae are however considered the postzygapophyses clearly do not reach beyond the margin of the centrum.

In dorsal view the third to the eighth cervicals show a prominent lateral ridge running from the pre- to the postzygapophyses. (see Fig. 57 S.A.M. 1327). These ridges are not present on the atlas or axis and from the ninth cervical onwards the ridges become less prominent and the area between the pre- and postzygapophyses depressed. A change in shape of the vertebrae is caused by an extension of the postzygapophyses while

the prezygapophyses is retracted. The prezygapophyses is retracted to such an extent that the articular facets are now moved posteriorly onto the anterodorsal surfaces of the transverse processes which are accordingly expanded. (This explains the enlarged processes visible in ventral view).

The dorsal vertebrae

These vertebrae are square in dorsal view because the prezygapophyses are now retracted altogether and lie on the level of the neural canal (see Figs 60, 59 and 61). The ridges between the pre- and postzygapophyses are not as conspicuous in the dorsal vertebrae as they are in the first few cervicals because the "swollen" arches of the dorsals obliterate the transversely concave areas between these ridges and the dorsal spine. In the last three dorsals the ribs are fused to the centra (see Fig. 63, U.S.S. 2/7/3) and become shorter posteriorly.

In ventral view the posterior articular surfaces of the centra can be seen to extend out posteriorly (S.A.M. 709, Fig. 62 and also Fig. 59) beyond the level of the articular facets on the prezygapophyses. The broad transverse process that lies anterolateral on the centrum extend laterally in a smooth curve from the posteriorly projecting surface of the centrum.

The sacral vertebrae

The two sacral vertebrae can readily be distinguished by the broad, blunt ending, ribs ankylosed to the centra. The anterior rib is the widest and between the anterior and pos-

terior ribs a recess is present on the lateral tips for the accommodation of the ilium. These elements are well preserved in dorsal view in specimen U.S.S. 1/7/3 (Fig. 64). This specimen shows that the two vertebrae are not fused.

The caudal vertebrae

At least 60 caudals are present amongst which three different types can be distinguished. These types are, the first few that carry ribs, those of the middle section with haemal arches but without ribs and the distal series without haemal arches or ribs.

Von Huene (1941) reports ribs on the first 12 caudals of M. brasiliensis but Araújo (1976) is of the opinion that only the first nine to ten vertebrae carry ribs. In Stereosternum, Osborn (1903) found ribs on the first eleven caudals. From the material in my collection it is clear that M. tenuidens, carries ribs on the first eleven caudal vertebrae only. These ribs are apparently not fully ankylosed to the centra for the ribs sometimes tend to separate from the vertebrae during fossilisation. This feature is illustrated well by specimens U.S.S. 3/1/5, 1/8/10 and 6/4/5 (Fig. 65).

In M. brasiliensis the rib on the second caudal vertebra is the longest and all the ribs point backwards (Von Huene 1941). In M. tenuidens the rib on the second caudal is also the longest but from the sixth caudal onwards the ribs point forwards. The first three of the last seven rib-bearing caudals carry short plump ribs while the last four ribs are reduced to mere laterally pointing projections. The long ribs on the first five

vertebrae are relatively more slender and longer than those on the last six vertebrae.

Araújo (1976) notes the presence of haemal arches on almost all the caudals of M. brasiliensis. The fact that in M. tenuidens only the ribless caudals, i.e. those from the 12th onwards, carry haemal arches must thus be purely coincidental. The breaking points noticed by Broom (1904) in the caudals of the Niewoudtville specimen of M. tenuidens are the sutural lines between centra and intercentra present in all the caudals from the 12th onwards (Fig. 66). In specimen U.S.S. 2/5/3, 47 of these, chevron bearing, caudals showing intercentra could be counted.

The haemal arches articulate with the intercentra in the usual way. Osborn (1903) reports the presence of a cross-connection between the proximal prongs of the haemal arches in M. brasiliensis but Von Huene did not find this to be the case in his material. The haemal arches of M. tenuidens do not show cross-connections either (see Figs 66 and 67).

The caudal vertebrae diminish in size distally and it seems that chevrons were present up to the fifth last vertebra. Dorsal processes are well developed in the proximal caudals and resemble those of the dorsals. From the seventh caudal onwards the processes tend to become more slender, almost rod-like in side view (Fig. 66) and develop a posteriorly directed slant. In the last + 26 caudals the slant in the dorsal processes become much more pronounced. The small posteriormost vertebrae are without haemal arches (Fig. 68).

RIBS AND GASTRALIA

The dorsal ribs bear a capitulum as well as a tuberculum with a long articulation facet situated between the two structures (Fig. 61). The distinct pachyostosis of the ribs probably developed to alleviate the natural positive buoyancy present in all lung-breathing animals and aided in diving. The heavy ribs therefore served the purpose of the "weight belt" of modern S.C.U.B.A. divers.

In M.tenuidens numerous rows of gastralium form an almost completely closed ventral field. Specimen U.S.S. 1/11/6 shows each transverse row to consist of a single straight median element and a pair of lateral elements. All elements are fusiform with the distal ends of the lateral elements distinctly bifurcated. The V-shaped or paired median elements mentioned by Romer (1956) are not shown by my material. Some isolated gastralium however are almost filiform in shape. Seeley's (1892) description of the gastralium therefore seems to be essentially correct. Broom (1904) proposes the possible presence of two or even three rows of lateral elements on each side of the median element. He also points out the apparent difference in thickness between the gastralium of the Niewoudtville specimen (U.S. Geology D 172) and that of Seeley's (1892) M.pleurogaster.

That such elements could indeed exist is illustrated by the presence of at least four relatively slender elements in a transverse row in specimen U.S.S. 1/11/15 (not figured). Whether this anomaly is an illusion caused by differences in preservation or whether it is a real difference with taxonomic implications is not clear at this stage.

THE GIRDLES: Pectoral girdle

Araújo (1976), although her material made a clear interpretation of the shoulder girdle impossible regards the interpre-

tation of McGregor (1908) and Von Huene (1941) on the girdle of M. brasiliensis as more correct than that of Seeley (1892) and Broom (1904) on M. tenuidens. It should be pointed out, however, that whereas McGregor (1908) and Von Huene (1941) studied South American material (M. brasiliensis), Seeley (1892) and Broom (1904) based their interpretations almost exclusively on a single specimen, the so called Cape Town specimen (S.A.M. 709) of M. tenuidens.

The difference in interpretation of the girdles in the two forms centres around the recognition of a double coracoid element in M. tenuidens while (as in Stereosternum) a single element only is said to be present in M. brasiliensis.

In his reconstruction, Seeley (1892) refers to the precoracoid as "the part of the bone which extends inwards from the scapula towards the clavicle" (p. 593) implying that the rest of the posterior and posteromedian parts of the plate form a coracoid. In a re-interpretation of the same specimen Broom (1904) interprets the posteromedian element (the coracoid of Seeley) as the precoracoid and the rest of the plate as the coracoid. Both these authors however acknowledge that the elements are so badly crushed in this specimen that it renders the recognition of sutures impossible. In the region where the posteromedian element of M. tenuidens attaches to the anterolateral scapula-coracoid plate, both McGregor (1908) and Von Huene (1941) noticed a "boss" on the outer surface of the coracoid plate immediately above the glenoid fossa.

Amongst the new material collected, isolated portions of the pectoral girdle show the relationship between the scapula, precoracoid and coracoid elements (U.S.S. 5/4/2 and 6/4/24

(Fig. 78). These specimens give unambiguous proof for the presence of two ossifications in the coracoid plate in M. tenuidens and show that the posteromedian element identified by Broom (1904) as the precoracoid is in fact the coracoid as Seeley (1892) said. The more anteriorly placed portion was correctly identified by Seeley (1892) as the precoracoid. The sutures between the scapula, coracoid and precoracoid are clearly visible in specimen U.S.S. 6/4/7. All three these elements take part in the formation of the glenoid fossa, with the scapula and precoracoid bordering on the coracoid for more or less equal distances immediately posterolateral to the coracoid foramen. The configuration of the three elements is reconstructed in Figs 69 and 70 in lateral and ventral views respectively.

The shape of the three-pronged scapula - coracoid - precoracoid is such that, whether it separates as a unit from a cadaver or remains in situ, it will always settle with at least one of the elements raised off the substrate and not in a flat plane. Any force or pressure exerted on such a structure will tend to snap it at the weakest point in the unit. The weak line seems to have been the narrow neck connecting the expanded median plate of the coracoid with its glenoid portion. This is illustrated by a number of specimens e.g. U.S.S. 5/4/2 and 6/2/24. In all these the median expanded portion of the coracoid, displayed by the Cape Town specimen (S.A.M. 709) is missing but the distal portion in contact with the scapula and coracoid is still in place showing the sutures between the three elements (U.S.S. 5/4/2 shows this condition bilaterally Fig. 78).

It is evident from the specimens in my collection that the

elements become better ossified and fused together in larger (older?) specimens while in small (young?) individuals the elements are usually separately preserved and in the smallest specimens the elements were not fully ossified and appear as disk-like structures. In large individuals even isolated girdle units are preserved intact but for the loss of part of the coracoid.

The two M. tenuidens specimens in which the pectoral girdles have been described previously show different views of the elements. The Paris type of Gervais (1864) exhibits the elements in outer view. The precoracoids and scapula had been displaced ventromedially, the righthand precoracoid being partially hidden by the stem of the interclavicle and the left coracoid element. These elements in turn obscure the median coracoid plates. The external "boss" below the glenoid cavity opposite the point of attachment with the precoracoid is visible.

In the Cape Town specimen (S.A.M. 709) of Seeley (1892) and Broom (1904) the precoracoid plates had been forced open anteriorly, flattening the precoracoids in ventral view by displacing them backwards. This had caused a rotation of the precoracoids through about 90° , twisting the narrow neck of the coracoid and drawing the scapula into an anterolateral position. This specimen therefore shows the coracoids in ventral view and the precoracoids and scapulae in inner view.

Judging from the literature there would appear to be a major difference in the morphology of the enchondral divisions of the pectoral girdles of the two species of Mesosaurus. This, like the apparent differences in the skull, could mean that a change in the classification is necessary. However, the stri-

king similarity between these forms in general, renders it more likely that a study of better material of M. brasiliensis and a direct comparison of material from the two continents will reveal the presence of these features also in M. brasiliensis.

Judging from the interclavicle of M. brasiliensis as figured by McGregor (1908 plate 11, Fig. 3) and the elements of M. tenuidens in my collection (e.g. U.S.S. 1/5/1) the elements in the two species are identical. The anterior plate of the long stemmed interclavicle, in ventral view (U.S.S. 1/5/11) clearly shows the broad areas of overlap where the expanded ventral portions of the clavicle overlapped onto the interclavicle (see Fig. 70). As in M. brasiliensis one of my specimens shows the tip of the stem to be smoothly rounded. Specimen (U.S.S. 6/5/1) on which the reconstruction in Fig. 70 is based, however, shows the stem to be clearly bifurcated.

With the interclavicles of specimen U.S.S. 1/5/11, a clavicle, was also preserved which shows these elements to be about half as long as the interclavicles. The clavicle has a medioventral spoon-shaped expansion that lies on the anterolateral ventral surface of the interclavicle. Between the areas of contact for the clavicles the interclavicles shows distinct surface sculpturing, typically found in amphibians and very primitive reptiles.

The pelvic girdle

This girdle in M. tenuidens was previously known only from the description of the Niewoudtville specimen (U.S. Geology D 172)

by Broom (1904). From this specimen the plate-like structure of the pubis and ischium is evident but the structure of the ilium was unknown prior to this study. The presence of a notch rather than a foramen in the lateral margin of the pubis as reported by Broom (1904) is confirmed by the newly collected material (e.g. U.S.S. 2/4/4). The notch in the pubis was also reported by Gürich (1889) in the young specimen of M. tenuidens he called Ditrochosaurus capensis. In the reconstruction of the elements by McGregor (1908) in M. brasiliensis the notch in the pubis is shown to be bordered by the ilium. I am however of the opinion that the notch in the pubis of M. tenuidens was bordered not by the ilium but by the ischium.

The ilium is preserved in lateral view in specimens U.S.S. 1/8/10 and 1/4/7. These specimens show a shallow acetabular depression formed almost exclusively by the blade-like ilium. Above the depression a prominent supra-acetabular buttress is developed. The posterior extension of the iliac blade of large specimens is absent from, and seems not to have been ossified, in small (young) individuals. In general the ilium is strikingly similar to that of most cotylosaurs.

As the ischia in my collection confirm the interpretation of Broom (1904) on the general form of this element the description will not be repeated here. The three elements are shown reassembled in Fig. 71 in lateral view.

THE APPENDAGES:

As the propodial and epipodial elements of both hind and front limbs have been adequately described by various authors (e.g. Seeley 1892, Broom 1904, McGregor 1908, Von Huene 1941 and Sikkama 1970) a full description will not be given here. Only new and relevant information will be covered. As confusion exists about the mesopodials, manus and pes, more attention will be given to these elements.

ANTERIOR LIMB

The Humerus

The proximal and distal ends of the bone lie in different planes almost at right angles to each other as is usual in primitive forms. The shaft of the bone is, however, in contrast to really primitive forms, well developed, a trend seen also in small cotylosaurs (Romer 1956).

The entepicondylar foramen for the passage of the median nerve (Williston 1925) is well developed and separates the entepicondyle from the capitellum (Fig. 72). Seeley (1892) describes two hollow areas on the distal end of the bone in S.A.M. specimen 709 which apparently corresponds with the capitular and trochlear areas. The ectepicondylar foramen of other forms is in Mesosaurus represented by a groove on the dorsal surface of the distal end of the bone and in this respect resembles the humerus in young plesiosaurs (Williston 1925). This groove separates the ectepicondyle from the supinator process which is placed far distally in Mesosaurus (Romer 1956). The bone

is nearly straight along its anterior border, concave along its posterior border arching slightly dorsally in length (Seeley 1892). In the humeri described in the literature and in my material, with one notable exception (U.S.S. 1/2/5 Fig. 72) the terminal epiphyses are invariably absent. Along the proximal posterior border of this exceptionally well preserved humerus a small spine and a shallow groove is present (Fig. 72). The proximal ventral area, posterior to the attachment of the short muscles to the shoulder on the deltopectoral crest (Romer 1956) is small in Mesosaurus.

The unusually large, distally placed supinator process for the attachment of the supinator muscle may indicate a well developed rotational ability of the front limbs. By rotating the front limbs and changing its angle the appendages could have served as steering organs in swimming.

Radius and Ulna

These two elements have been adequately described in M. tenuidens by Gervais (1864), Seeley (1892), Gürich (1889) and in M. brasiliensis by McGregor (1908), Romer (1956) and Sikama (1970). It should be mentioned however that the ventral ridge described by Seeley (1892) on the distal end of the radius in the Cape Town specimen of M. tenuidens seems to be an artifact. The two elements are subequal in length and as their ends are incompletely ossified no olecranon was found, which, as in many other aquatic forms, may well have been cartilagenous in life (Romer 1956). This would reduce the movement of the radius and ulna to a simple flexion on the humerus. In well preserved specimens the epipodials are invariably preserved in

line with the humerus and with the limb projecting from the body in a posterolateral direction at an angle of ± 45 degrees.

The ulna is curved slightly more than the radius because of the concavity of the inner border and the ends of the ulna is somewhat more expanded than those of the more rod-like radius. While the ends of the ulna are truncate the distal articular surface of the radius is slightly medially inclined. Araújo's (1976) remark that little difference exists in these elements between species is justified as was also shown in the statistical analysis of the data.

The carpus

The proximal carpalia:

Gervais (1864) originally described the proximal carpalia of M. tenuidens as consisting of two elements which he identified as a large radiale and a small "cubital" (or cuboid, mammalian terminology and ulnare, reptilian terminology, Romer 1956). Seeley (1892) recognised three bones in the proximal row of carpalia in the Cape Town specimen (S.A.M. 709) a cuneiform on the ulnar side (ulnare), a median lunar bone between the distal ends of the epipodials (an intermedium) and a centrale. The single large element in the right limb of the Paris specimen (radiale of Gervais (1864) is in the Cape Town specimen traversed by a shallow groove which must have led Seeley (1892) to interpret it as two elements. In the specimen Gürich (1889) named Ditrochosaurus capensis (a young individual of M. tenuidens), he noted three separate proximal elements which he identifies as an ulnare, a radiale (= the intermedium or lu-

nar of Seeley) and a centrale. Stromer (1914) identifies a radiale in addition to the three abovementioned elements in material from the Kalahari Karoo Basin in Namibia (the farm Kabus).

In M. brasiliensis McGregor (1908) recognised three elements in the proximal row and mentions the coalescence of two of the elements (the intermediocentrale?) but decided that it was an artifact. He identified a small ulnare, a large radiale and an intermedium distal to the radiale. Von Huene (1941) also identified an ulnare but found a single element in the area where McGregor (1908) identified a radiale and intermedium. This single element Von Huene calls an intermedium.

Both Von Huene (1941) and McGregor (1908) identify four distal elements opposite toes one to four. Sikama (1970) identifies four proximal carpals, a small ulnare, an intermedium, a centrale and like Stromer (1914) in M. tenuidens, also report the presence of a small radiale. Araújo (1976) identifies the ulnare and following McGregor (1908) calls the large proximal element a radiale and the smaller distal element the intermedium. Araújo (1976) is the first to note the presence of five elements in the distal row in M. brasiliensis. In Stereosternum tumidum, Osborn (1903) identifies an ulnare, an intermedium and a centrale and predicts the presence of an unossified radiale and a fifth element in the distal row. Cope (1886) however had at this time already found a radiale but mentions only four elements in the distal row. A radiale is also mentioned by Jaekel (1909).

Stromer (1914) in a description of specimens from Kabus in Namibia mentions the presence of nine carpals, therefore, a

radiale as well as a fifth element opposite the fifth toe. One of my specimens of M.tenuidens (U.S.S. 1/2/5) confirms the presence of nine carpal elements, a radiale, ulnare, a large intermedium with a more distally placed centrale and one element opposite each toe in the distal row (Fig. 72). In addition to these elements the latter specimen (as well as U.S.S. 2/8/3) show an additional central element between the ulnare and the elements opposite the fourth and fifth toes. The original interpretation of the elements by Cope (1886) and Osborne (1903) in M.brasiliensis and Seeley (1892) in M.tenuidens has therefore proved to be partly correct. It should be noted that the radiale and the distal fifth carpal seem to ossify only in older individuals and also tend to be lost very easily.

Phalangeal formula

The phalangeal formula for M.tenuidens is given as 2, 3, 4, 4, 3 which corresponds with the formula given by Seeley (1892) for the Cape Town specimen (S.A.M. 709). This count is confirmed by a number of specimens.

For M.brasiliensis the same phalangeal formula is given by McGregor (1908), Von Huene (1941) and Araújo (1976).

THE POSTERIOR LIMB

The Femur

Detailed descriptions of the femur of M.tenuidens has not been attempted other than general comments on length and form

(e.g. Broom 1904). Of M. brasiliensis more detailed descriptions are given by e.g. McGregor (1908) who comments on the fact that both genera of Mesosauridae, as fossilised, usually have the femur placed horizontally at approximately right angles to the body axis with the knee joint markedly flexed (p. 325). The two genera he refers to are M. brasiliensis and Stereosternum tumidum.

This observation is borne out also by the southern African material. The head of the femur of M. brasiliensis McGregor (1908) finds to be rounded and not very distinct; neither could he find any sign of a trochanter in his material. The distal articular surface he describes as convex and of a smooth triangular form. Von Huene (1941) comments on the similarity between the femurs of Mesosaurus and the pelycosaur Varanops, both showing large trochanters; presumably the internal trochanter (Romer 1956).

In a study of M. brasiliensis material housed in Japan, Sikkama (1970) denies the presence of any trochanters. Araújo (1976) supports McGregor rather than Von Huene (1941) on the proximal part of the femur, and Von Huene rather than McGregor on the distal end.

In the southern African material the shape and morphology of the femur could be determined with much more accuracy than was previously possible. It is clear that an anteroventral ridge is developed on the proximal part of the shaft. This ridge extends distally from the ventral apex of the triangular proximal articular facet. In terms of the femur morphology of primitive cotylosaurs the ridge would correspond to and include the posterior edge of the ridge system bordering the ventral intertrochantric fossa as well as the adductor

ridge (Fig. 73). The ridge terminates on the ventral edge of the posterior condyle on the distal end of the bone. A large flat intertrochantric fossa is developed but the internal trochanter seems to be only feebly developed at best. The distal end of the femur shows a posteromedially slanting articular area for accommodation of the proximal head of the tibia. The articular facet for the fibula typically present on the posterior surface of the posterior condyle in primitive reptiles (see Romer 1956 Fig. 170) in Mesosaurus occupies a shallow sulcus on the posterior surface of the distal end of the bone. The facet has therefore migrated from its original posterolateral position to a more medial position on the posterior surface of the distal end of the shaft and head of the femur (see Fig. 73 U.S.S. 1/7/3 and 2/8/1). The dorsal edge of the sulcus is strongly developed and the articular facet therefore faces slightly ventrally and the anterior condyle is displaced dorsally. No indication of an intertrochantric fossa could be found.

In dorsal view the femur is slightly S-shaped and is concave ventrally. In small (young) individuals the femurs are truncate (e.g. U.S.S. 0/1/11, 6/11/18 and 3/1/5) but seem to be more completely preserved in large (older?) individuals, which were presumably better ossified (e.g. U.S.S. 1/7/3). Apparent differences in the shape of the femur in different specimens seem to be the result of the exact angle in which the elements are preserved. This is illustrated e.g. by specimen U.S.S. 1/7/3 (Fig. 73) and the Niewoudtville specimen (U.S. Geology D 172; Broom 1904 Fig. 1). In both, the femur is seen in ventral view but in the Niewoudtville specimen the bone is rotated slightly with the result that the articular sulcus for

the fibula is not visible distally where only a narrow strip of bone is exposed. The proximal end of the bone however appears as a flat wide surface, as the intertrochantric fossa was brought into full view by the rotation. As a result the femur in this specimen appears to be slightly wider distally.

Tibia and Fibula

Like the radius and ulna these elements have been adequately described e.g. by Gürich (1889), in the specimen he named Ditrochosaurus capensis (actually a young individual of M. tenuidens) and in M. brasiliensis by McGregor (1908), Romer (1956) and Sikama (1970).

The fibula is the largest of the two elements. The concavity of the latter element is accentuated along its distal margin by the expansion of the distal end (Fig. 74). The slanting distal articular surface on the end fits snugly on the inter-medial part of the co-ossified intermedio-tibiale complex of the tarsus. The proximal end of the bone articulates on the posterodistal end of the femur in the shallow sulcus.

The tibia is more rod-like than the fibula with the ends less expanded. The distal end of the tibia fits on to the tibiale section of the co-ossified tibiale element. Both elements are slightly dorsoventrally flattened.

The Tarsus

Gürich (1889) and Broom (1904) were the first to describe the pes of southern African mesosaurid material (Gürich called his specimen Ditrochosaurus capensis). From Kabus (in Namibia)

Stromer (1914) described an incomplete foot of a specimen he referred to Mesosaurus. In a later work Broom (1913) described the foot of a specimen from Victoria West which he referred to a new genus of the Mesosauridae, Noteosaurus. This specimen shows six phalanges in the fifth toe and it was mainly on this feature that the new genus was based.

In Ditrochosaurus capensis (a young M.tenuidens), Gürich (1889) found two elements in the proximal row of the tarsus, which he identifies as a tibiale and a fibulare. Like the distal carpalia all the distal tarsalia are missing in D.capensis which is, according to Gürich (1889) a result of the failure of the elements to ossify. The phalangeal formula, based on specimens from Kimberley, he gives as 2,3,4,4,4.

In a study of the Niewoudtville specimen (which Broom (1908) calls Mesosaurus capensis) Broom (1904) identifies a fibulare and a large ankylosed intermedium and tibiale in the proximal row. Between the two elements a "fairly large foramen" (p. 105) is observed. Four elements are counted in the distal row with the fourth poorly preserved. The missing fifth element is said not to have been ossified. The phalangeal formula is given as 2,3,4,5,4.

In Noteosaurus africanus, Broom (1913) mentions two proximal tarsal elements which he does not identify other than stating that they resemble the elements of M.brasiliensis more closely than that of M.capensis (the use of Mesosaurus capensis is puzzling but probably refers to the Niewoudtville specimen which he referred to M.tenuidens in the original description of the specimen (Broom 1904)). In the latter paper he refers to Gürich's (1889) specimen as a young Mesosaurus and the re-

ference to the Niewoudtville specimen in his 1908 paper as M. capensis implies that he judged these two specimens (the Niewoudtville and Gürich's) to be of the same species but different from the Cape Town (S.A.M. 709) and Paris type specimens of Mesosaurus tenuidens.

In M. brasiliensis McGregor (1908) identifies a fibulare and an ankylosed tibiale-intermedium element in the proximal row of tarsalia. In the distal row five elements are present and the phalangeal formula is given as 2,3,4,5,3. The fibulare is illustrated as medially elongated. On the phalangeal formula as given in the text by McGregor (1908 p. 321) both Stromer (1914) and Wiman (1925) point out that it differs from his reconstruction of the pes in figure 1 (p. 309). In the figure the formula can be counted as 2,3,4,5,4. Wiman (1925) gives the formula as 2,3,4,5,5 (from his study of the Stockholm collection) and mentions that the additional fifth element is also mentioned by Williston (1925). He also illustrated the feet of a young and an older individual and the fibulare is shown to be more elongated in the older individual. He observed five elements in the distal row.

The observations of Von Huene (1941) on the pes in general agree with those of McGregor (1908) and Wiman (1925). Von Huene, however, claims six elements in the fifth toe which brings the phalangeal formula of M. brasiliensis to the same as that of N. africanus Broom (1913). That confusion still exists about the formula is illustrated by the fact that Araújo (1976) in the latest study of Brazilian material repeats the formula of McGregor (1908) as correct.

In the original description of Stereosternum tumidum, Cope (1886) mentions two proximal and five distal tarsal elements. He iden-

tifies the proximal elements as a large fibulare + intermedio-calcaneum and a smaller elongated tibiale. From his figures it is clear that he has mistaken the tibiale for the fibulare as he has also mistaken the tibia for the fibula. The tibia and tibiale of Cope (1886) therefore are the fibula and fibulare of e.g. Osborn (1903) and Broom (1904, 1913) and his fibulare + intermedio-calcaneum corresponds with the tibiale-intermedium complex of other authors. (It should be noted that in a later work, Cope's (1887) mistake led also to the incorrect phalangeal formula of -,4,4,4,3 (second to fifth toe) which should actually read 2,4,4,4,- for apart from having mistaken the first for the fifth phalange his figure 1 clearly shows two and not three phalanges in the first digit. Osborn (1903) identifies a fibulare and an element which he sees as a complex of the intermedium, centrale-tarsi + tibiale in the proximal row and five elements in the distal row. The fibulare is figured as an elongated element similar to that of M. brasiliensis.

From the new material collected for this study it is clear that there are indeed two elements in the proximal row of tarsalia. The fibulare in small (young?) specimens do not show the prominent elongation so conspicuous in older specimens (Fig. 74). A fifth element in the distal row present in large specimens apparently was not ossified in young individuals for it is invariably absent from small specimens.

The large element is formed by the ankylosis of two elements. This is illustrated well by the X-ray photograph of specimen U.S.S. 3/1/5 (Fig. 75). The two elements involved seem to be the intermedium and tibiale. In most of the specimens the foramen between the two proximal elements is preserved.

One exceptionally large foot, (U.S.S. O/1/8 Fig. 74) shows in addition to the five elements in the distal row and two elements of the proximal row, an extra element between the tibiale-intermedium and the first and second elements in the distal row. This centrale was anticipated by Williston (1925) who had added this element in dotted lines to his reconstruction of the foot of M. brasiliensis (see his Fig. 153). This element was eventually observed by Sikama (1970) in M. brasiliensis material housed in Japan and he refers to the element as a "medial centrale" (p. 46). The element could either be a lateral centrale, a mediocentrale, or what is most likely a product of the fusion of the two.

The abovementioned specimen U.S.S. O/1/8 in addition seems to have a double element opposite the fifth toe. If not an artifact this element (between the small distal element opposite the fifth toe and the fibulare in Fig. 74) could only be a somewhat displaced proximal centrale element. If this proves to be correct the tarsus of Mesosaurus will be almost identical to that of a young Captorhinus (Romer 1956).

TAXONOMICAL INTERPRETATIONS

Araújo (1976) has established beyond doubt that in the South American material, at least three different mesosaurid genera can be recognised on statistical grounds, (Mesosaurus brasiliensis, Stereosternum tumidum and Braziliosaurus sanpauloensis).

Through lack of information about the southern African M. tenuidens no comparison could be made to establish the relationships and taxonomy of the material from the two continents.

The material from southern Africa has been referred to a number of genera and species. Apart from the type species of the genus Mesosaurus (M. tenuidens Gevais 1864) two more genera and four more species have been created. These are Ditrichosaurus capensis Gürich (1889), Mesosaurus pleurogaster Seeley (1892), Mesosaurus capensis and Noteosaurus africanus Broom (1913).

Subsequent authors have invariably treated Ditrichosaurus capensis Gürich (1889) as a junior synonym of M. tenuidens (e.g. Broom 1908, Araújo 1976). M. pleurogaster Seeley (1892) was based on an incompletely preserved and exceptionally large individual and is also regarded as a junior synonym of M. tenuidens. The Niewoudtville specimen (U.S. Geology D 172; Broom 1904), along with Gürich's Ditrichosaurus capensis specimen, were transferred by Broom (1908) to the genus Mesosaurus as the species Mesosaurus capensis. These specimens cannot be distinguished from M. tenuidens and M. capensis should also be considered a junior synonym of M. tenuidens.

Noteosaurus africanus Broom (1913) poses more of a problem. This species was based on the larger number of digits in the fifth toe and as has been pointed out there are indeed six elements present in the fifth toe of this specimen. It is

furthermore possible that the sacral ribs are wider than in M. tenuidens if the preservation of these elements in N.africanus is not an artifact.

The stratigraphic position and exact locality of this specimen is unfortunately unknown which complicates matters. The locality is given by Broom (1913) as the Victoria West district but the Whitehill Formation does not outcrop in this district. The matrix of the slab containing the specimen does not at all resemble Whitehill shale (in spite of Broom's claim that it does) and upon analysis was shown to differ chemically from Whitehill shale. (The results of X-ray diffraction analysis of five specimens of Whitehill shale from representative outcrops over the entire outcrop area of the Great Karoo Basin and that of the *Noteosaurus* slab, are given in table 1).

The green mudstone matrix of the N.africanus slab can either be from the intercalated green mudstone in the Whitehill Formation or from the overlying Tierberg shale Formation. The intercalated green mudstone (silty-shale) member is not developed in the Whitehill outcrops to the north of the Victoria West district (near Vosburg) while the Tierberg shale outcrops extensively in this area. It is therefore most likely that the specimen was derived from the latter Formation if Broom's (1913) statement on the origin of the specimen (Victoria West district) is correct.

If the specimen is indeed from the lower Tierberg Formation it could be considerably younger than those from the Whitehill Formation which might explain the apparent anatomical differences.

The higher phalangeal count of the fifth digit on which Broom

(1913) based the genus Noteosaurus, becomes doubtful in view of Von Huene's (1941) report of the presence of an equal number of elements in the fifth toe of M.brasiliensis. Nevertheless, as will be shown in the following section, the relative proportions of the pro- and epipodial elements and the bones of the foot in Noteosaurus differ sufficiently from those of other genera to warrant the retention of this species. An effort should however be made to investigate the shales of the lower Tierberg Formation to verify whether N.africanus indeed occurs in these younger strata. The treatment of Noteosaurus as a junior synonym of Mesosaurus by e.g. Von Huene 1941, Kuhn 1969, and Araújo 1976, is considered to be incorrect.

To date the Whitehill Formation has therefore yielded only M.tenuidens. One specimen in my collection, shows a close relationship with the Brazilian genus Stereosternum. The specimen was presented to me by D. Strydom who collected it on the farm Maritzdam, a subdivision of Buffelbout 42 in the Carnavon district. The differences between Stereosternum and Mesosaurus is given by Araújo (1976) as follows.

Stereosternum: 34 presacrals, length of skull = neck, teeth short, conical, straight.

Mesosaurus: 29 presacrals, skull longer than neck, teeth longer than in Stereosternum, oval in section, recurved.

The Maritzdam specimen has 34 presacrals with the head and neck of equal length, the teeth are short and straight. The number of cervical vertebrae of this specimen (12) equals that of Stereosternum and excludes the possibility that it could be more closely related to Braziliosaurus. It therefore seems certain that we are dealing with Stereosternum or a closely

related form rather than with Mesosaurus tenuidens. Apart from the Maritzdam specimen two more specimens in my collection could also possibly differ from Mesosaurus in the same way but as these specimens lack the skull and neck a final decision is impossible.

If the presence of Stereosternum tumidum or a closely allied form is confirmed in the southern African Formations it will have far reaching implications and will support the arguments in favour of a former junction of the African and Brazilian Basins. Before a final decision on the taxonomical status of these specimens can be reached a comparison with South American Stereosternum material is essential.

THE BIOLOGY OF MESOSAURUS

Several authors have in the past speculated on aspects of the biology of Mesosaurus and the climate of the water body in which it lived e.g. McGregor (1908), Wiman (1925), Romer (1956, 1968), Fabr  (1967).

The mere presence of a reptile in the Whitehill sea indicates a considerable amelioration of the climate since the preceding period of continental glaciation. There is no way of knowing whether the winters were mild enough to enable Mesosaurus to remain active throughout the year. In view of the history of glaciation and the suggested cold climate (Fabr  1967) and the seasonal variation evident from the presence of contemporaneous deciduous vegetation on nearby land (Plumstead 1969) it seems logical to infer that the climate necessitated the hibernation of Mesosaurus on land. It is however unlikely that it was able to dig into the mud for hibernation as Bakker (1974) suggested.

Visits on land must have been a periodic phenomenon with the whole population converging on favourite beaches for the laying of eggs during the breeding season (like modern marine turtles) or for hibernation in Autumn. If natural catastrophes had befallen the reptiles during such times it would have resulted in dense accumulations of disarticulated skeletal material. Episodes such as this may have resulted in the formation of bone beds in nearshore facies as e.g. at Doros in the Huab Basin and at Gross Daberas in the Kalahari Karoo Basin. Similar occurrences of bone beds in coarse clastic material are also recorded from the Iraty (Martin 1961).

The weakly developed and oddly placed front limbs must have

made locomotion on land somewhat laborious and for the burial of eggs (if the eggs were covered at all) the hind limb only, could have been employed.

Mesosaurus must have been a very competent swimmer for even very small (young?) individuals of only 35 cm (the largest individuals reached a length of more than two meters) are found in areas of the basin that must have been hundreds of kilometers from the nearest shore. In swimming the small front limbs presumably functioned only as rudders with the tail acting as the main propulsive organ. The tail in Mesosaurus was strongly developed compared to that of a modern semi-aquatic reptile of comparable size e.g. Varanus niloticus. The relatively strongly developed caudal ribs on the first caudal vertebrae of Mesosaurus indicate that very strong musculature stretched between the pelvic girdle and the base of the tail. The tail therefore seems to have been powerful although no indication of the degree of lateral flattening can be deduced from the form of the caudal vertebrae. Judging from the caudals in Varanus niloticus the tail in Mesosaurus could quite well have been flattened to at least the same degree.

The role of the pes of Mesosaurus in swimming is not clear although it is regarded as enlarged and thought to have been webbed (Romer 1968) to perform such a function. It is true that the toes, especially the fourth and fifth, are widely spaced which could indicate the presence of webs but in comparison to the pes of V. niloticus that of Mesosaurus is not all that much enlarged. Since V. niloticus is clearly less aquatic than Mesosaurus the fact that it lacks webs between the toes cannot be used to extrapolate conditions in Mesosau-

rus. This feature therefore remains pure speculation. With or without webs the hind feet would in any case most likely have been used in intricate manoeuvring. The idea of Wiman (1925) that Mesosaurus used the outer edges of the webbed hind feet and the nails on the outer toes to propel itself on the substrate seems to be a fair assumption but this could have been possible only in very shallow nearshore areas or on land.

The food source and manner of feeding of Mesosaurus remains problematic. McGregor (1908) depicted Mesosaurus as piscivorous and Romer (1956 p. 455) points out that a "high degree of concentration of small crustaceans is present in some Mesosaurus bearing beds" implying that it fed on these Crustacea. From the small size of the head of Mesosaurus and its seemingly fragile teeth it is unlikely that it fed on the relatively large "tough scaled" palaeoniscid fish of the Whitehill sea. Romer's (1956) idea seems to be more acceptable but the study of the biozonations of the Formation revealed that the dense Notocaris acme zone of crustaceans barely overlaps with the top of the Mesosaurus range zone. In the major part of the Mesosaurus zone no trace of crustacea was found. Mesosaurus could have fed on juvenile fish but to have sustained a large population of reptiles a more reliable and abundant food source must have been available (the fish probably utilized the same food) although no record of it is preserved in the shales. It was suggested by Ziegler (1972) that the fine battery of long teeth of Mesosaurus was used as a filtering apparatus. Small, soft bodied, planktonic organisms (which would have included fish larvae and eggs)

could thus have served as its main food supply. Such a mode of feeding would not have placed excessive strain on the extremely long and presumably fragile, loosely attached teeth of Mesosaurus. Wiman's suggestion that Mesosaurus was a bottom feeder is ruled out by the indications of the presence of toxic bottom brines and the resultant absence of a benthonic fauna.

STATISTICAL TREATMENT OF MATERIAL

Collection of data:

Detailed measurements of the newly collected southern African mesosaurid material were made with veneer calipers to the nearest 0.1 mm. A list of parameters collected for use in this study is given as Appendix 1.

The measurements were treated with the S.P.S.S. system and T-tests, scattergrams and biplots of data were executed. To the new information, data on South American species available from the literature were added (mainly from Araújo 1976) and the compound data analysed.

Parameters used in comparisons are skull length, cervical length, tooth length and width and rib width. These parameters were chosen because data on these elements of the South American species are available from the work of Araújo (1976).

T-test results (see Table 2).

(1) T-test results of a comparison between M. tenuidens and M. brasiliensis are given in Table 2. Significant differences between the two species were found in the length of the skull ($P \leq 0.0001$) length of the neck ($P \leq 0.05$) and length of the teeth ($P \leq 0.05$). No statistical difference could however be illustrated in rib and tooth width (diameter) between the two species.

(2) T-test results of a comparison between M. tenuidens and Stereosternum tumidum are given in Table 3. From this it is clear that significant differences exist between these two

forms in only two of the elements tested, skull and cervical lengths ($P \leq 0.05$). My results confirm those of Araújo (1976) who found significant differences in skull lengths ($P \leq 0.05$) between M. brasiliensis and S. tumidum; and S. tumidum and Braziliosaurus sanpauloensis.

If the mean skull length of M. tenuidens (52.108 mm, $n = 12$; table 2), S. tumidum (59 mm, $n = 14$; tabel 3) and M. brasiliensis (75.94 mm, $n = 17$) is considered it would seem to be unwise to discard the possibility that we are dealing with a growth series. The different presacral count of S. tumidum naturally excludes this from such a growth series but it is still a possibility for the two species of Mesosaurus. The apparent difference in size (as shown by the T-test results) could however also result from factors such as sample bias. Smaller individuals will tend to be represented at a higher ratio than larger individuals for they will tend to be less fragmented by weathering after exposure. It is well known that blocks or slabs of shale, large enough to contain a fairly large individual rarely remain unfragmented. This is especially true of the southern African Whitehill material. Another factor that might have played a role is food availability in different parts of the basins. In this respect the higher carbon content of the Iraty shales reflect a higher amount of detritus and possibly a better food staple. This could eventually have resulted in producing a stock of relatively large consumers.

In the biplot, skull/cervical lengths (Fig. 79) the clustering of data for the two species of Mesosaurus does not refute the possibility that they form part of an allometric growth series, with M. tenuidens the smaller and M. brasiliensis the

larger individuals (see Fig. 79). This impression is strengthened if the biplots of e.g. Humerus/Radius length (Fig. 80) is considered where the plots for all four species form an almost straight line. In order to clear up this point further statistical treatment of the data to test for allometric growth was carried out.

Statistical analysis for allometric growth

Allometric growth or the study of relative growth was characterised by Gould (1966) as the analysis of size and its consequences. Such growth can be assessed and described quantitatively and a statistical test to this effect was developed by Tollman, Grine and Hahn (1980). The data compiled in this study was treated with the computer program developed by these authors (for a full description of the methodology and mathematical basis of the program see Tollman, Grine and Hahn 1980). The main basic steps only will be reiterated here for the sake of clarifying the data given in the accompanying tables (Tables 4, 5, 6, 7).

Growth can be assessed and described quantitatively when measurements are fitted to the biparametric power function $Y = ax^{\beta}$, where y = a variable whose increase relative to that of another parameter, x , is considered; a is a numerical constant and β is the slope of the rectilinear plot. By converting the equation to a logarithmic form the problem is reduced to the fitting of a straight line.

$$\log y = \log a + \beta \log x$$

$$\text{or } Y = \alpha + \beta x.$$

Where $Y = \log y$; $x = \log x$ and $\alpha = \log a$. The slope of the

best straight line is given by β (the allometric coefficient) which can be given as the value of y when $x = 0$. Thus values of $\beta > 0$ indicate positive allometry which implies a differential increase of Y relative to X with an increase in the absolute magnitude of X . Isometry is indicated by $\beta = 1$ and represents the maintenance of geometrical similarity with increase in size. $\beta < 1$ implies negative allometry.

In determining the slope of the best straight line through the data the process utilised was that of Bartlett's (1949) best fit which was preferred and used by the majority of workers in this field (Tollman et al 1980).

Two parameters, cranial and cervical lengths (variable one and three respectively) were utilised as comparative (x) measurements in the present study. These were selected because Araújo (1976) has shown that these are the discriminatory features between the South American species. Bivariate quantitative assessments for the four species involved and combinations of species e.g. M.tenuidens and M.brasiliensis were made. Results of these tests are shown in tables 4, 5, 6, 7.

Interpretation of the allometric data

Linearity was rejected in every case which indicates that we are not dealing with different size fractions of an allometric growth series but with different species in which different allometric ratios were operative. It is of special interest to note that the two species of Mesosaurus on the strength of these results should be regarded as different.

In most cases the individual elements show a positive allometric growth in relation to skull and / or cervical length,

thus a positive β (slope) for the line of best fit is obtained (positive β in tables 4,5, 6, 7). If these elements are plotted against the X variable a configuration as e.g. in Fig 81, humerus / skull length is obtained. Some elements (e.g. metacarpals and phalanges of the foreleg, elements 14 - 22 and Fig. 82) however show a negative β . This implies that these elements, in contrast to those with a positive slope, grow slower than the X parameter (skull or neck in this case). Hatchling mesosaurs thus had relatively long lower forelegs and large forefeet which enlarged at a slower rate than the rest of the body throughout life. Large (old) individuals therefore had relatively small lower forelimbs and feet and the distance between the girdles were relatively short.

Conclusions

(1) Both T-test and allometric growth methods indicate that, on available data, the conclusion can be drawn that M.tenuidens and M.brasiliensis are two separate species. Allometric results confirm the results of Araújo (1976) that M.brasiliensis, Stereosternum tumidum and Braziliosaurus sanpauloensis are valid species.

(2) The observations of Araújo (1976) who indicated that cervical and skull lengths are the discriminatory factors are confirmed by the present study. These factors are also shown to be important differences between the two species of Mesosaurus from the two continents. M.tenuidens is shown to have relatively shorter skulls than M.brasiliensis as is illustrated by the biplot of Cervical / Skull length (Fig. 79). If

this biplot is compared with the plot of e.g. the humerus / ulna (Fig. 80) it is evident that very little variance exists between species in the latter elements. as all plots cluster along a straight line.

(3) If the biplot of the Femur / Metatarsal-total-length is considered (Fig. 84) it is evident that the ratio of these elements differs in M. tenuidens and the specimen Broom (1913) referred to Noteosaurus africanus. The matatarsal elements and phalanges of the hind limb of Noteosaurus are relatively shorter than that of Mesosaurus. This shortness of the phalanges and metatarsals was partly compensated for by the addition of a sixth element in the fifth toe of Noteosaurus.

The low correlation coefficient obtained is probably caused by two factors. It might be regarded as an indication that some of the specimens included in this study and treated as M. tenuidens in fact belong to other genera or species (e.g. the Maritzdam specimen with a presacral count equal to that of Stereosternum and Braziliosaurus, as well as Noteosaurus). A second factor might be the difficulty of accurately measuring often disjointed and badly crushed elements e.g. necks and skulls. The master list of the data used in the statistical analysis is available in computer printout format, upon request.

SUMMARY AND CONCLUSIONS

The dual goal of the present work comprises a study of the mesosaurid-bearing shales to gather information on the palaeo-environment and contemporary fauna of the Whitehill waters as well as an attempt to unravel the cranial anatomy and taxonomy of this Permo-Carboniferous reptile. Mesosaurus is of particular interest and importance for it occurs both in southern Africa and South America in almost identical strata. To date most of the anatomical work on the genus has been done on the more abundant South American M. brasiliensis, the southern African form being relatively poorly known. No direct comparison of the two species has thus hitherto been possible.

PALAEOECOLOGY

The results of this study on the palaeoenvironment of the water body in which Mesosaurus occurred can be summed up as follows:

From an epicontinental sea arm that invaded along a N-S extending zone of (-) epeirogenesis between Africa and South America in early Permian times the Whitehill sea was formed as two separate embayments onto the southern African landmass. The sea arm may have been in the position of the suture along which Africa and South America separated during the breakup of Gondwanaland very much later. Remnants of the larger, more southern, embayment are at present preserved in three separate basins, the main Great Karoo Basin, the Karasburg Karoo Basin and the Kalahari Karoo Basin. The smaller northern embayment, the Huab Karoo Basin was se-

parated from the southern Basins by the Windhoek Highlands. The presence of identical biozonations in the Worcester outlier prove that the Basin extended much further south and that the Whitehill Formation predates the Cape Orogeny. The Orogeny however probably followed soon after the deposition of the Formation.

The Whitehill embayments are visualised as relatively shallow (calculated depth < 150 m), sediment starved, euxinic marine water bodies surrounded by low lying marshland. The water of the Whitehill sea was stratified with evaporitic minerals precipitating in small amounts from highly sulphuretted, toxic, bottom brines. The poor quality of the bottom waters prevented the establishment of a bottom fauna and this accounts for the impoverished fauna of the sea, consisting of but two vertebrates, two crustaceans, a possible cephalochordate and a few other problematic forms. All these forms were pelagic and flourished in the relatively fresh oxygenated top water layers. Surplus organic material from primary producers of the food chain in the top water layers was decayed in the bottom layers by anoxic bacteria resulting in the formation of sulphuretted black muds. From the low lying adjacent land very little material was shed into the basins and the bulk of the sediments is probably of aeolian origin. The most striking single impression gained is that the sediments were deposited in an almost energyless environment as no indications of vectorial sediment distributing agents are preserved in the monotonously homogeneous, thinly layered sediments. Low amplitude oscillation ripples and the orientation of fossils however registered an oscillatory movement of a tidal nature in the

bottom waters over vast tracts of the basins.

The anoxic conditions were upset only once for a short period which resulted in the development of a green silty shale member in the middle of the Formation. It was only during this period that benthonic and fossorial organisms colonised the Whitehill sea floor leaving evidence of their presence in the form of a variety of trace fossils and feeding trails. These ichnofossils are described and figured.

Systematic collection of fossils on a Basin wide basis led to the recognition of Mesosaurus, fish, Notocaris and ichnofossil range zones. (The lower half of the Formation, with the exception of a yet undescribed crustacean in the black dolomitic layers, proved to be unfossiliferous). The consistency of the biozones has conclusively shown that the Formation is a chronostratigraphic unit and any of the zones may be used in correlations (time-stratigraphic) between the different basins. The implementation of the biozones in the course of this study has already proved to be of practical value as a local, post-Whitehill-pre-Tierberg shale, erosion cycle could be recognised in the area north of Hopetown by the absence of the topmost biozones in some outcrops.

The biostratigraphy, lithology and fossil faunas of the South American Iraty and the southern African Whitehill Formations show an almost unbelievable similarity. This similarity results from the fact that the two Formations were deposited in contemporary embayments of a central sea arm on landmasses which had an identical immediate prehistory of glaciation. The fact that these two Formations are almost mirror images of each other can be explained only in this way.

ANATOMY AND TAXONOMY

In the study of the cranial anatomy of Mesosaurus tenuidens it was conclusively proved that the temporal area is completely roofed over. The mesosaurids may thus prove to be anapsid, in spite of Von Huene's (1941) interpretation of M. brasiliensis as synapsid, and their current uncertain systematic position in an order (Proganosauria) of their own (often tentatively regarded as allied to Euryapsida) may be clarified. A better understanding also, of the individual elements of the skull was possible and a new interpretation of the morphology of the palate could be made. Elements like the supratemporals, tabulars and ectopterygoids allegedly not present in M. brasiliensis are demonstrated in M. tenuidens.

The elements of the mesosaurid palatoquadrate and braincase and their inter-relationships are described for the first time.

In cranial morphology and also in features of the post cranial skeleton Mesosaurus resembles the cotylosaurs with its closest relative undoubtedly being the primitive form Limnoscelis.

Mesosaurus and Limnoscelis are both aquatic forms (Romer 1956) of contemporaneous age. Unique among reptiles both show remnants of labyrinthodontine tooth infolding. They also share a few unique and apparently non-adaptive cranial features e.g. the pterygoid meeting the maxilla behind the ectopterygoid and the slightly backward projecting basal processes.

The atlas complex is described for the first time in any mesosaurid. The presacral vertebral count for M. tenuidens was established at 29, with 12 cervicals and 17 dorsals which is

identical with the count for M. brasiliensis. Two free sacral vertebrae and at least 60 caudals are present. The first 11 caudals bears ribs and haemal arches are present from the 12th onwards up to the last few vertebra. Sutural lines are present between centra and intercentra of the middle series of caudals.

In the pectoral girdle of M. tenuidens a three pronged scapula-coracoid-precacoracoid plate is described in contrast to M. brasiliensis where a single coracoid ossification is allegedly present. A new interpretation and reconstruction of the pectoral girdle is thus attempted.

In the pelvic girdle the presence of a notch in the pubis rather than a foramen is confirmed.

Ten carpal elements are described in M. tenuidens of which five form a distal row, one opposite each toe. In the proximal row a radiale, ulnare and a large intermedium are present and two central elements are present between the elements of the proximal and distal rows. The phalangeal formula of 2, 3, 4, 4, 3 is identical to that of M. brasiliensis.

In the hind limb additional information on the morphology of the femur was gained. It was established that the two proximal elements of the tarsus is an elongated fibulare and a large element formed by the ankylosis of an intermedial and tibiale element. Between the five elements in the distal row and the elements of the proximal row a proximal central and a central element are present. The phalangeal formula for the pes of M. tenuidens is 2, 3, 4, 5, 5.

It was established that only one Mesosaurus species is present in southern Africa and that all other species named

(M.capensis, M.pleurogaster, Ditrochosaurus capensis) should be considered as junior synonyms of M.tenuidens Gervais (1864).

Morphological characters, matrix analyses and statistical tests however indicate that Noteosaurus africanus Broom (1913) is a valid species probably from somewhat younger strata.

In addition to the two abovementioned forms a few specimens with a presacral vertebral count identical to that of Stereosternum were recovered from the Whitehill Formation. A comparison of these specimens with Stereosternum material is essential to establish whether this South American form occurs also in South Africa.

If future research should prove M.brasiliensis (and other mesosaurid forms) also to be anapsid, the family Mesosauridae, i.e. all the members of the order Proganosauria will have to be transferred to the order Cotylosauria. If M.tenuidens is to be regarded as typical for the Mesosauridae, the family's closest relatives amongst the cotylosaurs would seem to be the Limnoscelidae. These two groups could quite feasibly be derived from a common ancestral Carboniferous cotylosaur.

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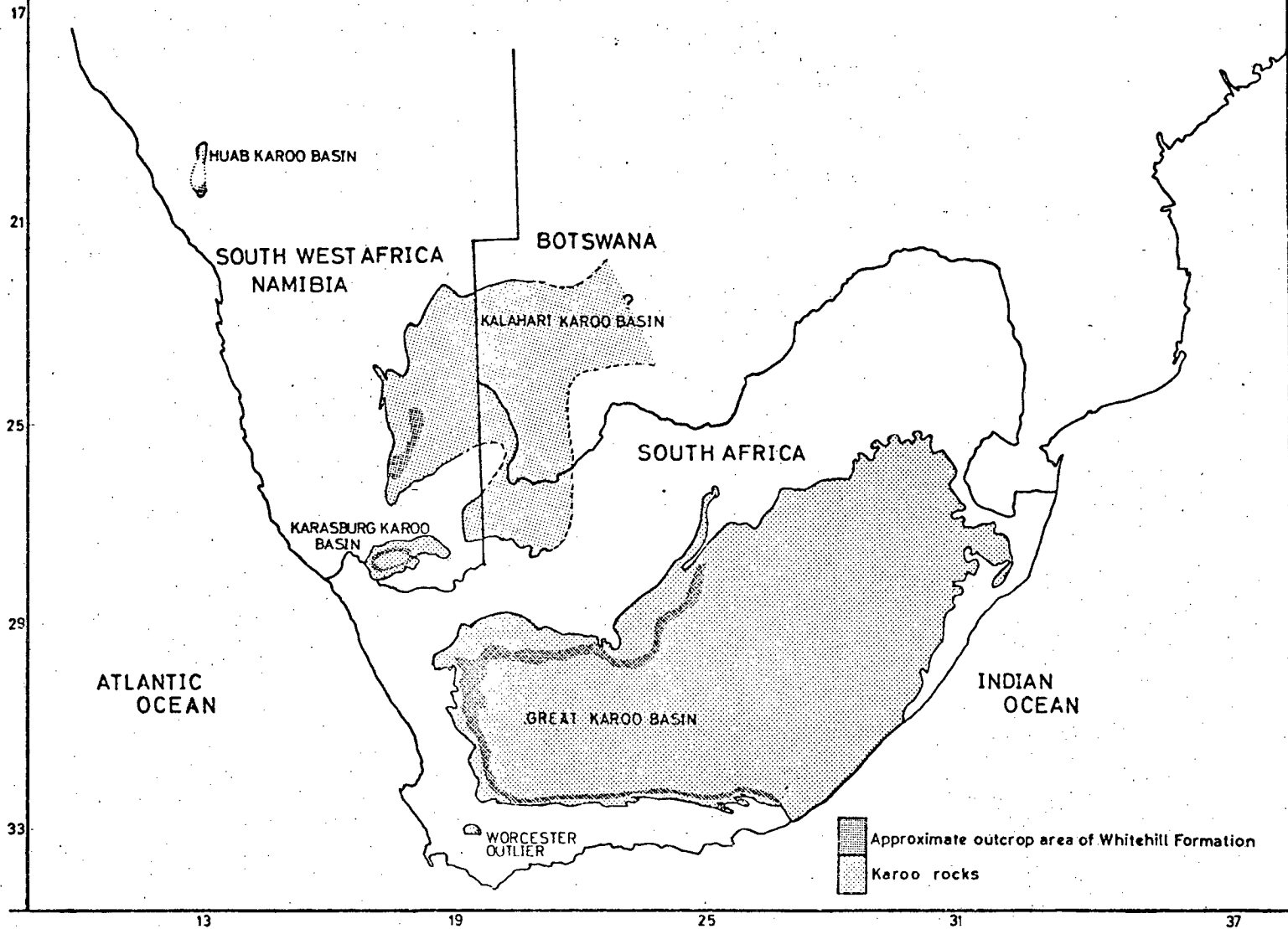
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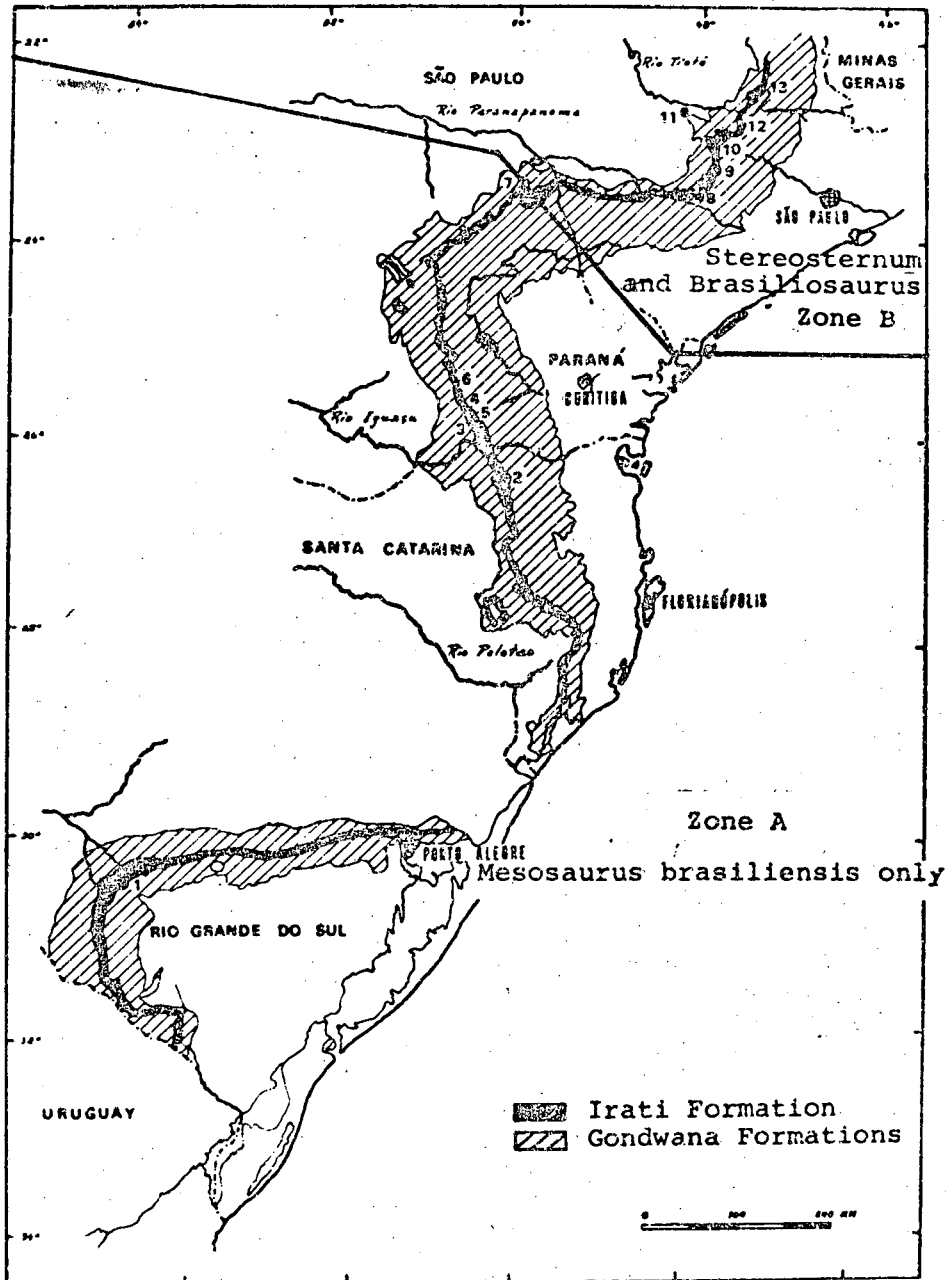
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Fig. 1A Distribution of Whitehill outcrops in the major basins in southern Africa





Geological map of the Gondwana Formation of the Paraná Basin with the localities where fossils of mesosauria were collected.

- 1 Passo de Sao Borja 2 Papandura 3 São Mateus
 - 4 Eng. Guttierres 5 Estiva 6 Irati 7 Gaupiraina
 - 8 Ilapetininga 9 Tietê 10 Laranjal Paulista
 - 11 Piracicaba 12 Rio das Pedras 13 Rio Claro
- (After Arujo 1976)

Figure 1B

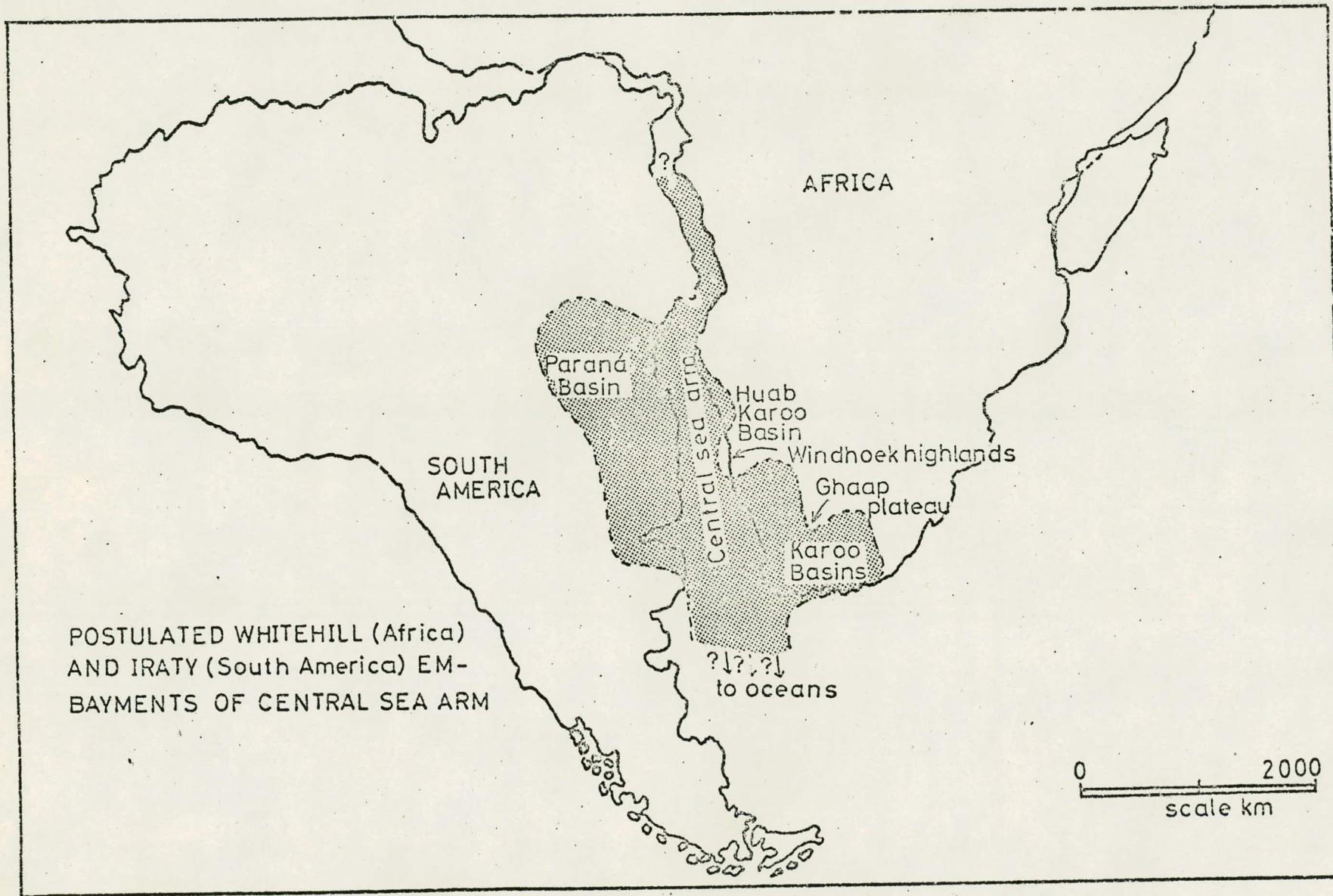


Figure 1C

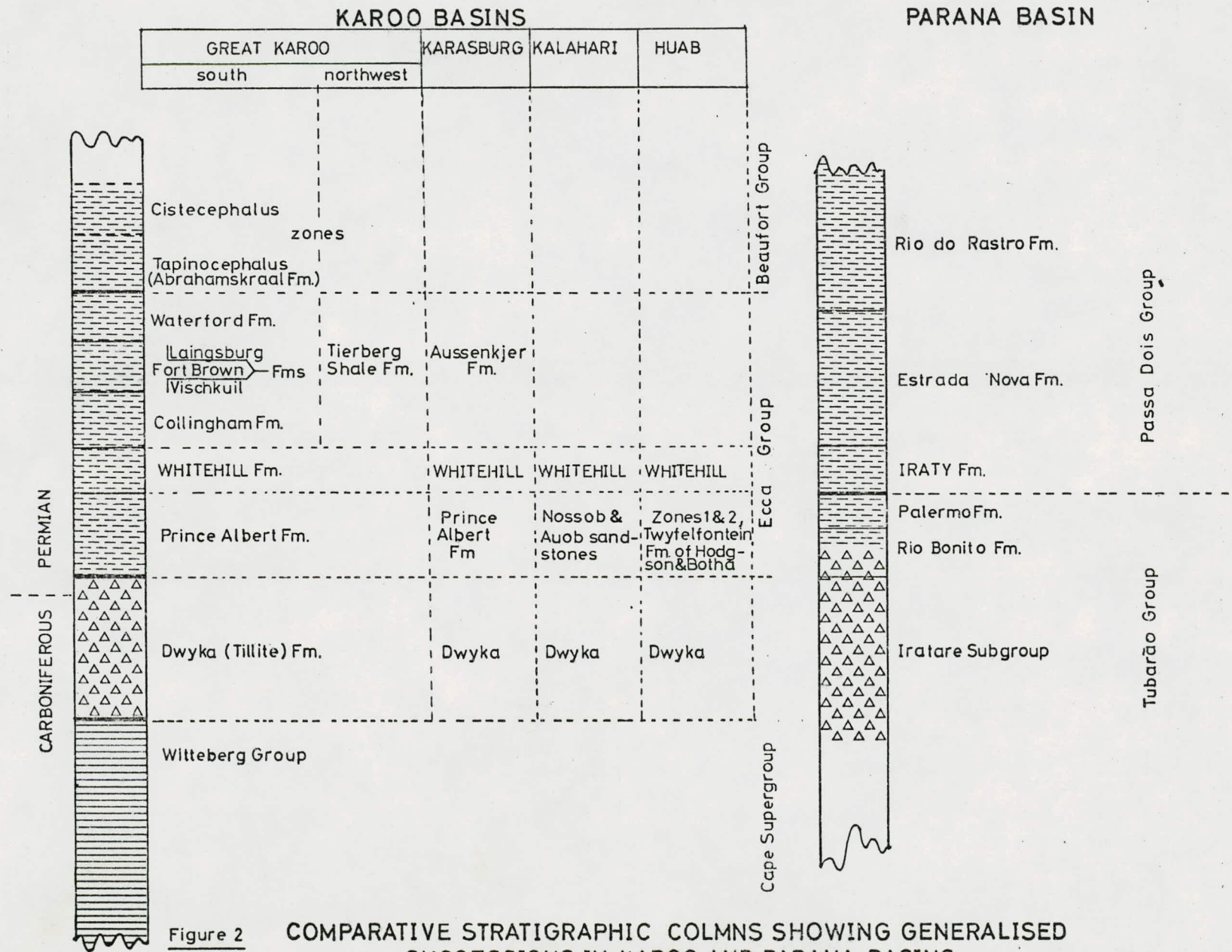


Figure 2

COMPARATIVE STRATIGRAPHIC COLUMNS SHOWING GENERALISED SUCCESSIONS IN KAROO AND PARANA BASINS.



Figure 3A: Whitehill Formation in typical outcrop near Loeriesfontein, Great Karoo Basin. Note dark dolerite sill in middle of Formation.



Figure 3B: Whitehill Formation in Kalahari Karoo Basin on the Gellap plateau. Car parked on contact of Whitehill Formation and Green siltstone with worm tracks, see Fig. 36.

Figure 4 The distribution of Mesosaurus in the Whitehill out-crops.

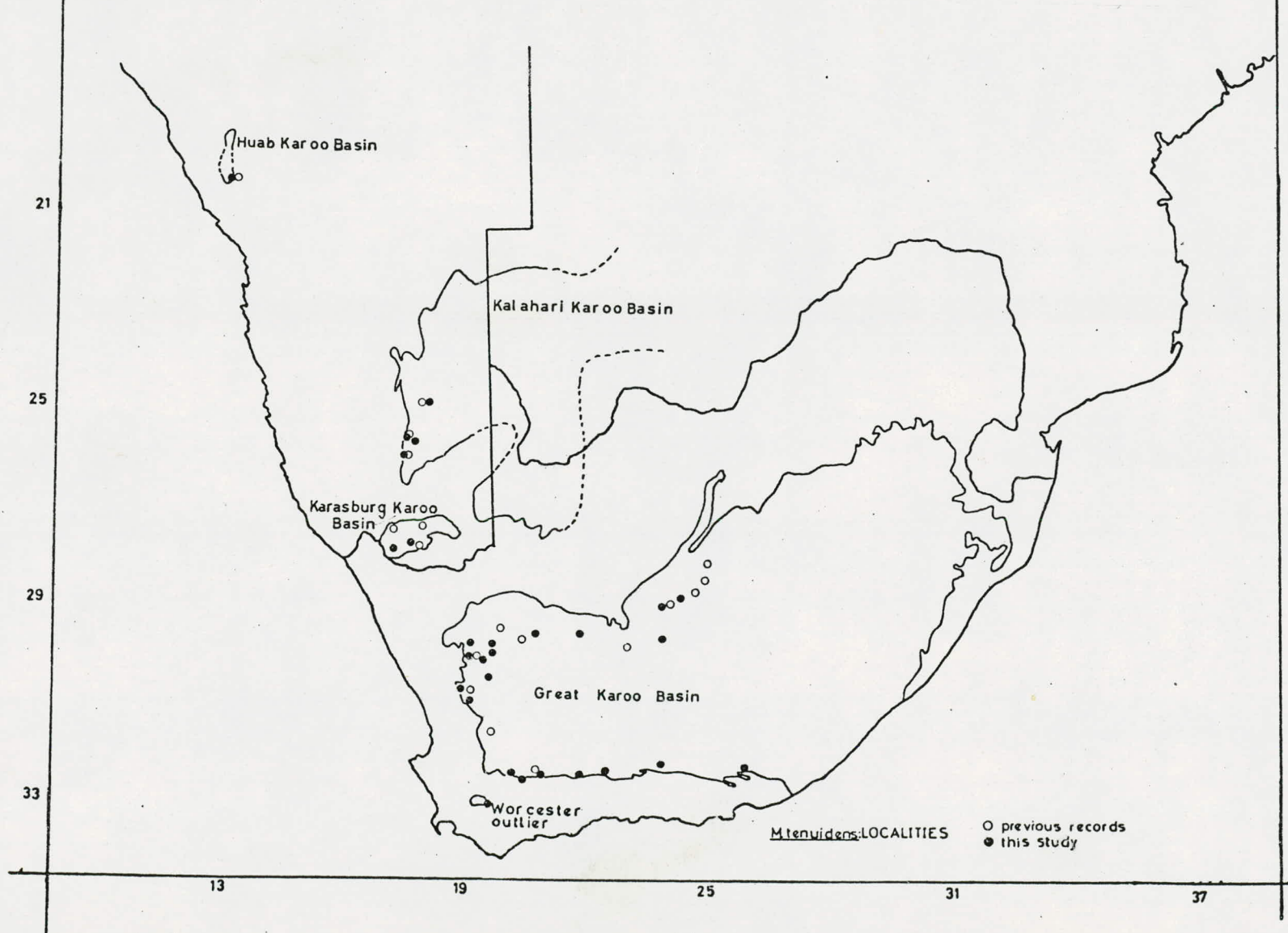


Figure 5 The distribution of insect wings in the Whitehill outcrops.

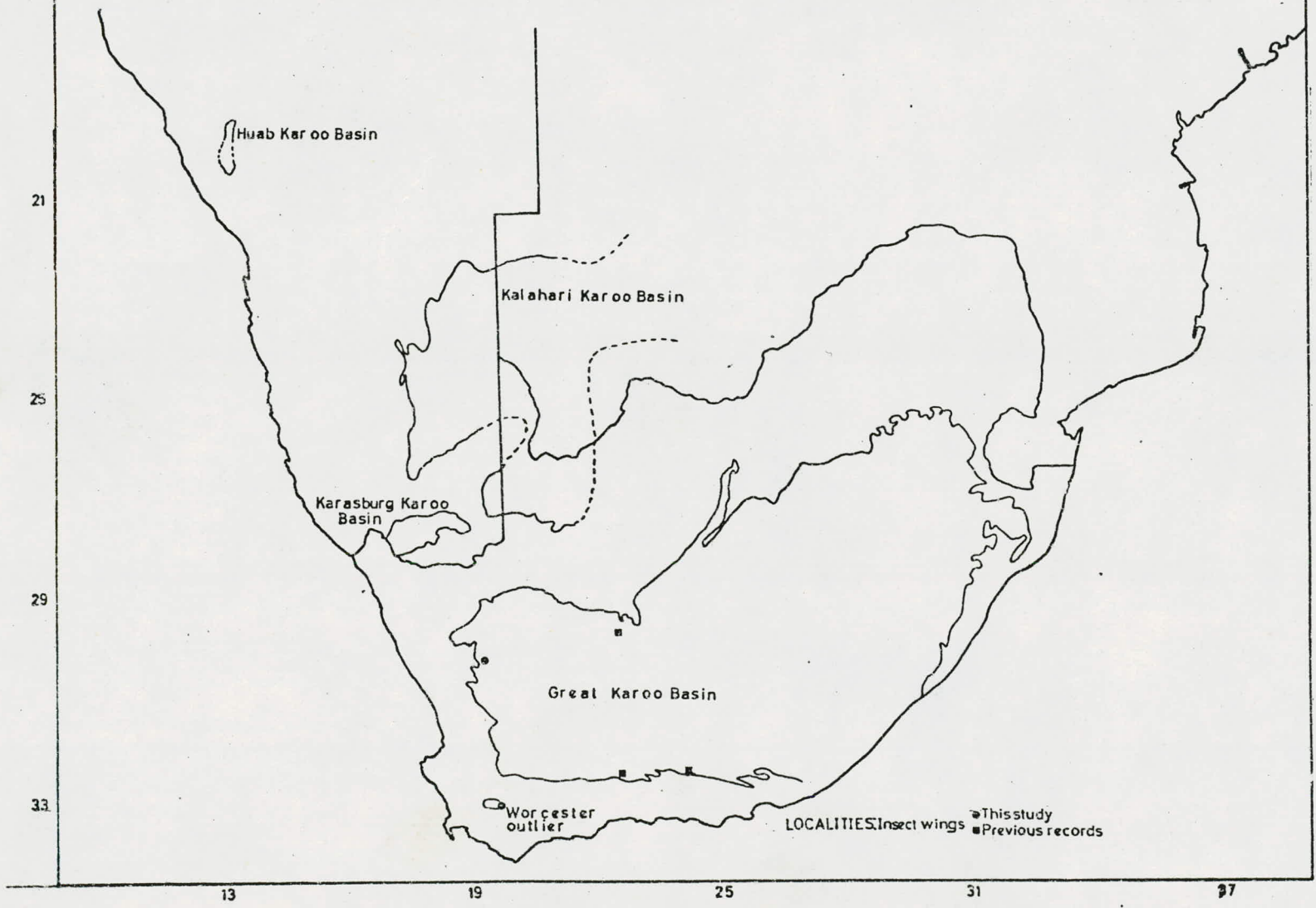
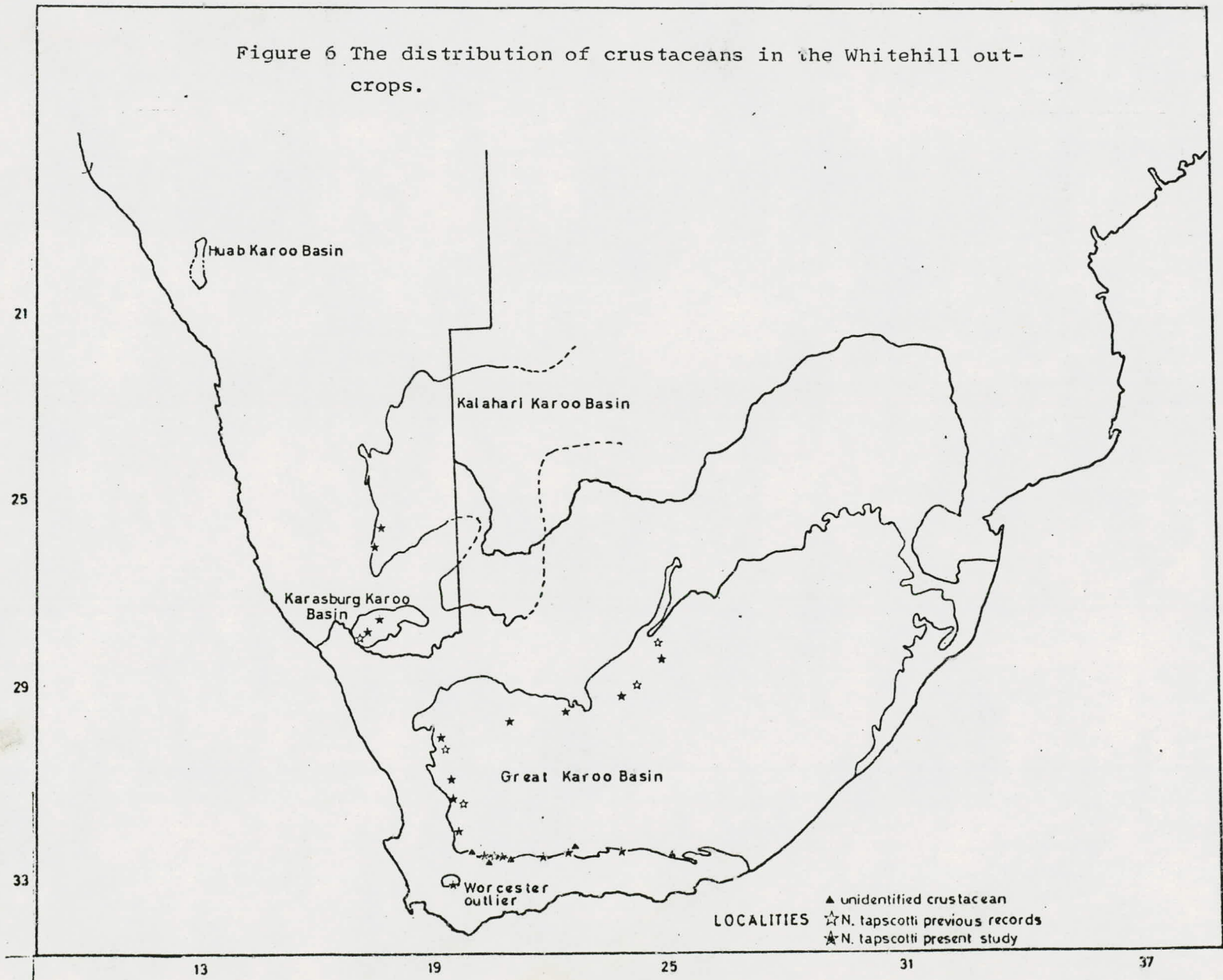


Figure 6 The distribution of crustaceans in the Whitehill outcrops.



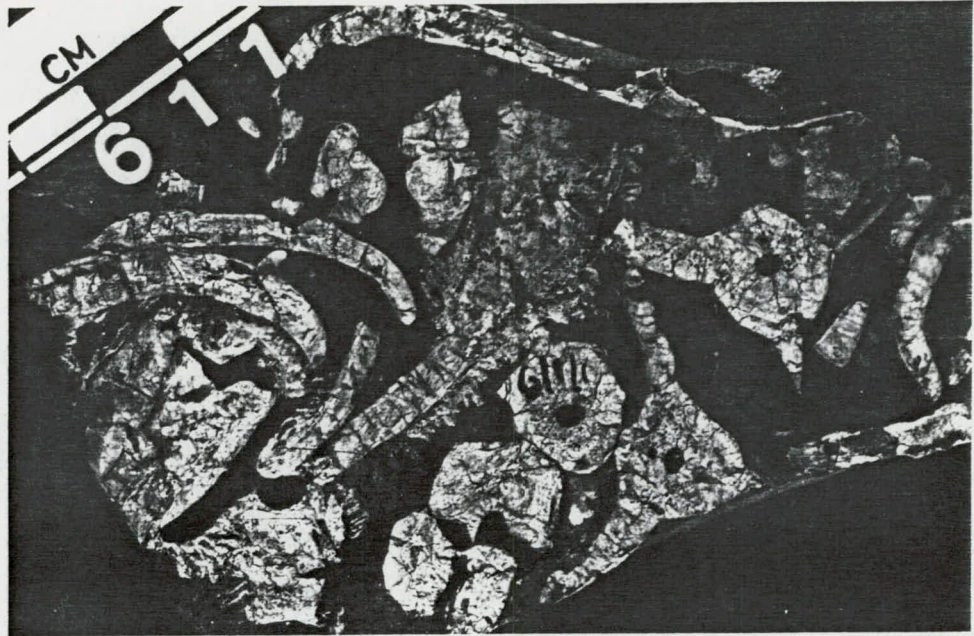


Figure 7: Rolled, disarticulated mesosaurid bones in limestone. Gross Daberas, Kalahari Karoo Basin.

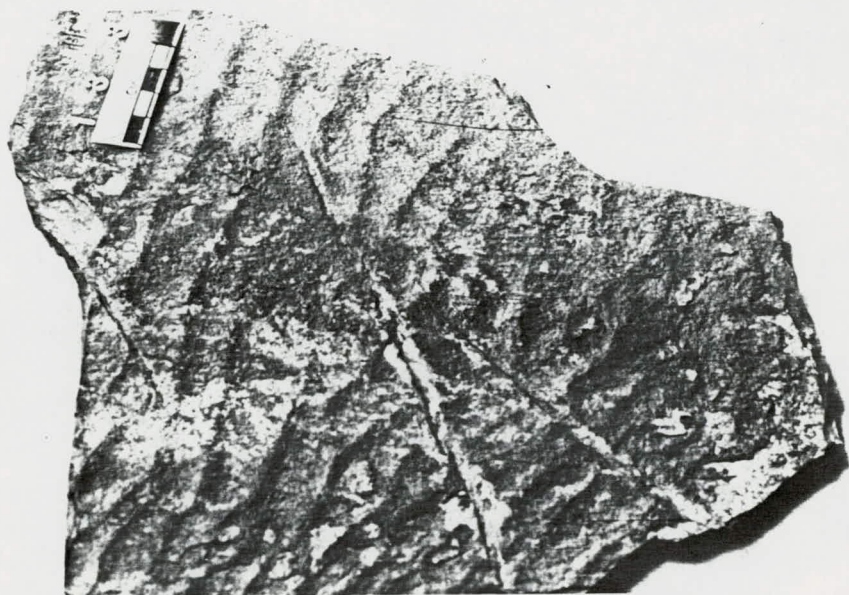


Figure 8: Low amplitude oscillation ripples from the intercalated sandy shale member of the Whitehill Formation, Loeriesfontein, Great Karoo Basin.

Figure 9 Rose diagrams to illustrate in situ orientation of mesosaurid fossils n = number of specimens measured.

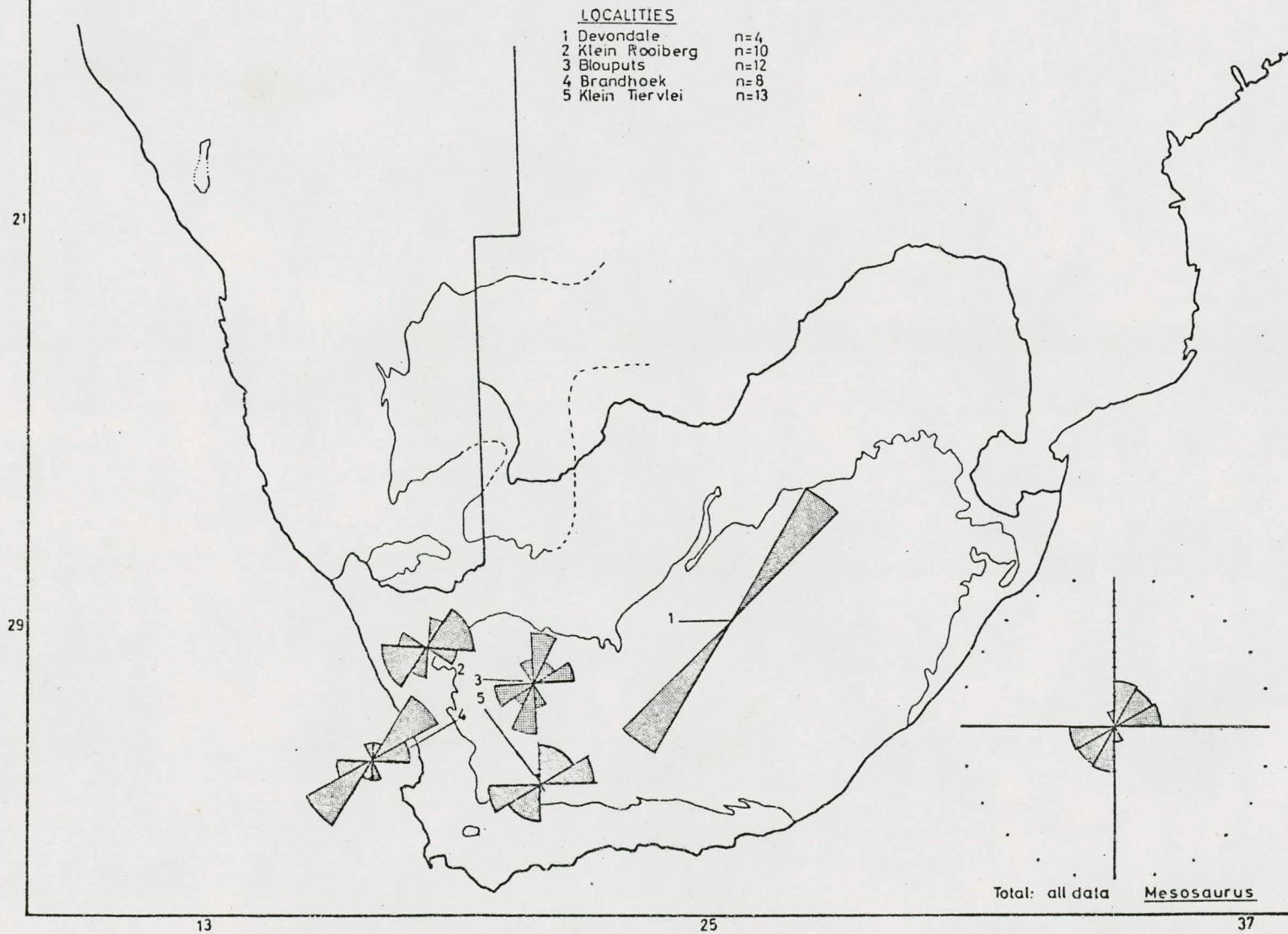
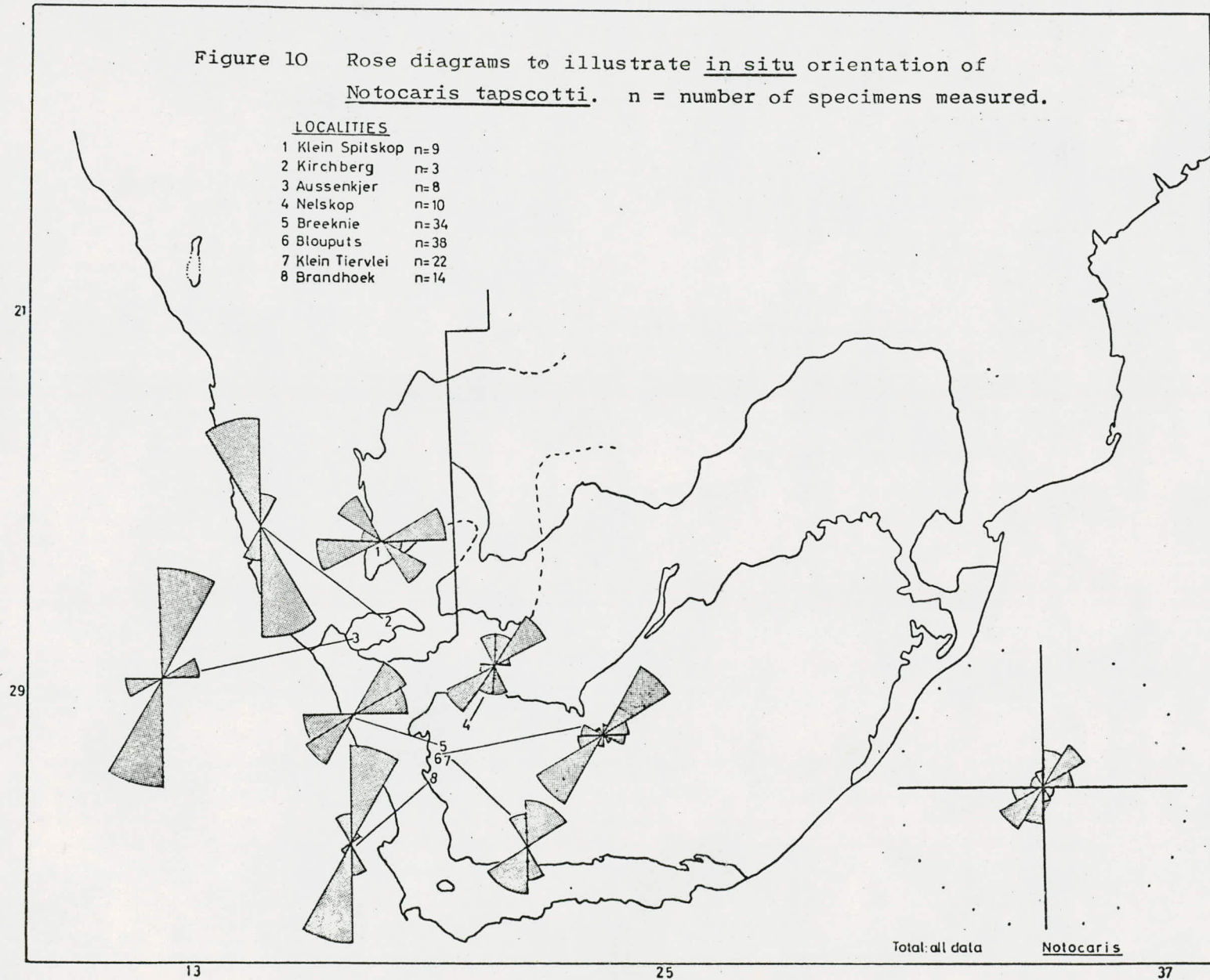


Figure 10 Rose diagrams to illustrate in situ orientation of Notocaris tapscottii. n = number of specimens measured.

LOCALITIES

- 1 Klein Spitskop n=9
- 2 Kirchberg n=3
- 3 Aussenkjer n=8
- 4 Nelskop n=10
- 5 Breeknie n=34
- 6 Blouputs n=38
- 7 Klein Tiervlei n=22
- 8 Brandhoek n=14



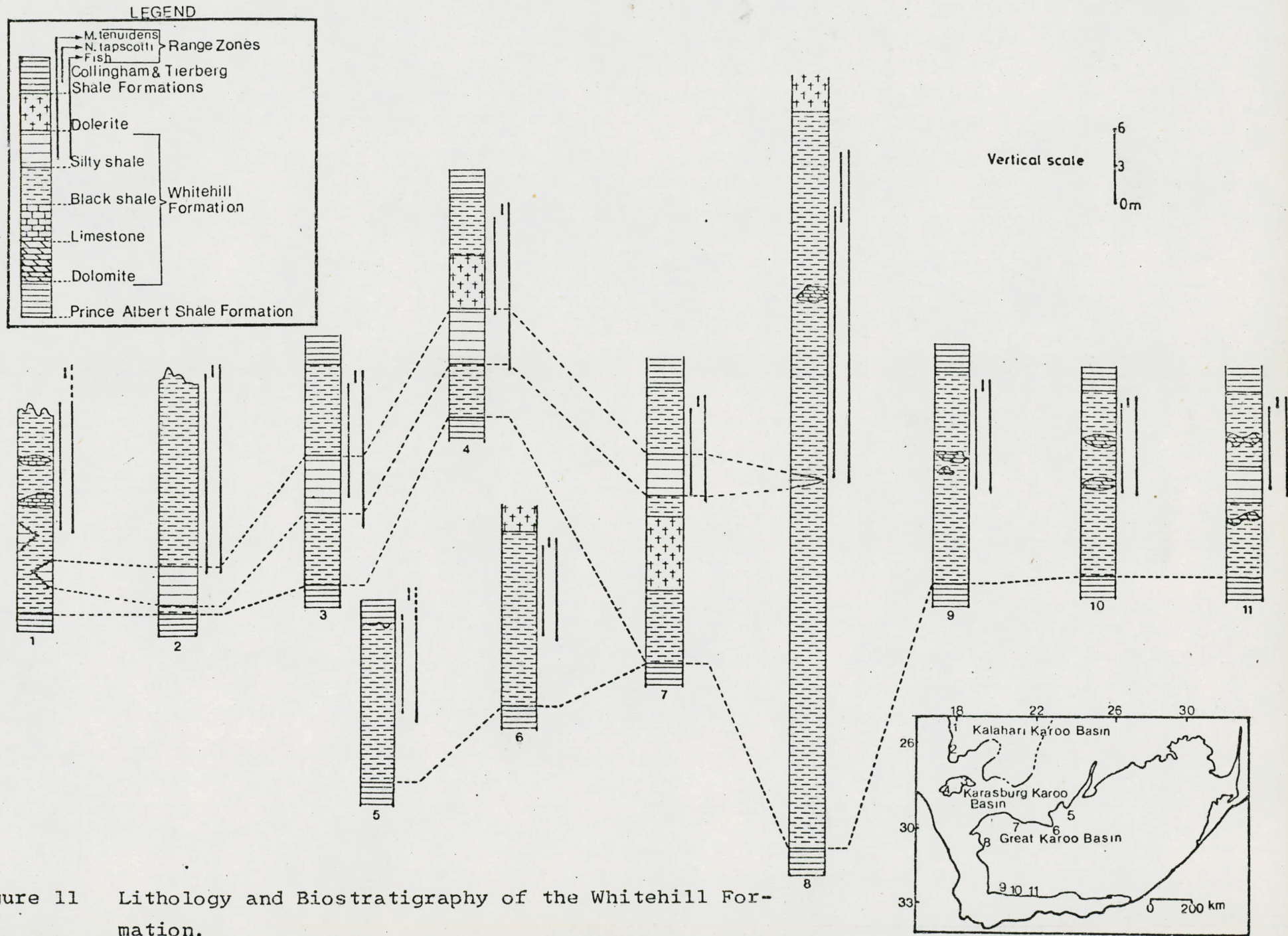


Figure 11 Lithology and Biostratigraphy of the Whitehill Formation.

Figure 12 Lithology and Biostratigraphy of the Iraty Formation:
Zone A & B refer to the map in figure 13.

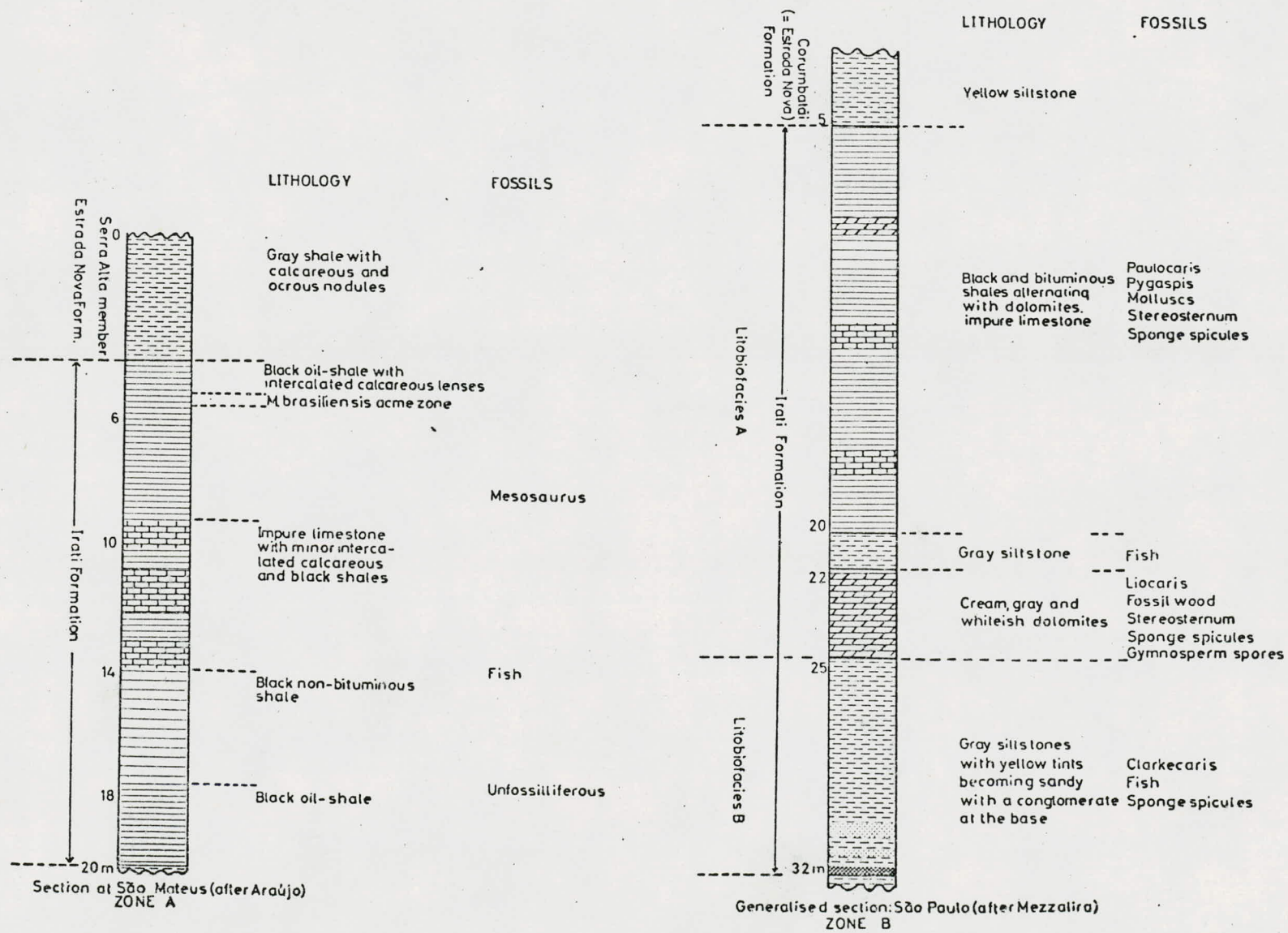


Figure 13 Distribution of fish in the basins of the Whitehill Formation.

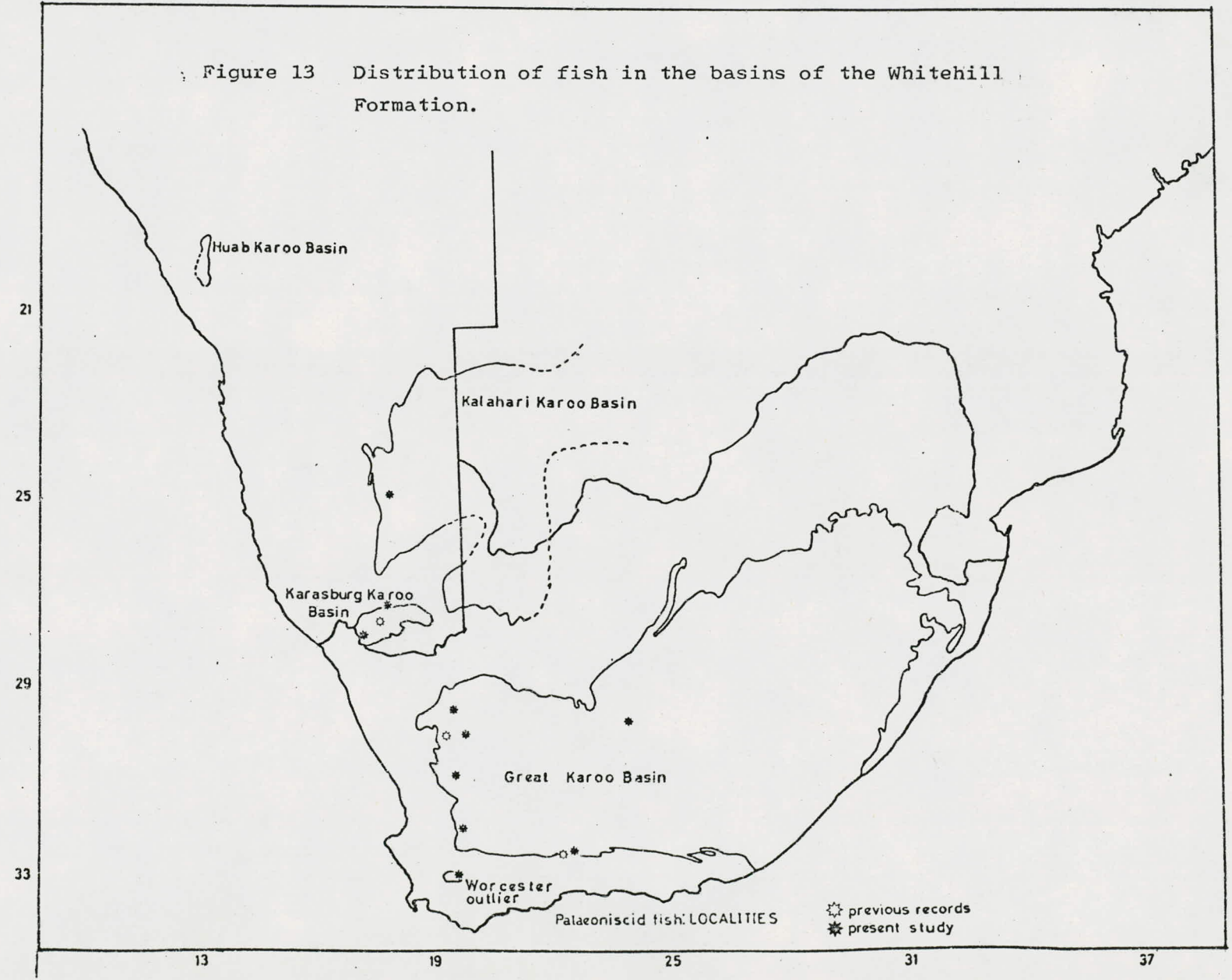




Figure 14A: Whitehill Formation outcrops at Doros crater, Huab Karoo Basin, Fossiliferous site marked with X.

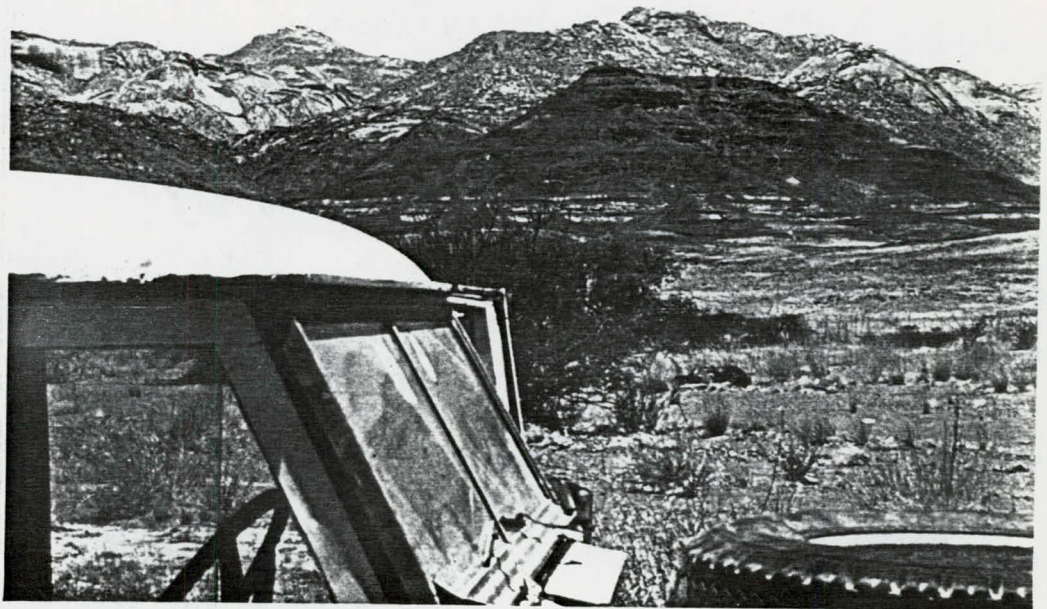


Figure 14B: Outcrops (horizontal layers in middleground) correlated with the Whitehill Formation; western flank of the Brandberg, Huab Karoo Basin.

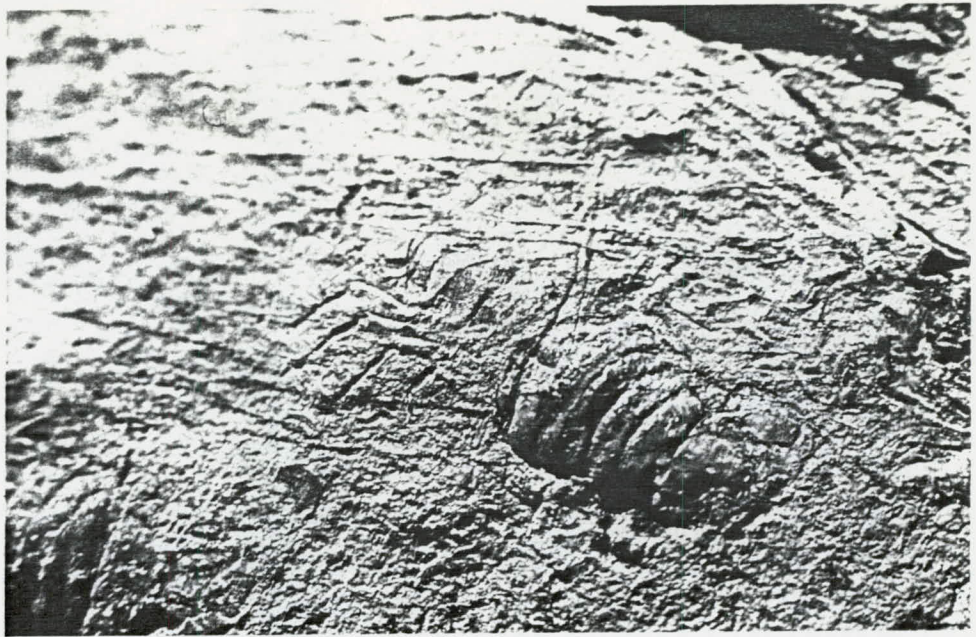


Figure 15: Unidentified crustacean from black dolomite layers, Great Karoo Basin. Specimen (length \pm 2.5 cm) in collection of R.D.F. Oosthuizen.

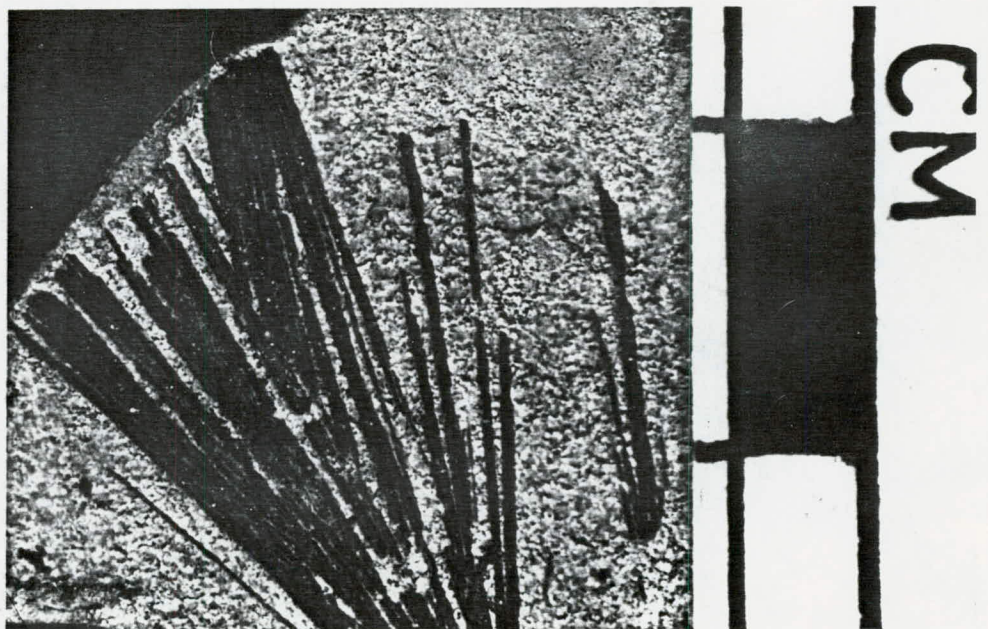


Figure 16: Problematic imprint; possibly of sponge spicules.

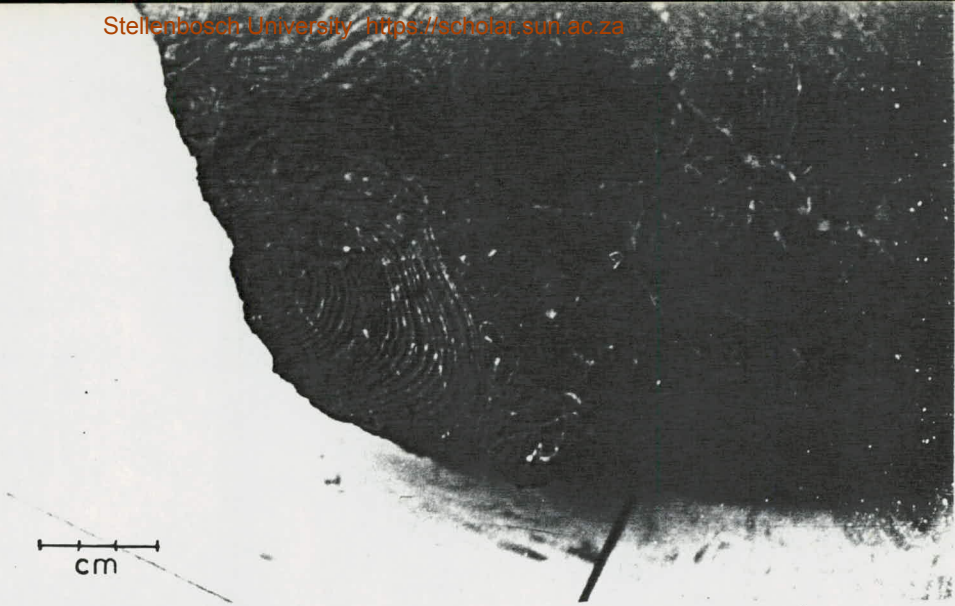


Figure 17A: Black stromatolite-like, slumped dolomite.



Figure 17B: Cream coloured dolomite lenses in Whitehill Formation; Driekoppen, Worcester.



Figure 17C: Black dolomite lense, Kalahari Karoo Basin (Hammer for scale).



Figure 18: Fish trail. Gannavloer, Great Karoo Basin.

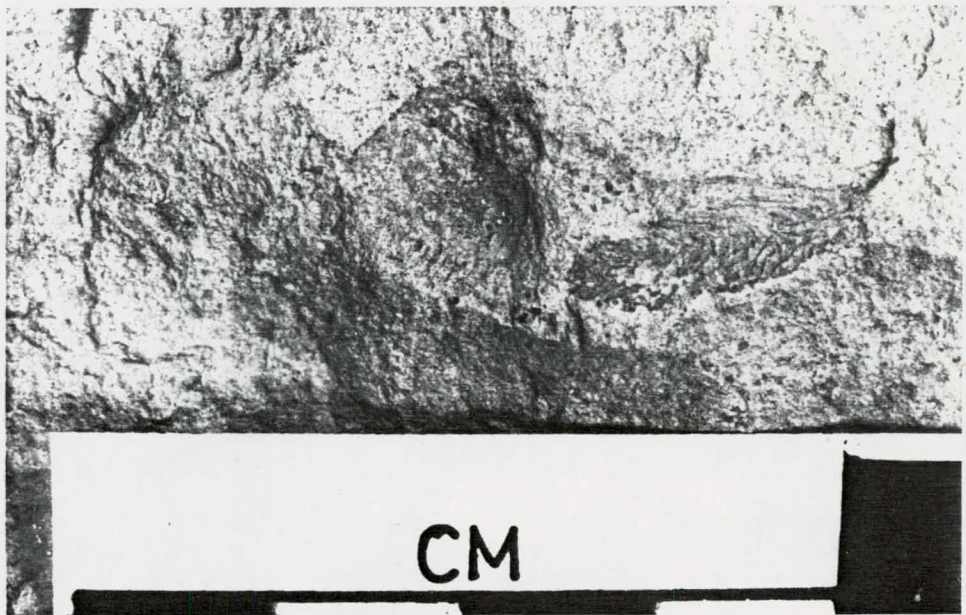


Figure 19: Bony plate of fish skull; Gross Daberas, Kalahari Karoo Basin.



Figure 20: Insect wing; Worcester outlier, Great Karoo Basin.

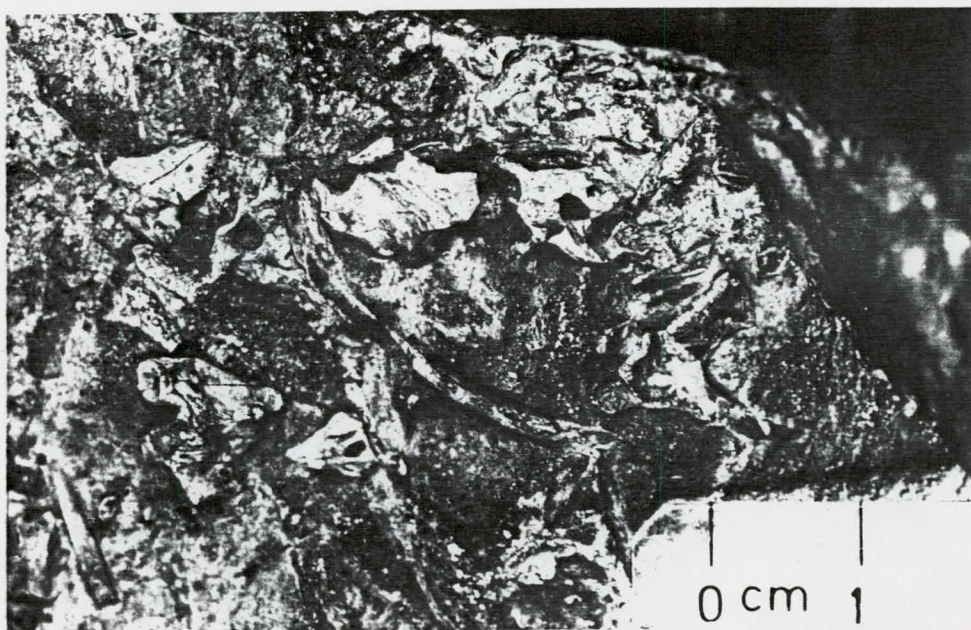


Figure 21: Vertebrae in limestone, Kalahari Karoo Basin.

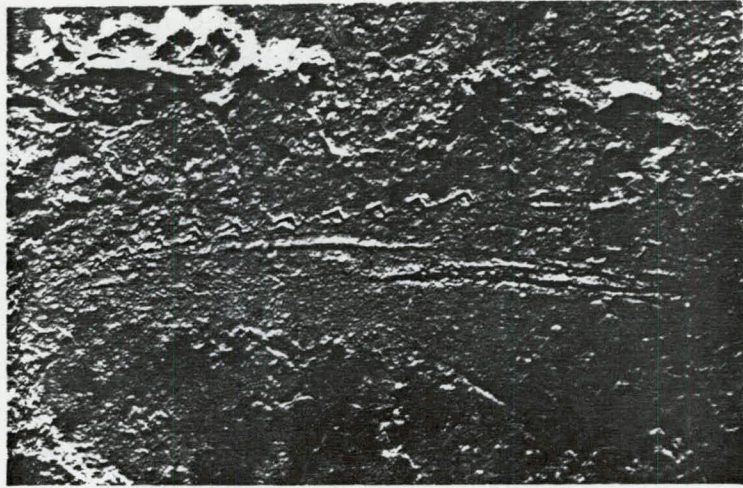


Figure 22: Fossil imprint of problematic cephalochordate-like organism

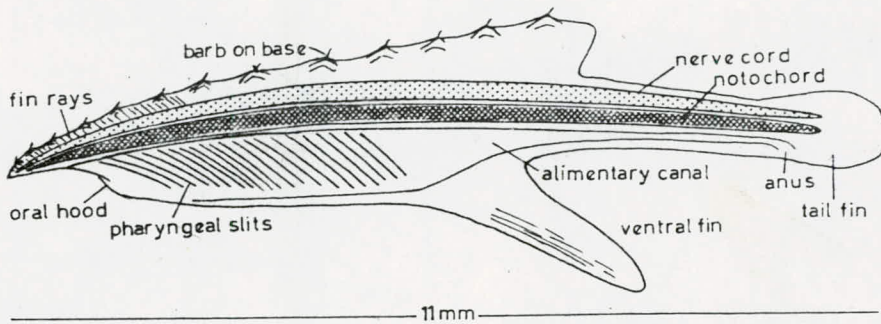


Figure 23: Diagrammatic interpretation of fossil imprint in figure 22.

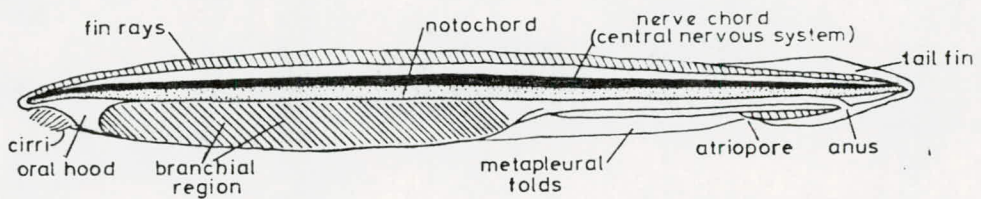


Figure 24: Schematic drawing of modern Cephalochordate (after Hildebrand).



Figure 25: Silicone rubber casts of echinoderm-like hollow spheroids; Loeriesfontein, Great Karoo Basin.



Figure 26: Brachiopod-like imprint; Devondale, Great Karoo Basin.



Figure 27: Arthropod trail; Kafferdam, Great Karoo Basin.

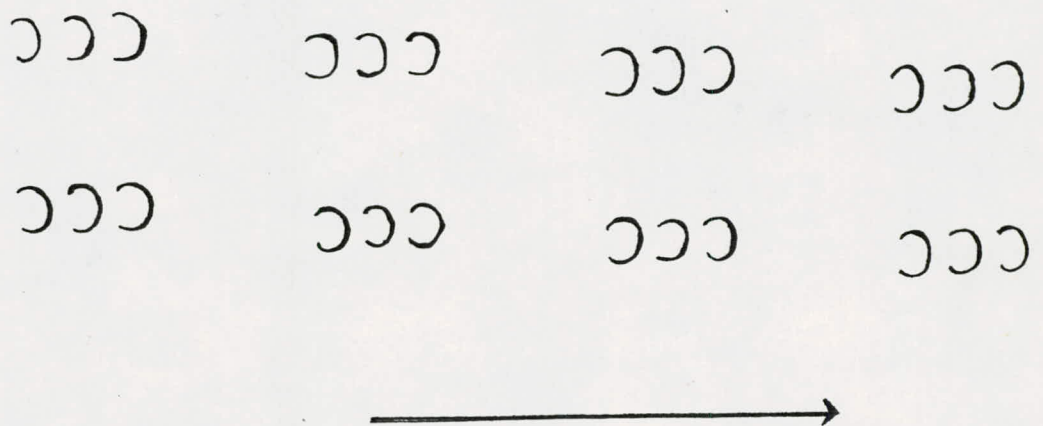


Figure 28: Arthropod trail; Kafferdam; shown in figure 27. Notice slight offset to right suggesting crab-like movement.



Figure 29: Umfolosia-type trail; Haib, Karasburg Karoo Basin.



Figure 30A: Body imprint of crustacean; Haib, Great Karoo Basin.

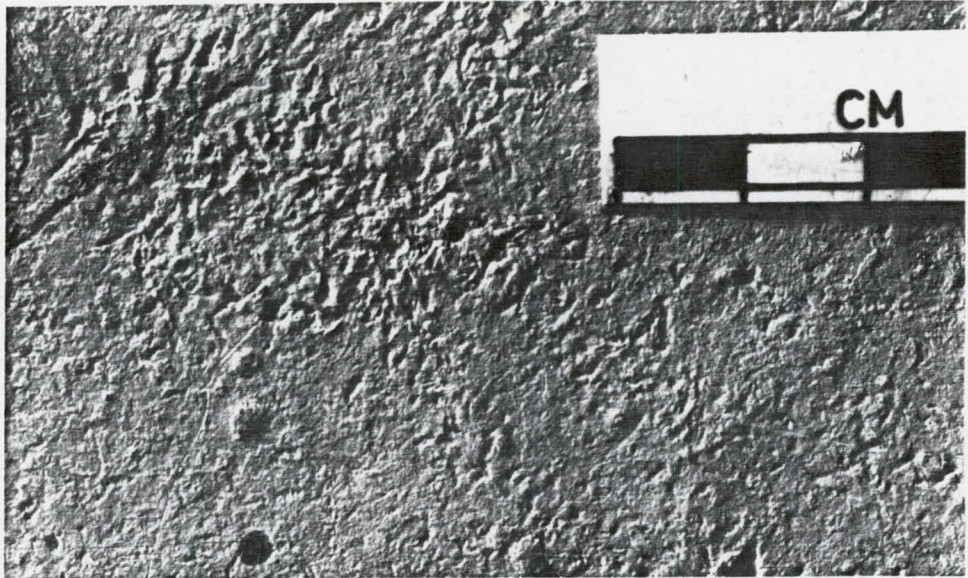


Figure 30B: Trail leading up to body imprint of crustacean; Haib, Karasburg Karoo Basin.



Figure 31: Small bilaterally simmetrical trail; Haib, Karasburg Karoo Basin.

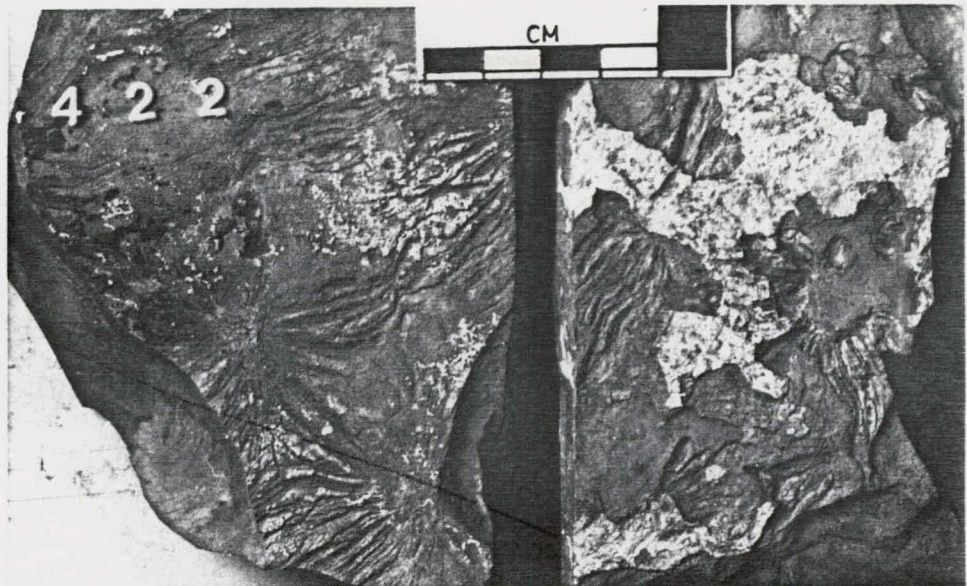


Figure 32: Star-like trace fossils; Great Karoo Basin.



Figure 33: Zoophycos from the intercalated siltstone member of the Whitehill Formation; Vlake onder Hangklip, Great Karoo Basin.



Figure 34: Type of Rosaichnus witbandicus; Kafferdam, Loeriesfontein.

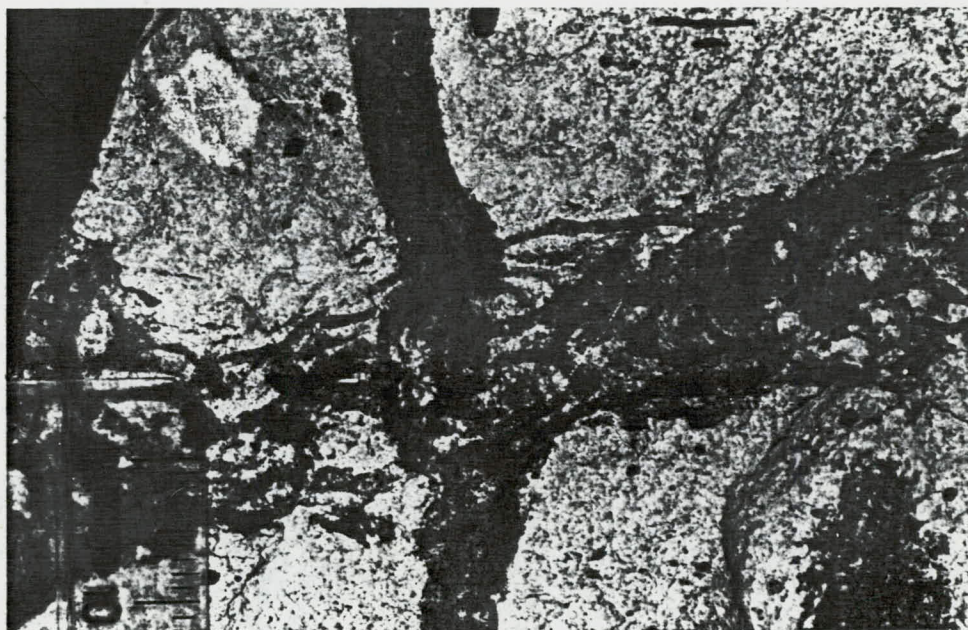


Figure 35: Scolicia-like worm trails, type A with small sub-trails, type B trail smaller without sub-trails. Notice rounded corners at intersection indicating sub-trails to be associated with both trail types.

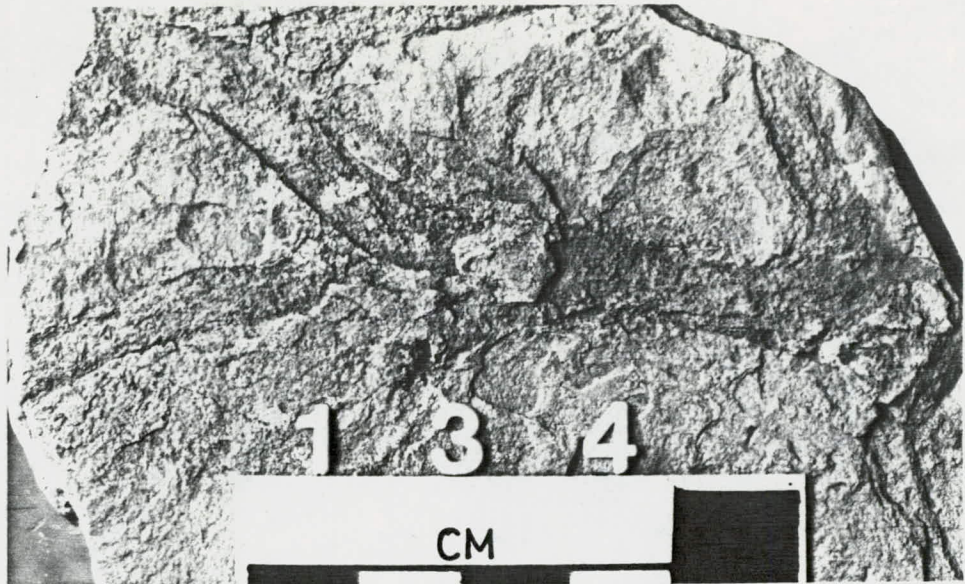


Figure 36A: Scolicia-like worm trails, type B from intercalated silty shale member, Great Karoo Basin.

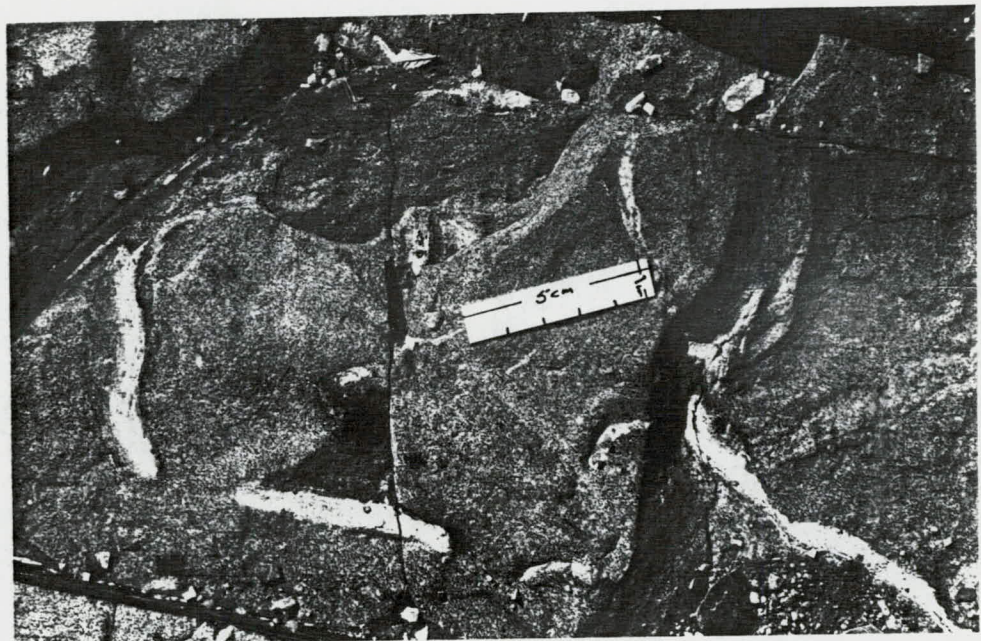


Figure 36B: Type B Scolicia-like wormtrails from mottled green shale below Whitehill Formation, Kalahari Karoo Basin.

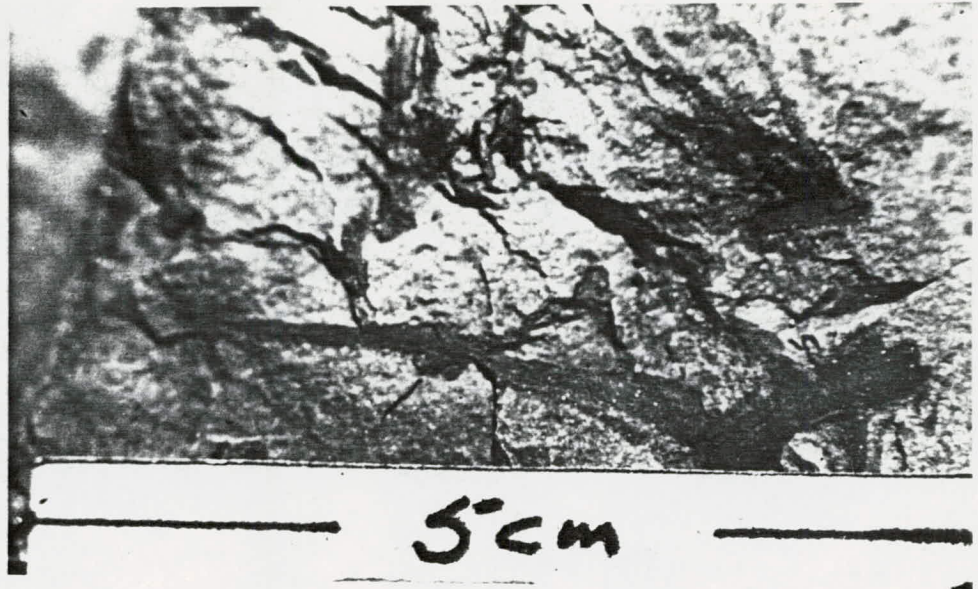


Figure 36C: Type B. Scolicia-like wormtrails from below the Whitehill Formation, Huab Karoo Basin, Brandberg area.



Figure 37: Bifungites-like trace from Lower Collingham Formation, Worcester Outlier.

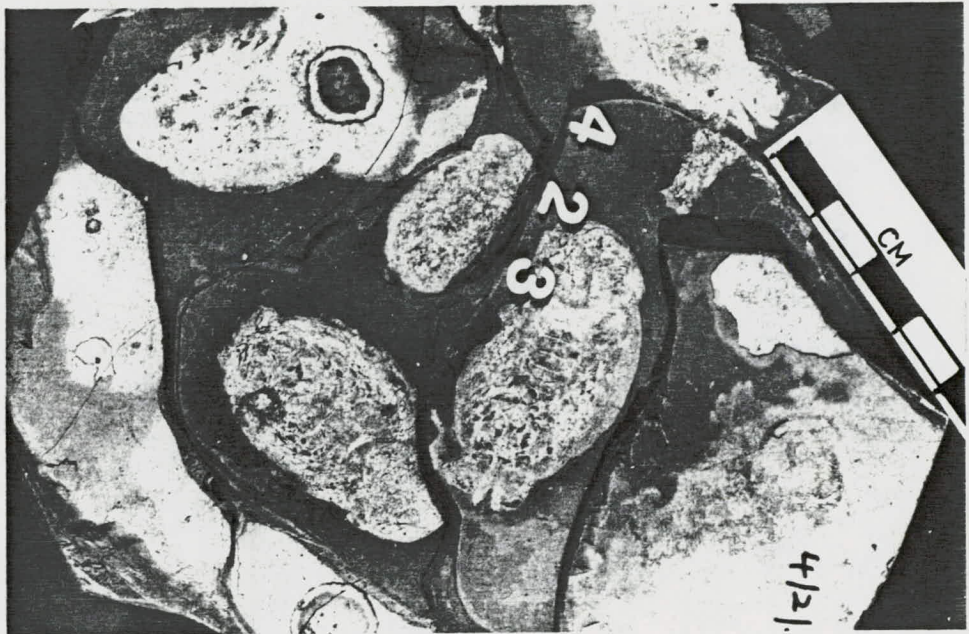


Figure 38: Imprints of Notocaris tapscotti; Brandhoek, Calvinia, Great Karoo Basin. Notice abundance of fossils in acme zone.

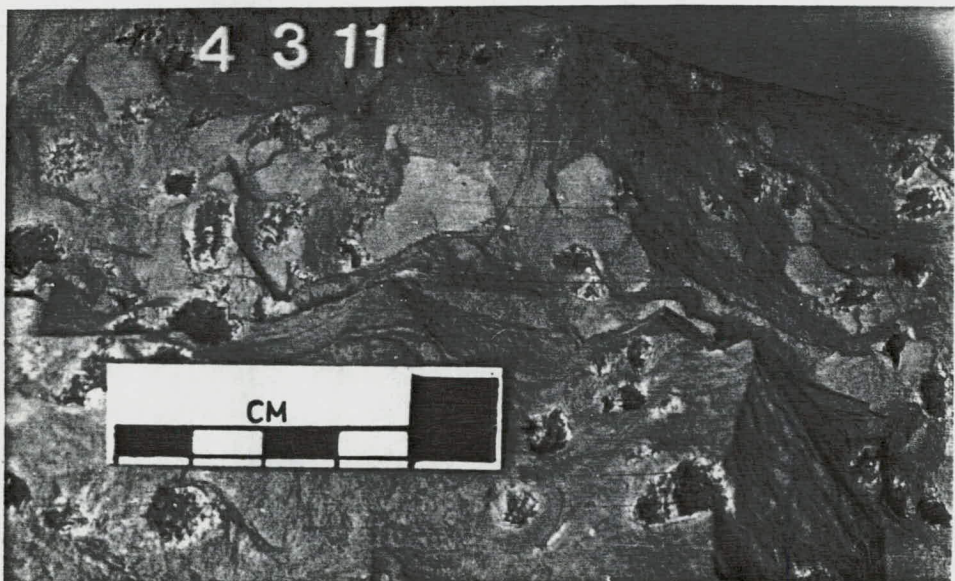


Figure 39: Impressions of small gypsum resettes, Whitehill Formation; Groote Brak, Tanqua Karoo, Great Karoo Basin.

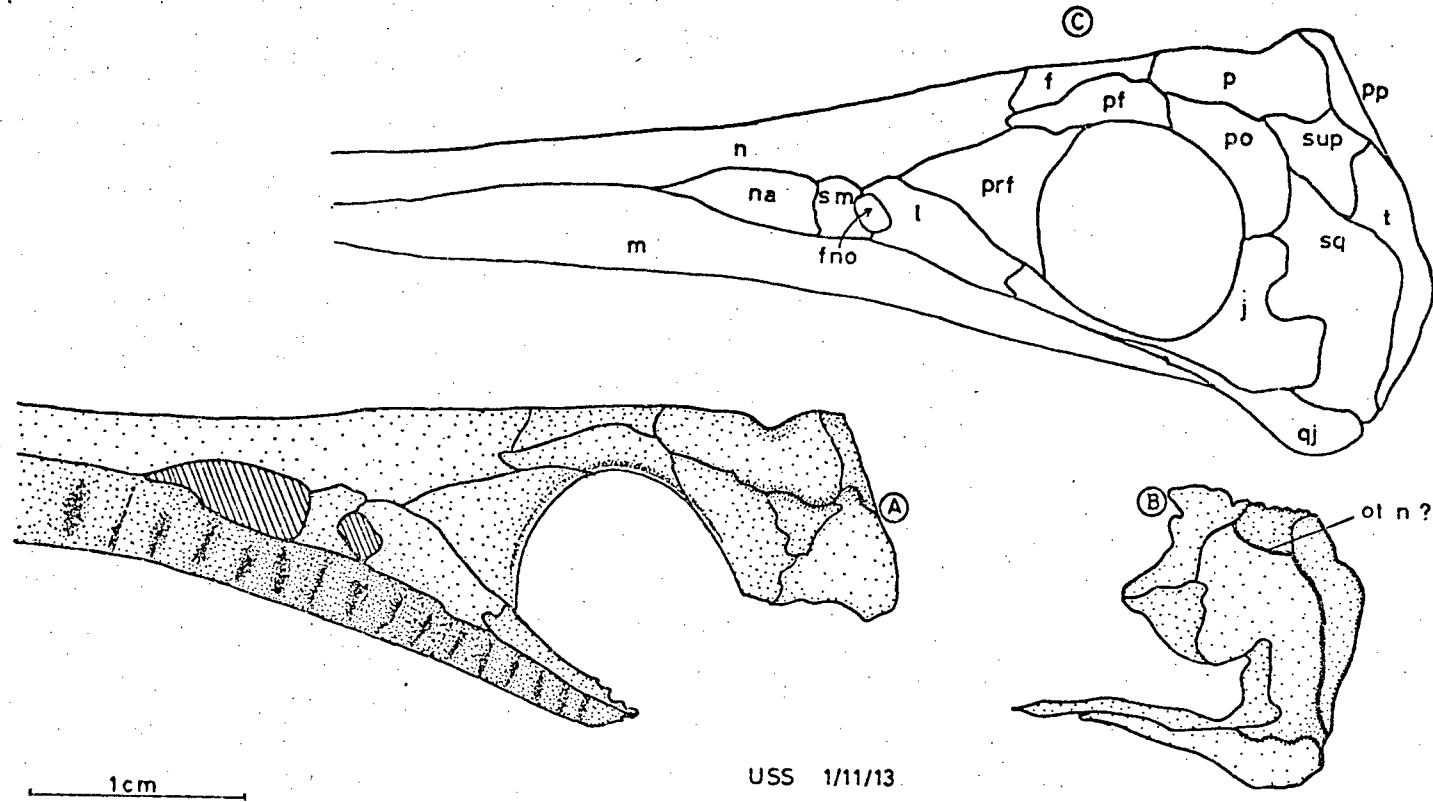
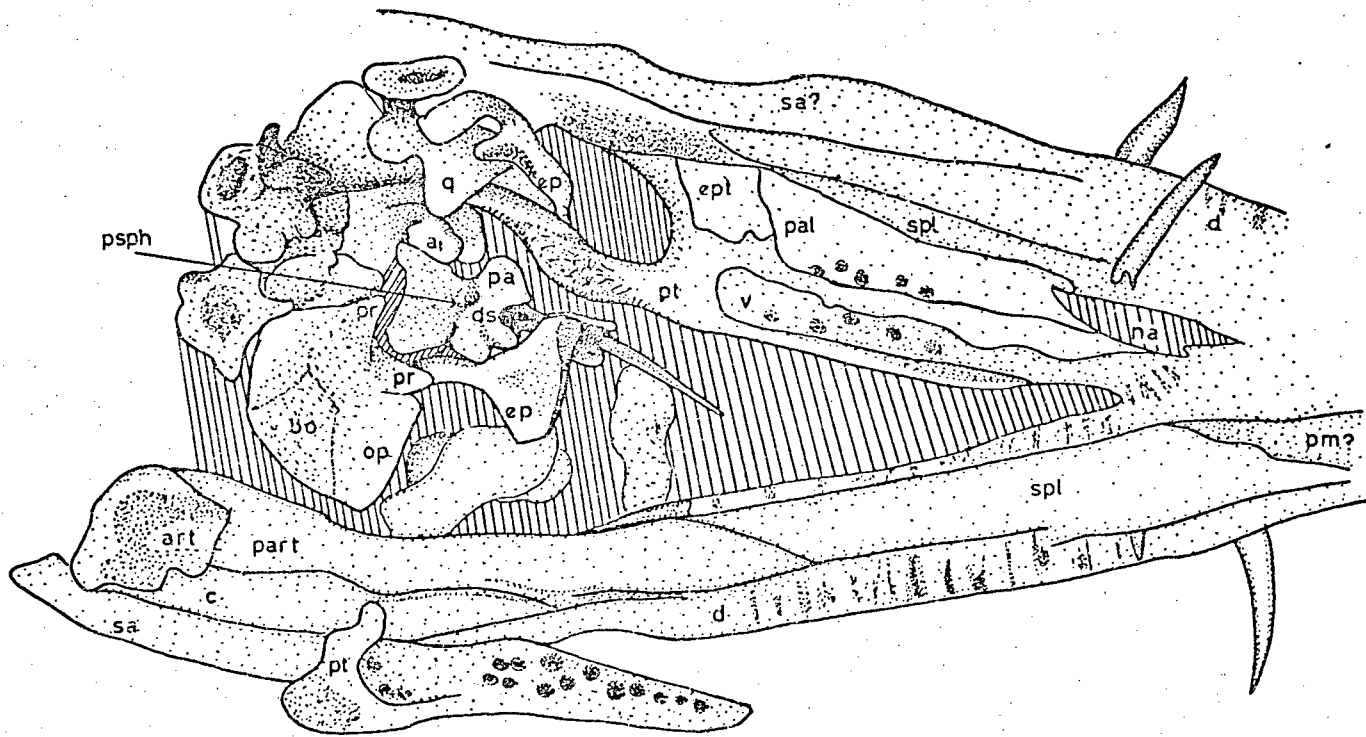


Figure 40: Camera lucida interpretation of broken sidewall of skull, specimen U.S.S. 1/11/13. Two illustrated sections (A & B) reconstructed in C. (See composite photograph in Fig. 76).



USS 1/11/13

1 cm

Figure 41: Camera lucida interpretation; dorsal view of palate and floor of braincase. (Silicone rubber cast of specimen U.S.S. 1/11/13).

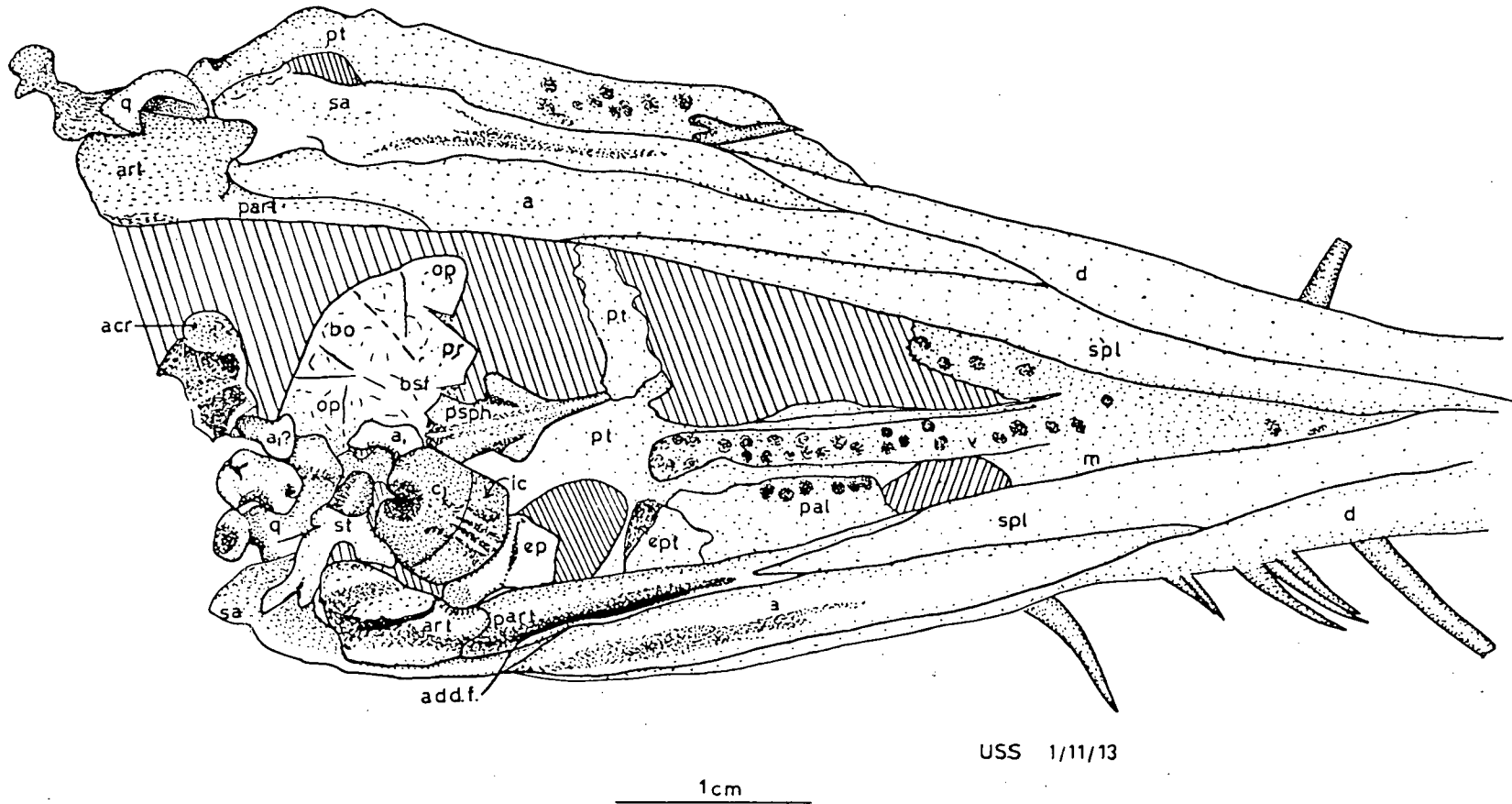


Figure 42 Camera lucida interpretation of ventral view of palate and skull base (silicone rubber cast of specimen U.S.S. 1/11/13)

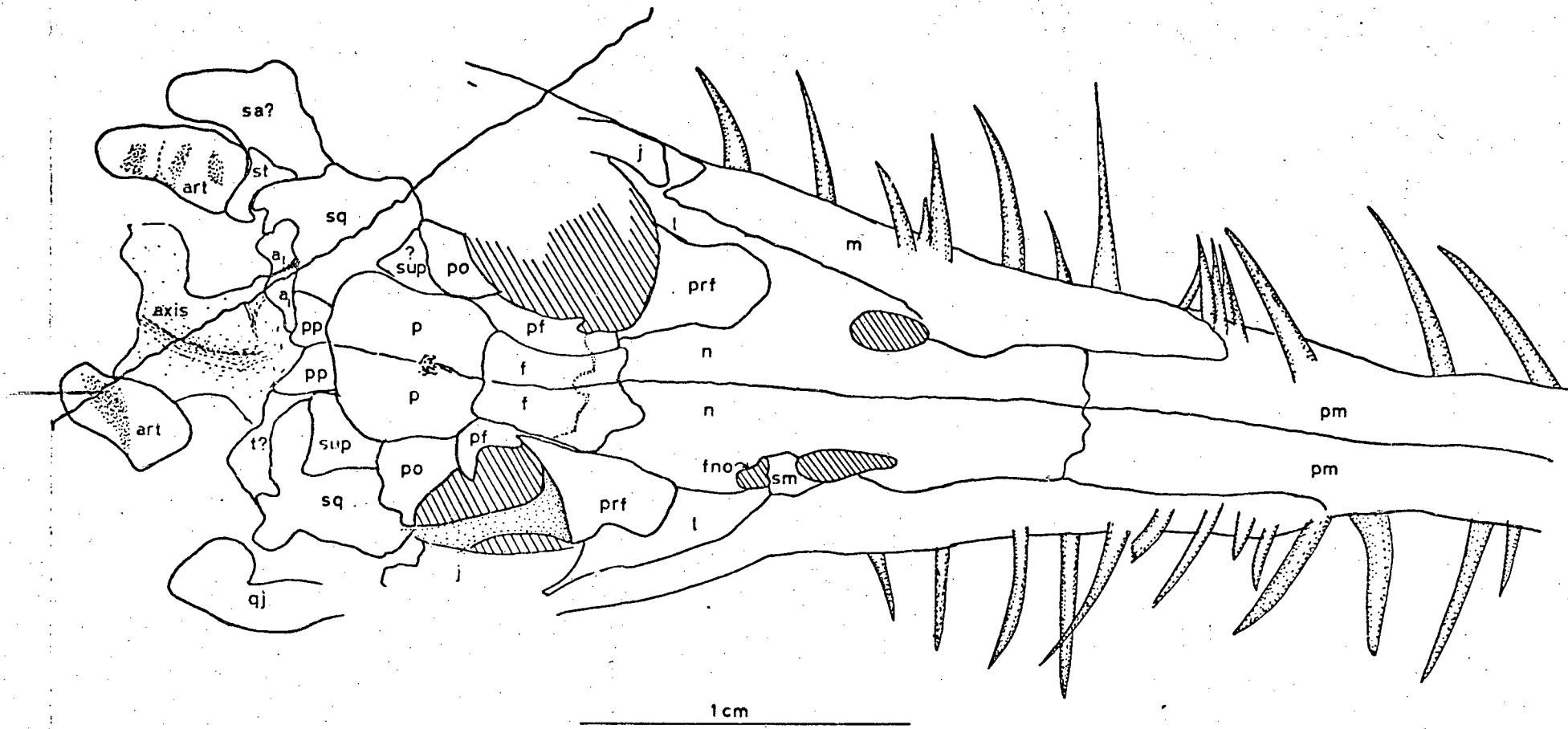


Figure 44: Camera lucida interpretation of silicone rubber cast of skull roof. Specimen in collection of R.D.F. Oosthuizen, Zwartskraal, Prince Albert.

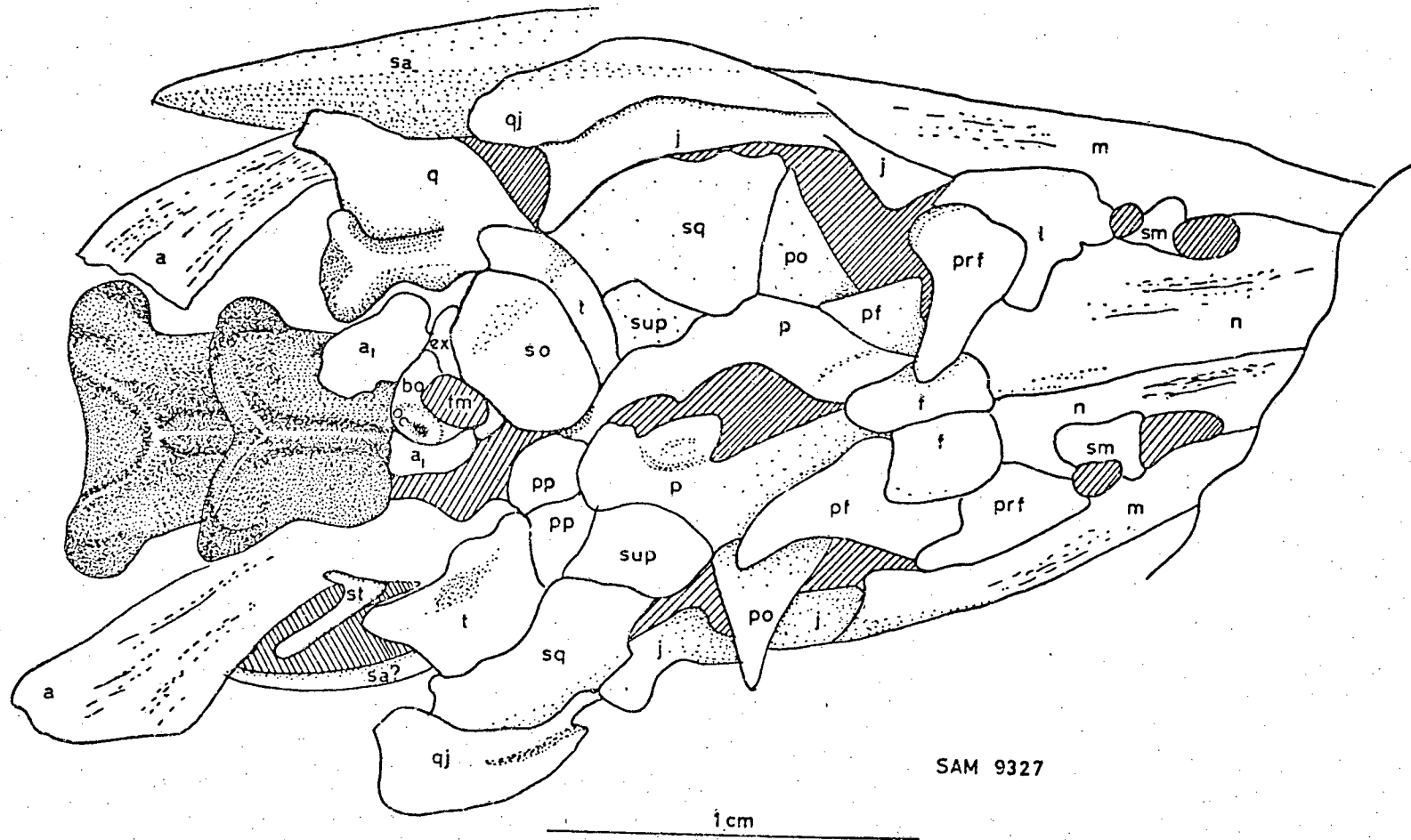


Figure 45: Camera lucida interpretation of silicone rubber cast of skull roof. Specimen S.A.M. 9327.

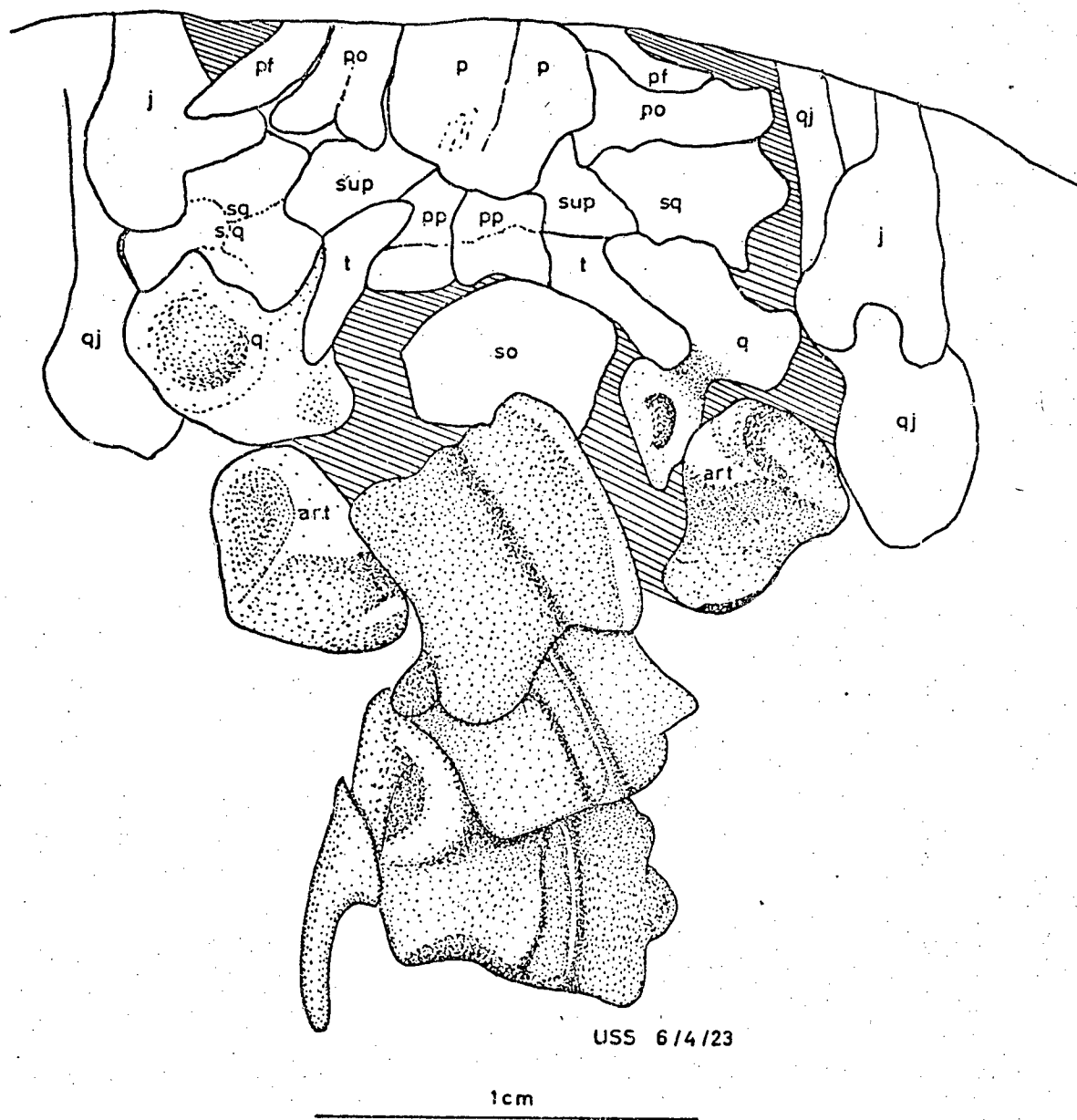


Figure 46: Camera lucida interpretation of skull roof. Specimen U.S.S. 6/4/23.

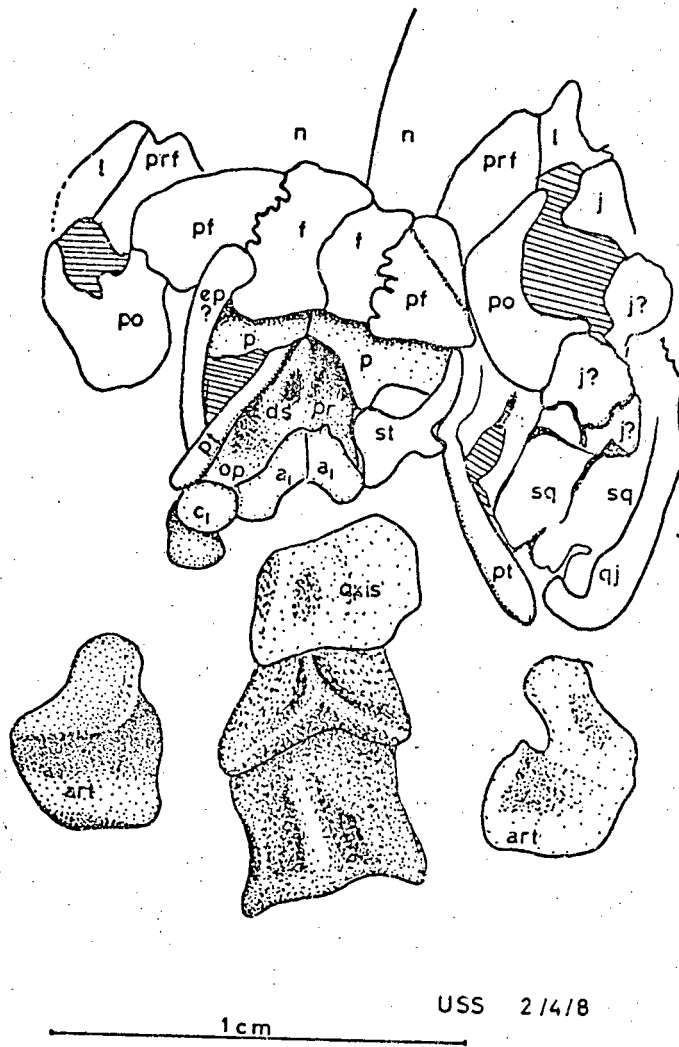


Figure 47: Camera lucida interpretation of silicone rubber cast of dorsal view of skull. Specimen U.S.S. 2/4/8. Skull base partly exposed.

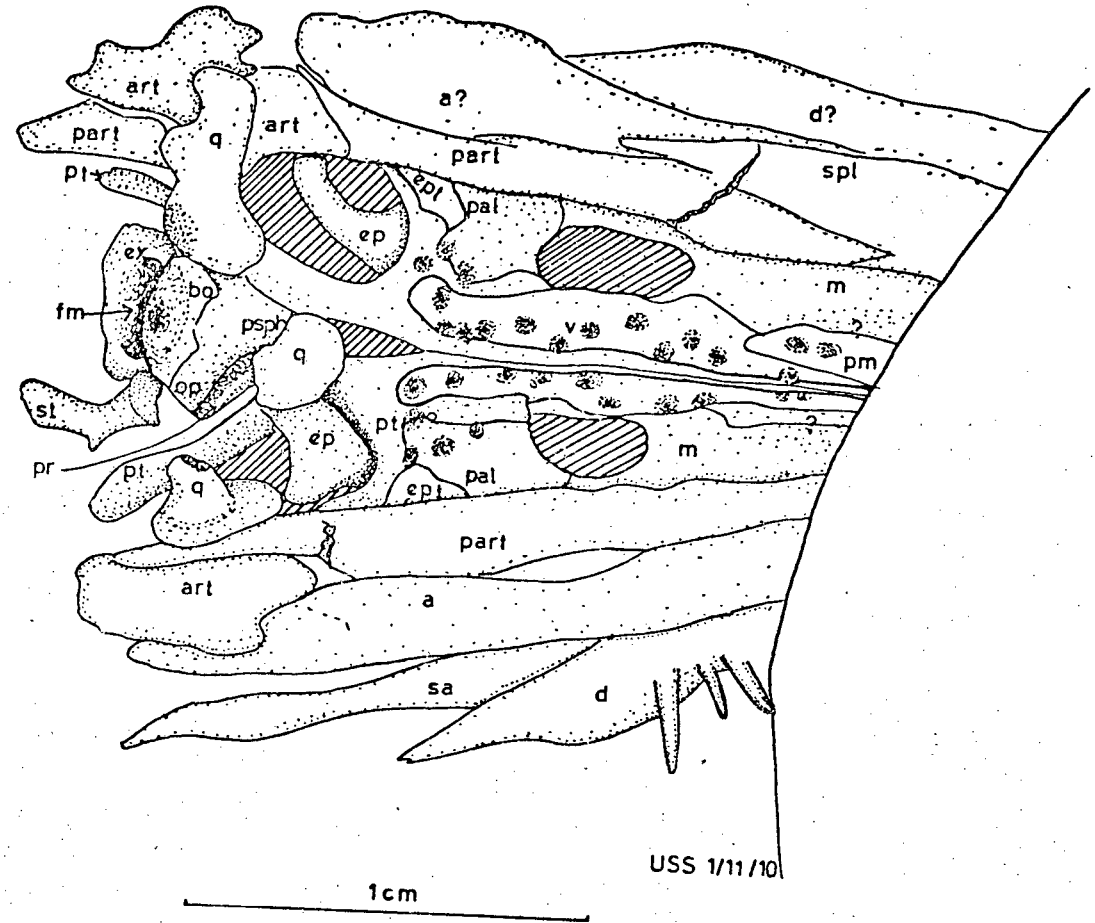


Figure 48: Camera lucida interpretation of silicone rubber cast of palate and skull base. Specimen U.S.S. 1/11/10.

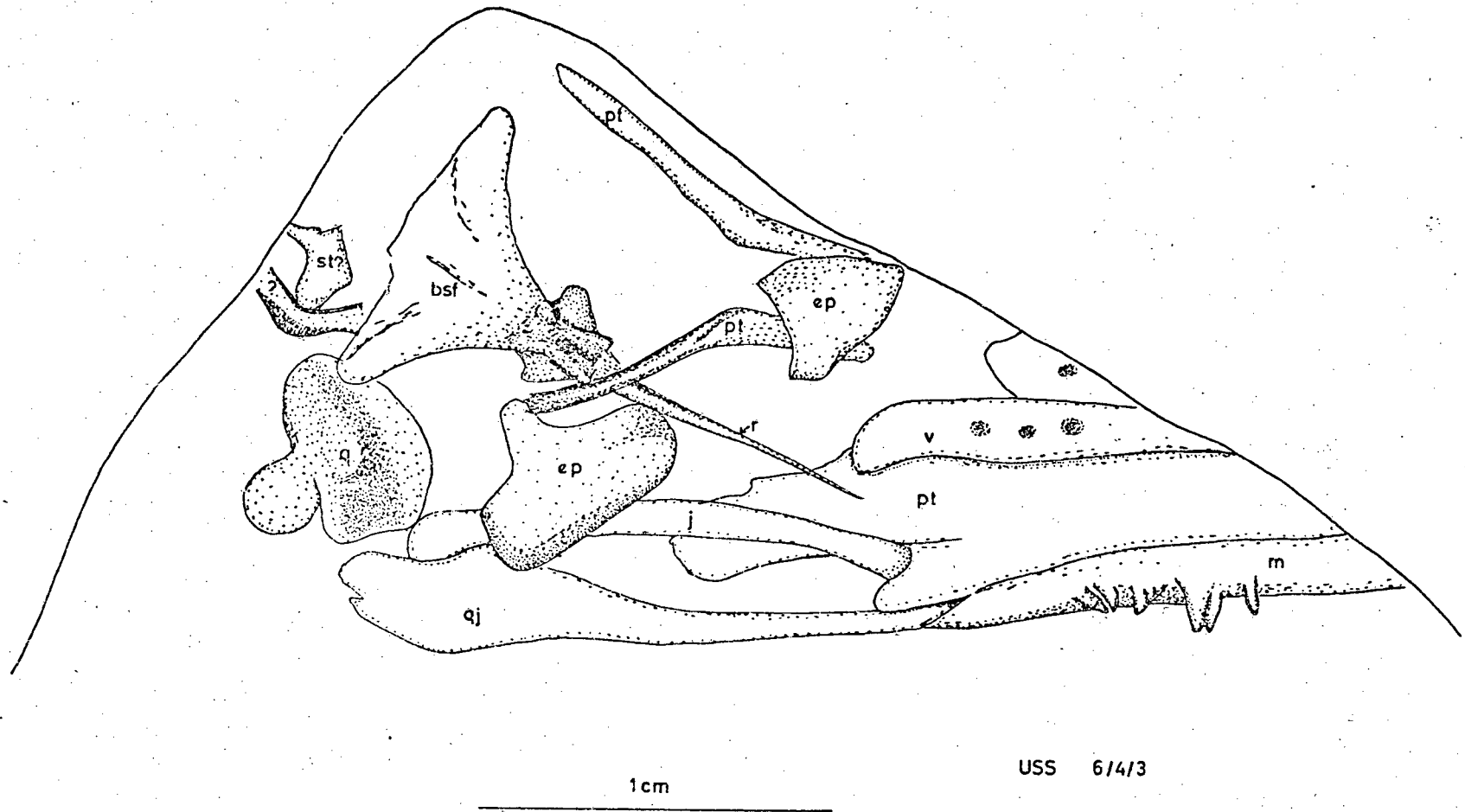


Figure 49: Camera lucida interpretation, dorsal view of skull base and elements of palatoquadrate based on silicone rubber cast of specimen U.S.S. 6/4/3. (Palatal tooth sockets appear to have been pressed through very thin palatal bones).

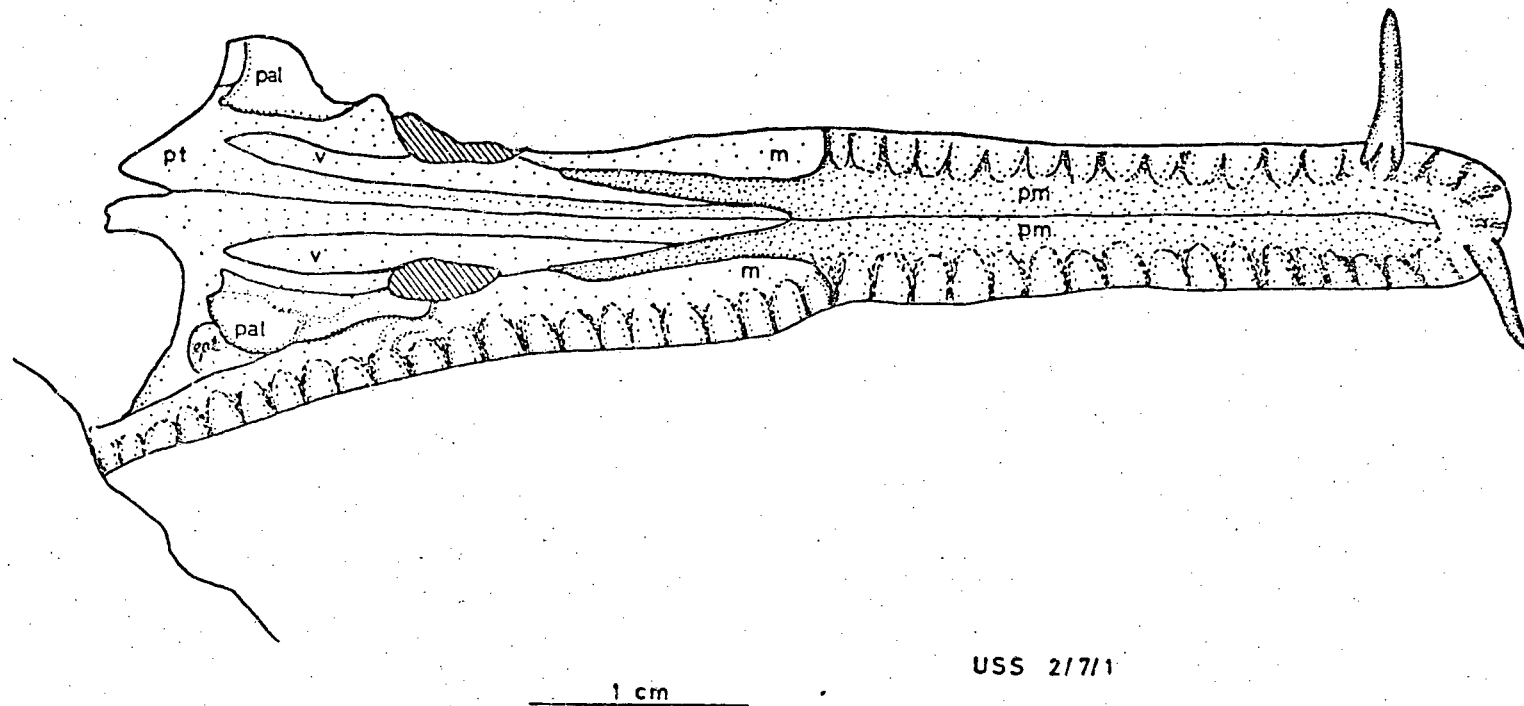


Figure 50: Camera lucida interpretation of impression of palate in dorsal view. Specimen U.S.S. 2/7/1.

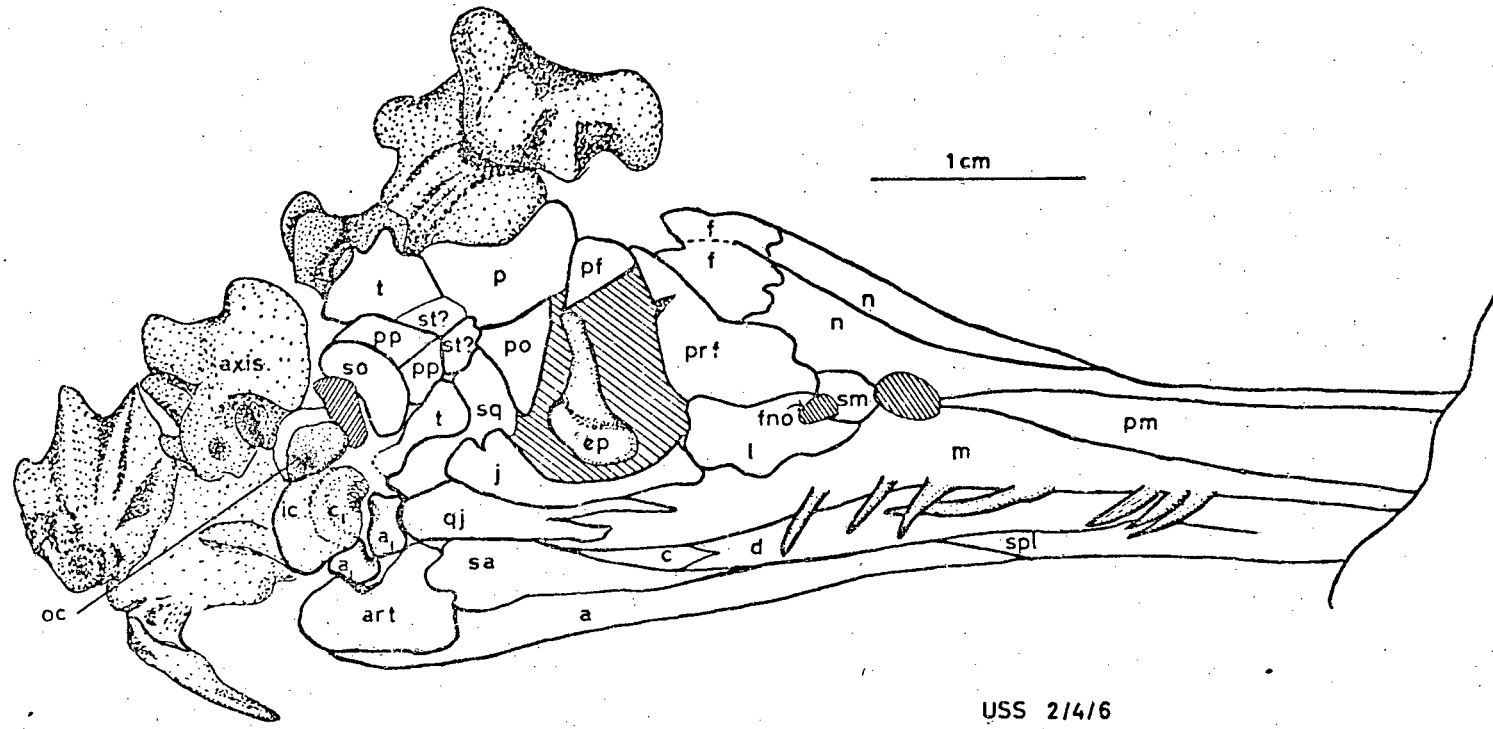
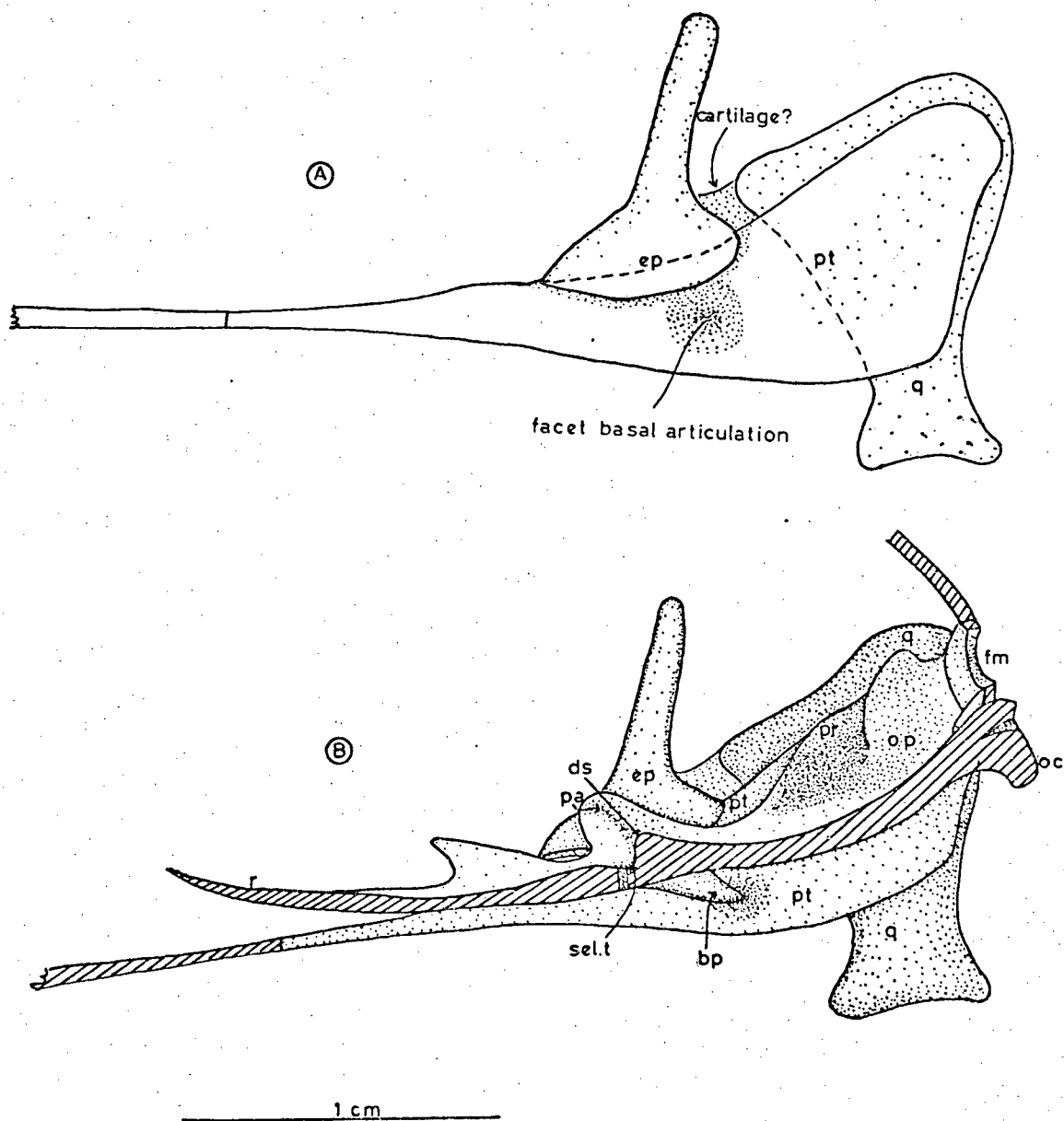


Figure 51: Camera lucida interpretation of silicone rubber cast of skull in lateral view. Specimen U.S.S. 2/4/6.

USS 2/4/6

Figure 52: Tentative reconstruction of palatoquadrate in median view. A, without cranial floor, B, with section through cranial floor added.



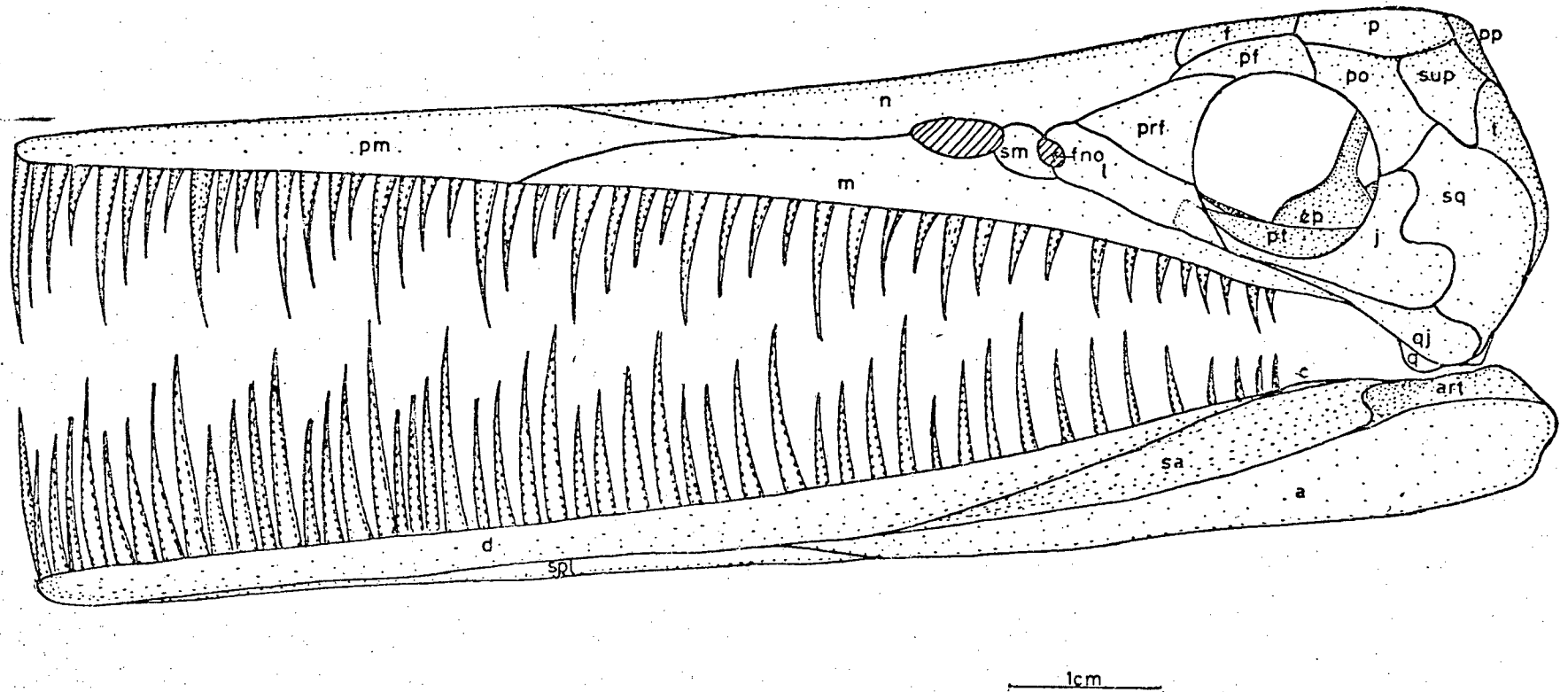
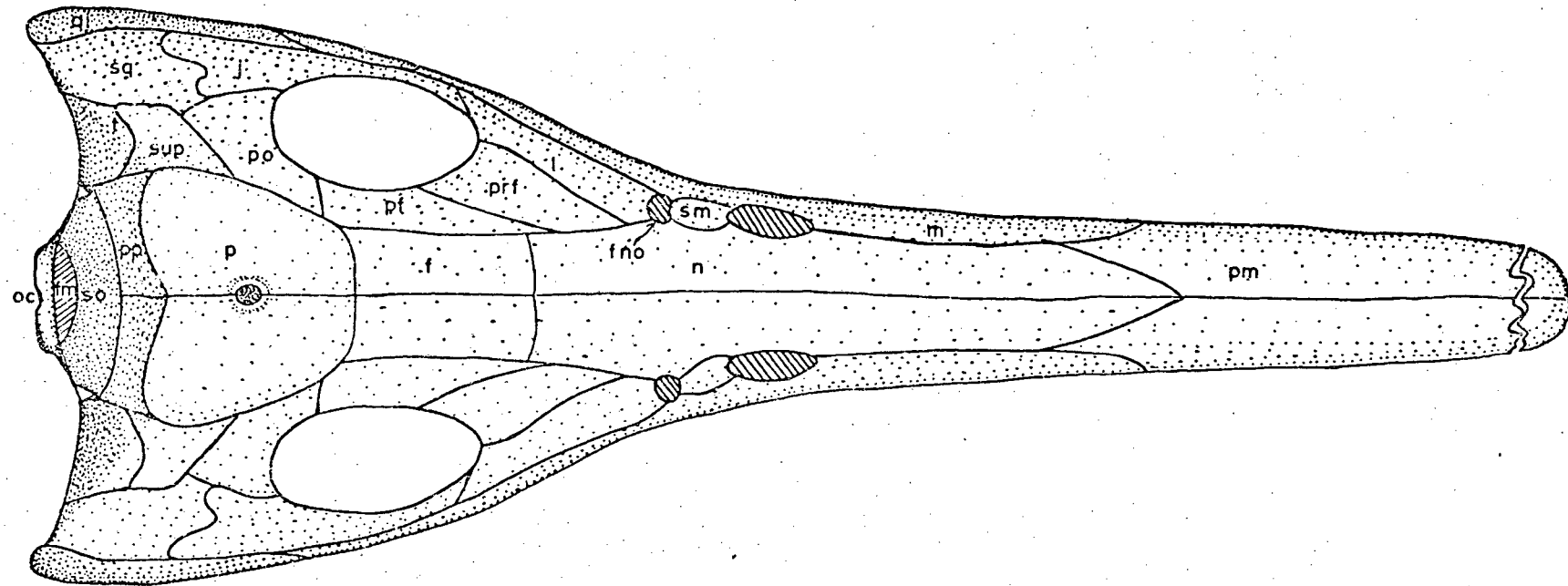


Figure 53: Reconstruction of skull of Mesosaurus tenuidens in lateral view.



1 cm

Figure 54: Reconstruction of skull of Mesosaurus tenuidens in dorsal view (teeth and lower jaw omitted).

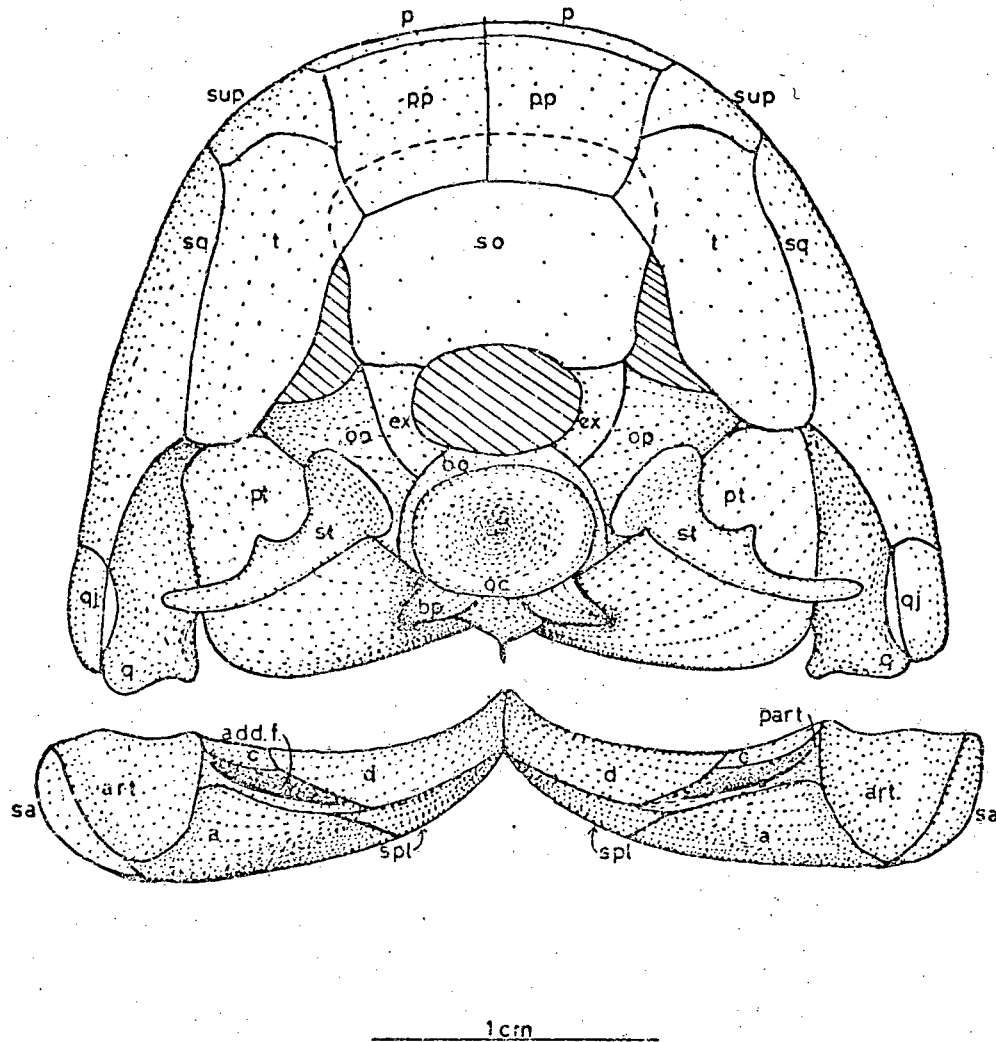


Figure 55: Tentative reconstruction of skull and lower jaw in occipital view (teeth omitted).

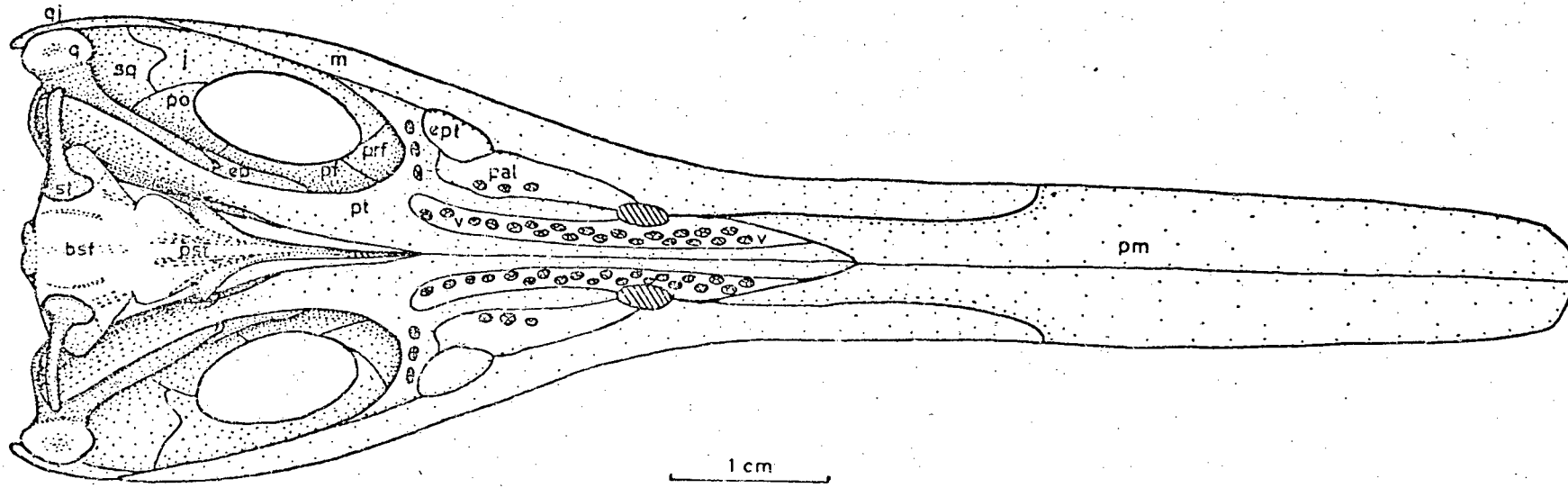
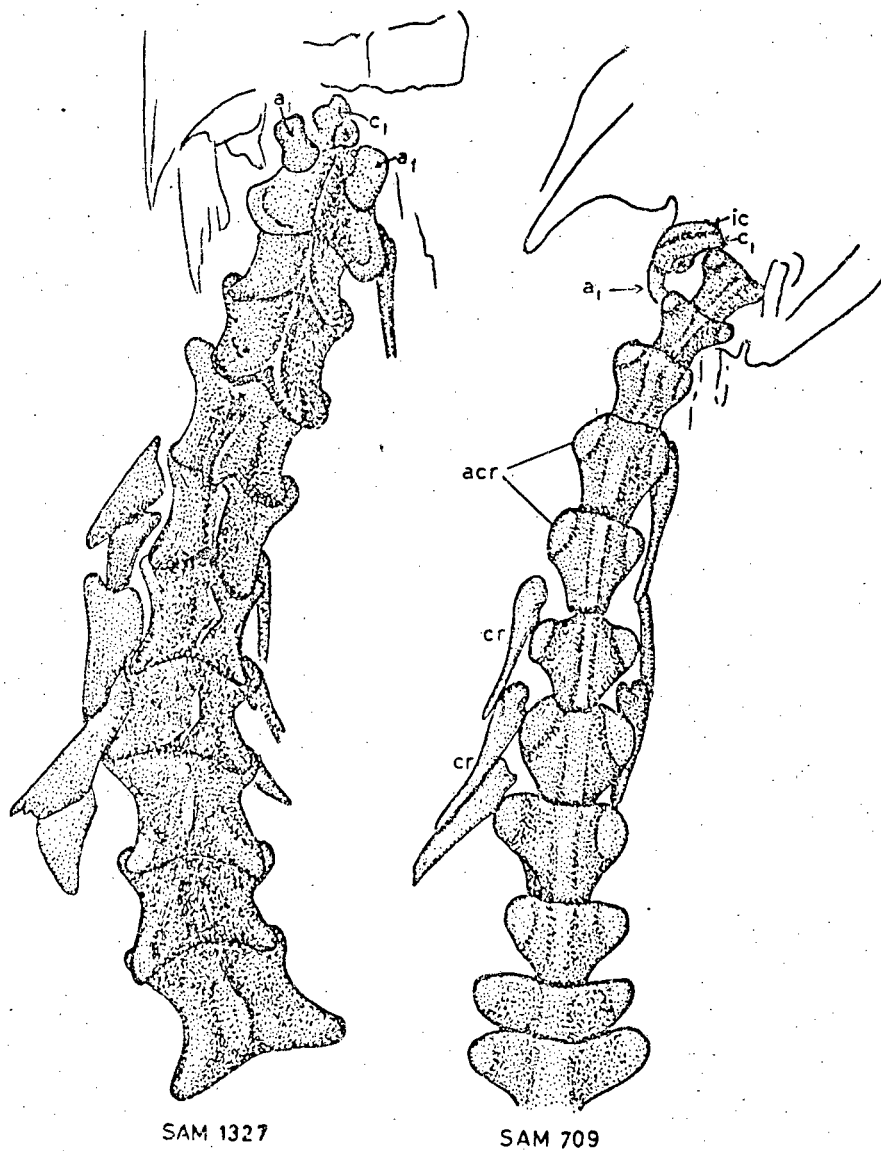
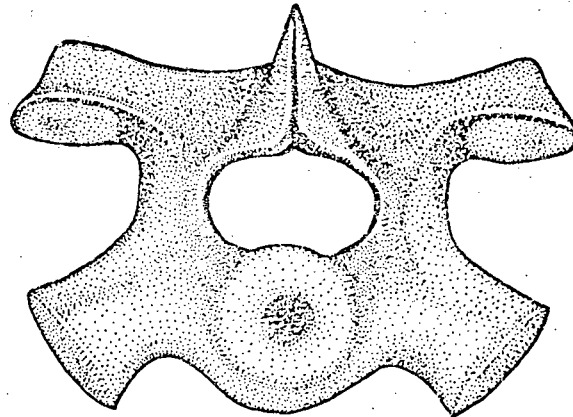


Figure 56: Reconstruction of skull in ventral view, marginal teeth and lower jaw omitted.

Figure 57: Cervical vertebrae with ribs. Specimen S.A.M. 1327 in dorsal view and S.A.M. 709 in ventral view.

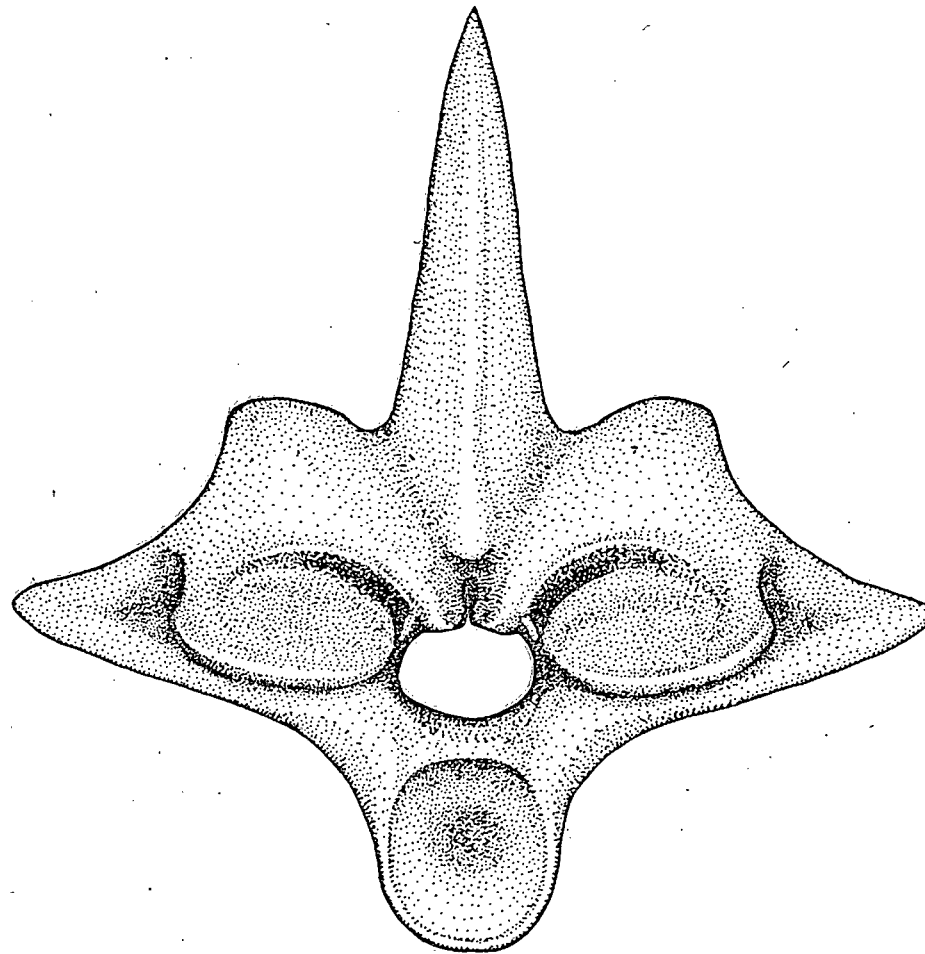




USS 6/4/9

1 cm

Figure 58: Posterior view of isolated cervical vertebra.
Specimen U.S.S. 6/4/9.



USS 614124

1cm

Figure 59 Anterior view of isolated dorsal vertebra. Specimen U.S.S.

6/4/24.

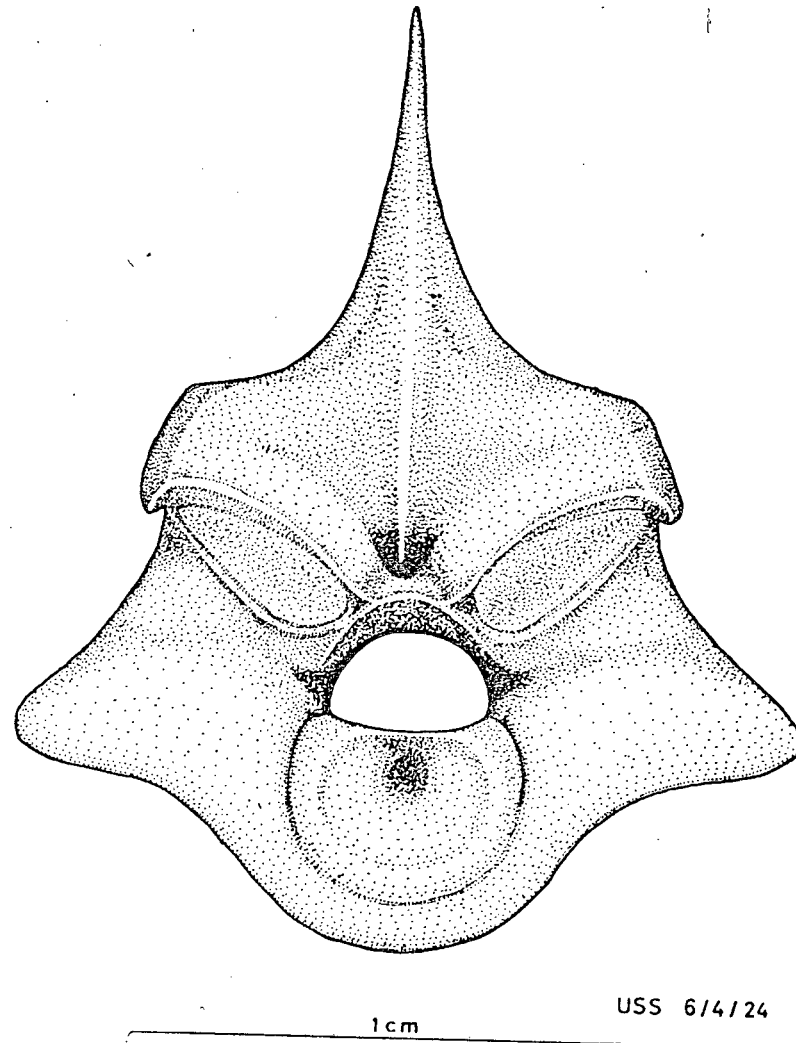


Figure 60 Posterior view of isolated dorsal vertebra. Specimen U.S.S.
6/4/24.

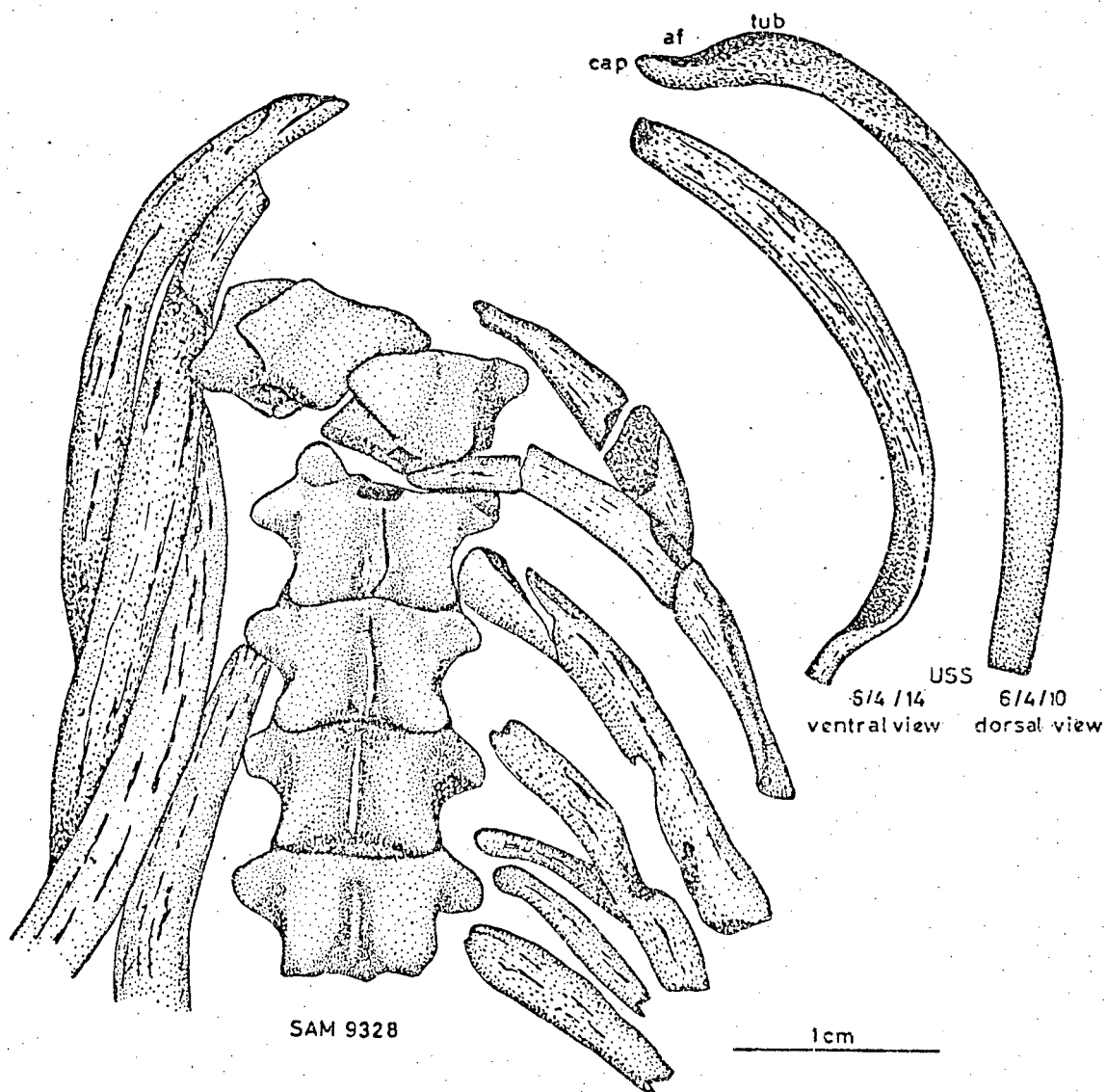


Figure 61: Dorsal vertebrae and associated ribs in dorsal view, S.A.M. 9328. Ribs, specimens U.S.S. 6/4/14 and 6/4/10 in ventral and dorsal views respectively.

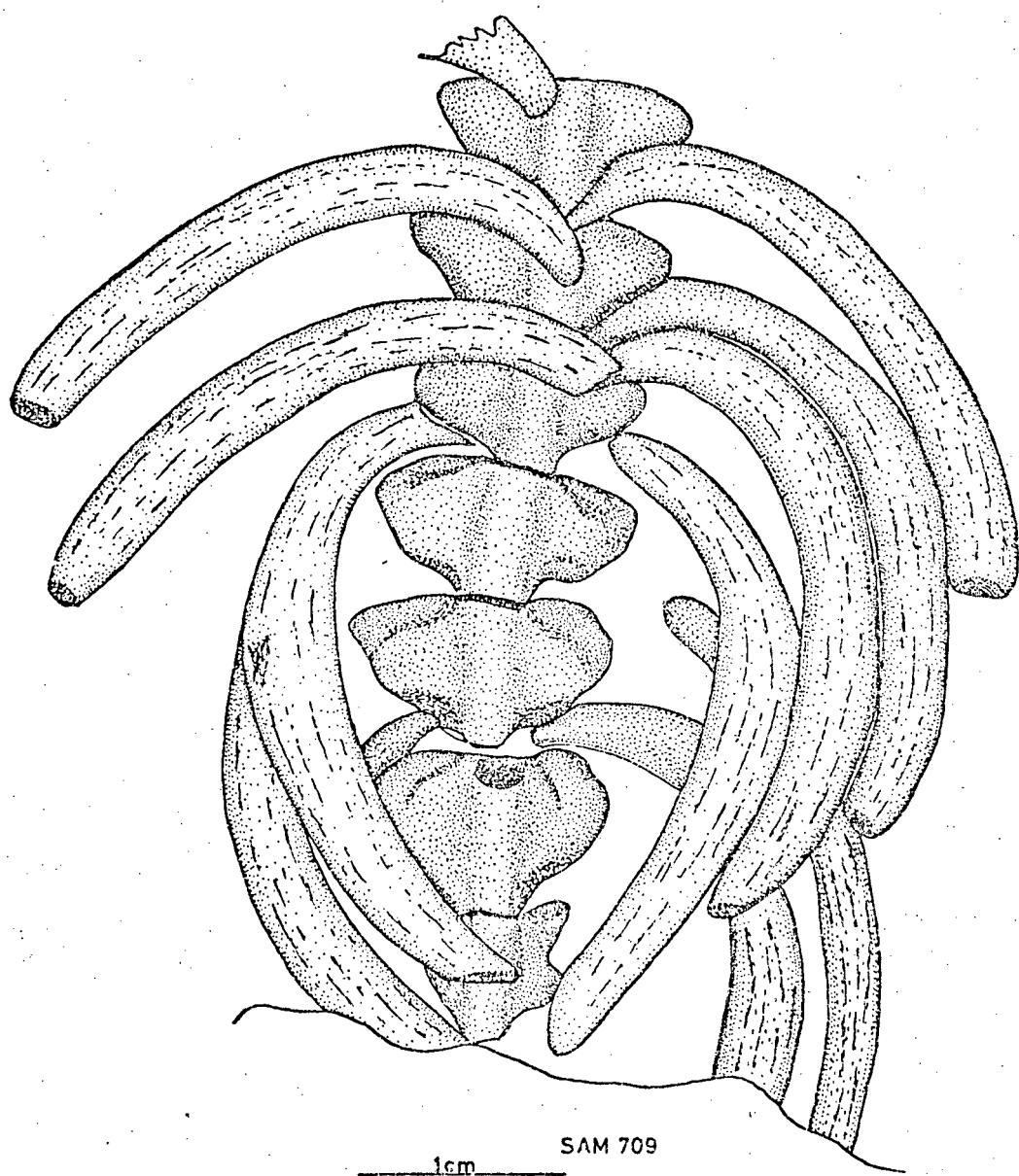


Figure 62: Articulated dorsal vertebrae and ribs in ventral view, S.A.M. 709.

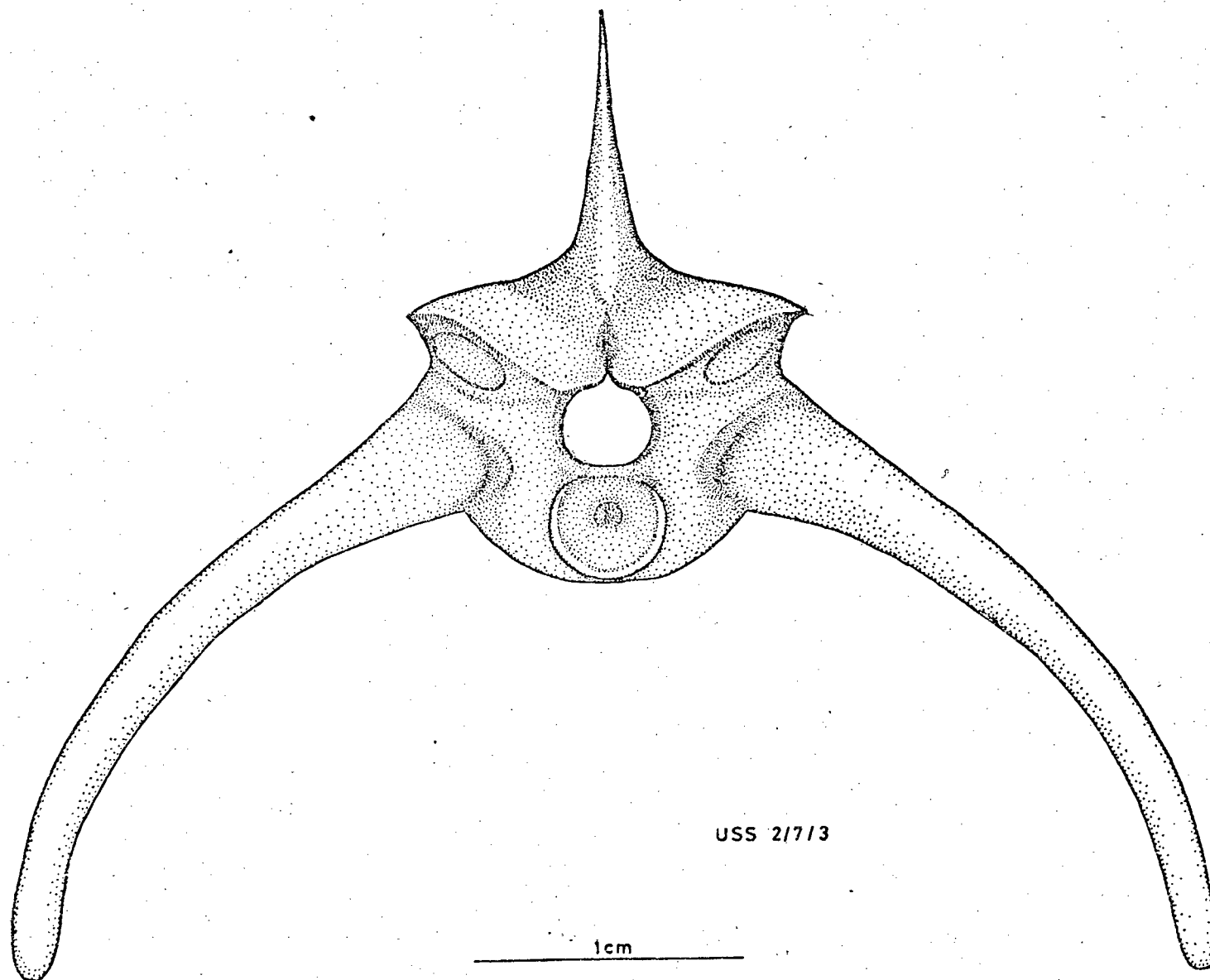
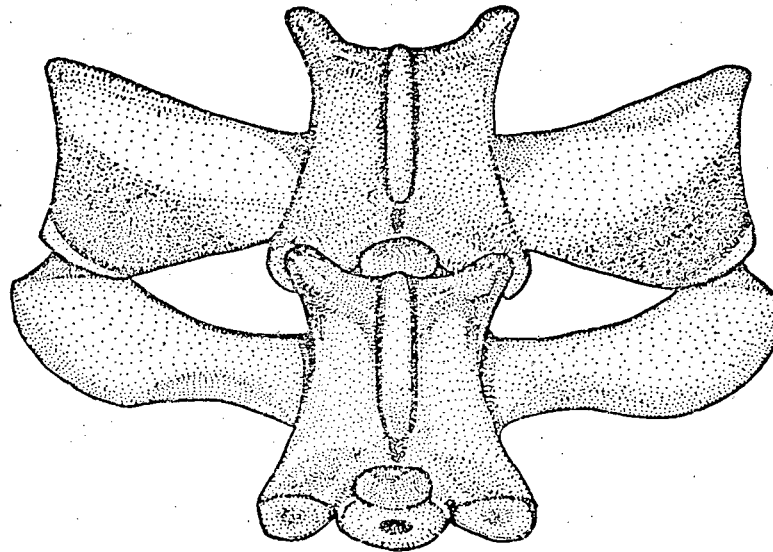


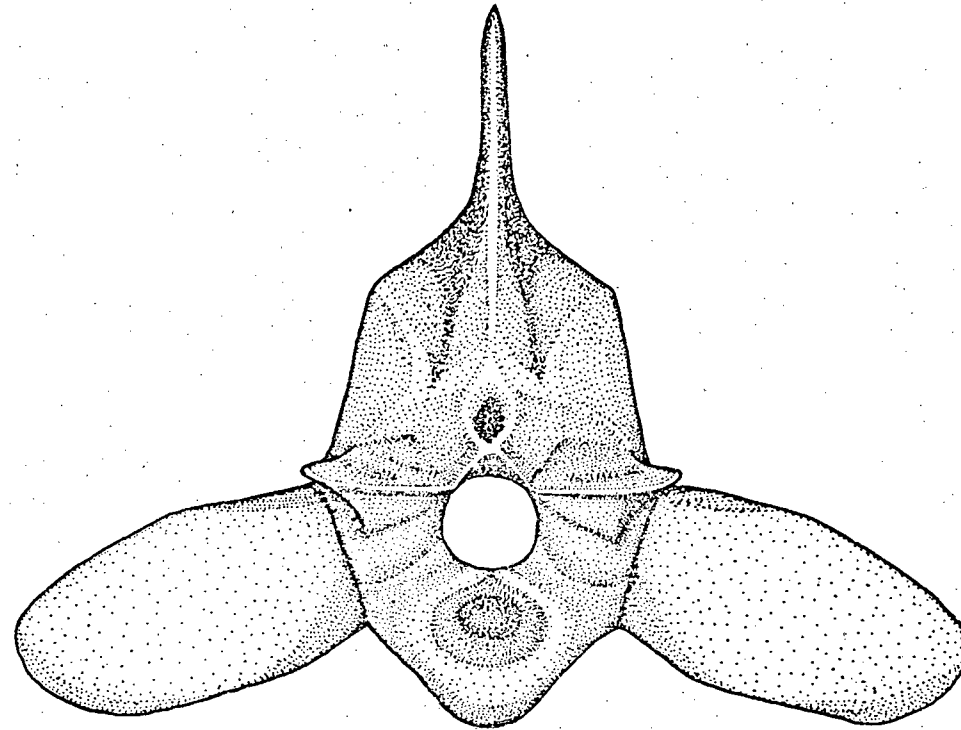
Figure 63: Posterior view of isolated presacral dorsal vertebra with ankylosed ribs. Specimen U.S.S. 2/7/3.



USS 1/7/3

1 cm

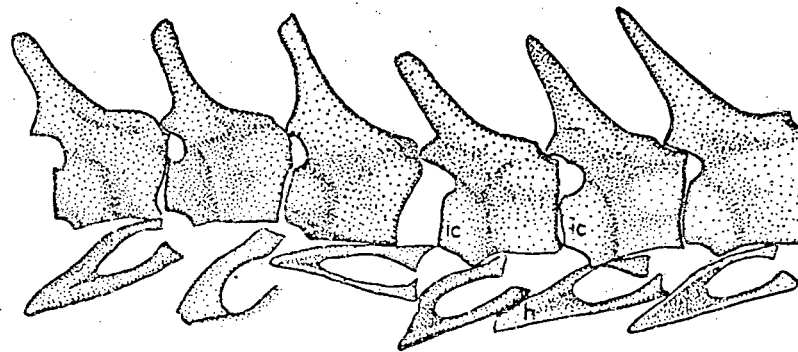
Figure 64: Posterodorsal view of isolated sacral vertebrae. Specimen U.S.S. 1/7/3.



1 cm

USS 6/4/5

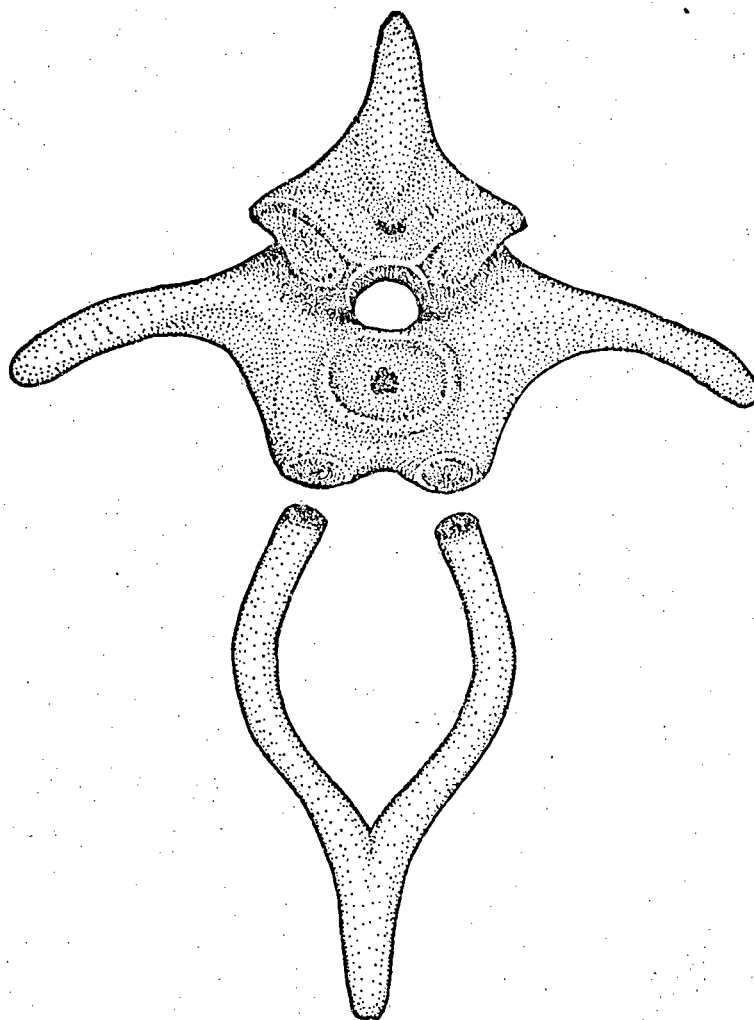
Figure 65: Rib-bearing caudal vertebra in anterior view. Note the line of separation between caudal rib and centrum of vertebra. Specimen U.S.S. 6/4/5.



USS 2/5/3

1 cm

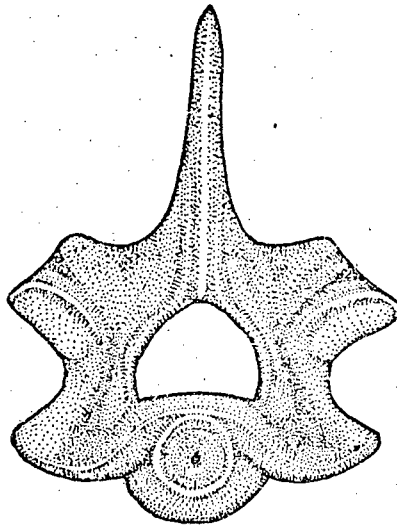
Figure 66: Lateral view of caudal vertebrae showing intercentra and haemal arches. Specimen U.S.S. 2/5/3.



USS 614/24

1cm

Figure 67: Posterior view of caudal vertebra with associated arch in posterior view. Specimen U.S.S. 6/4/24.



USS 6/4/9

1cm

Figure 68: Posterior view of one of the last caudal vertebrae without ribs or haemal arches. Specimen U.S.S. 6/4/9.

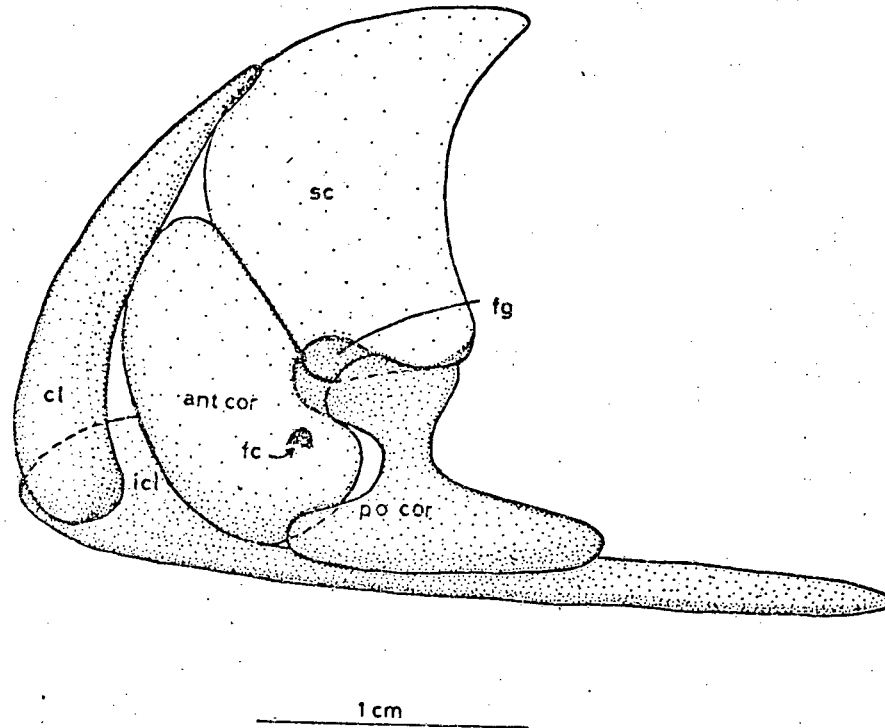


Figure 69: Reconstruction of pectoral girdle in lateral view.

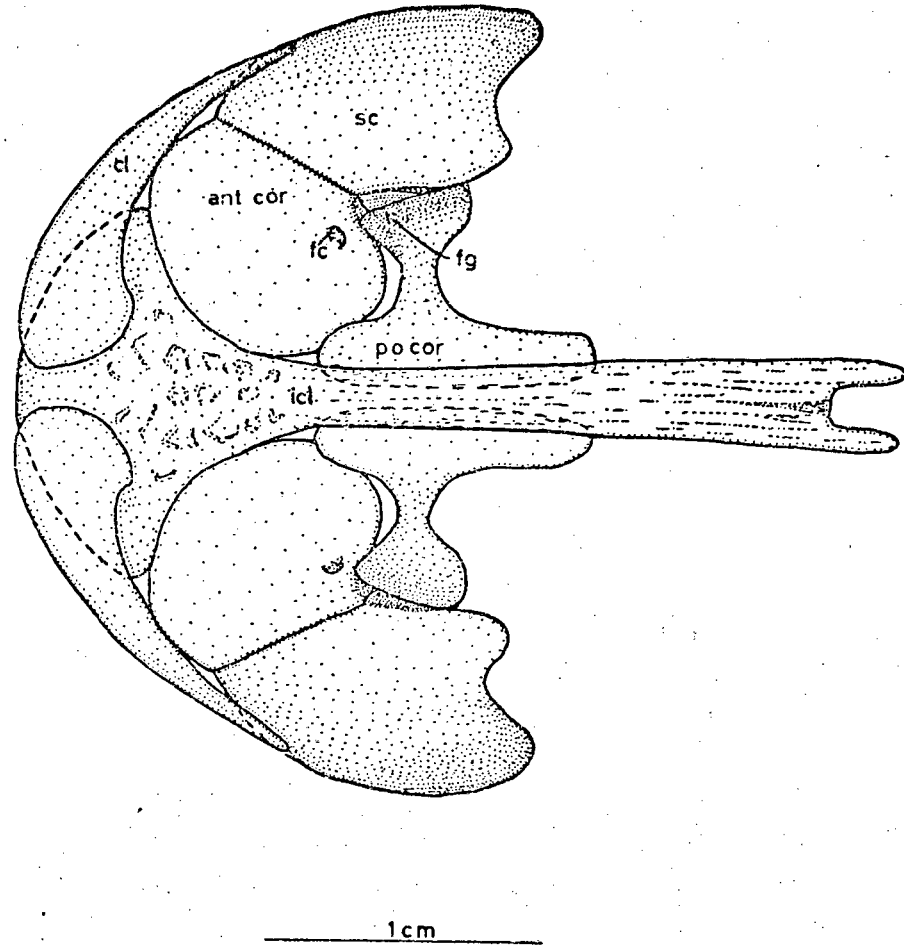


Figure 70: Reconstruction of pectoral girdle in ventral view.

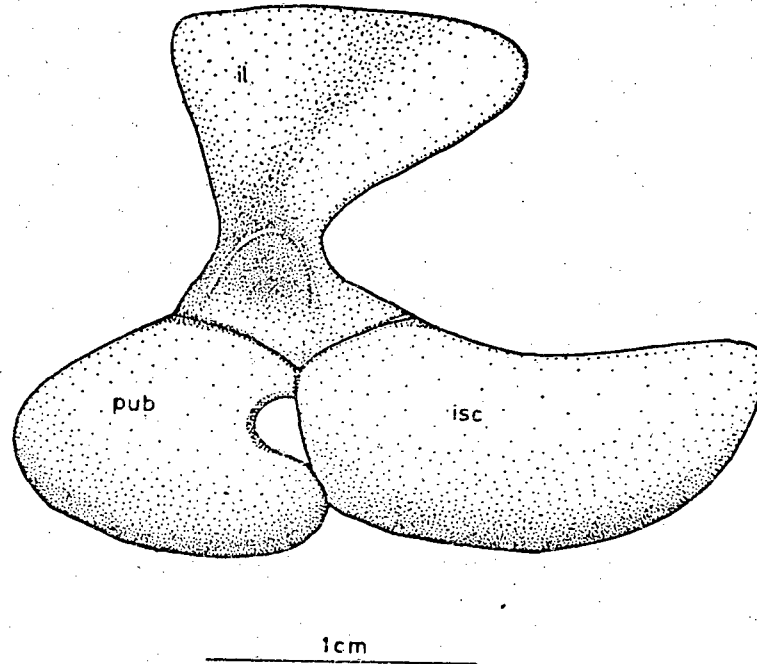


Figure 71: Reconstruction of pelvic girdle in lateral view.

Figure 72: Elements of the front limb of Mesosaurus.

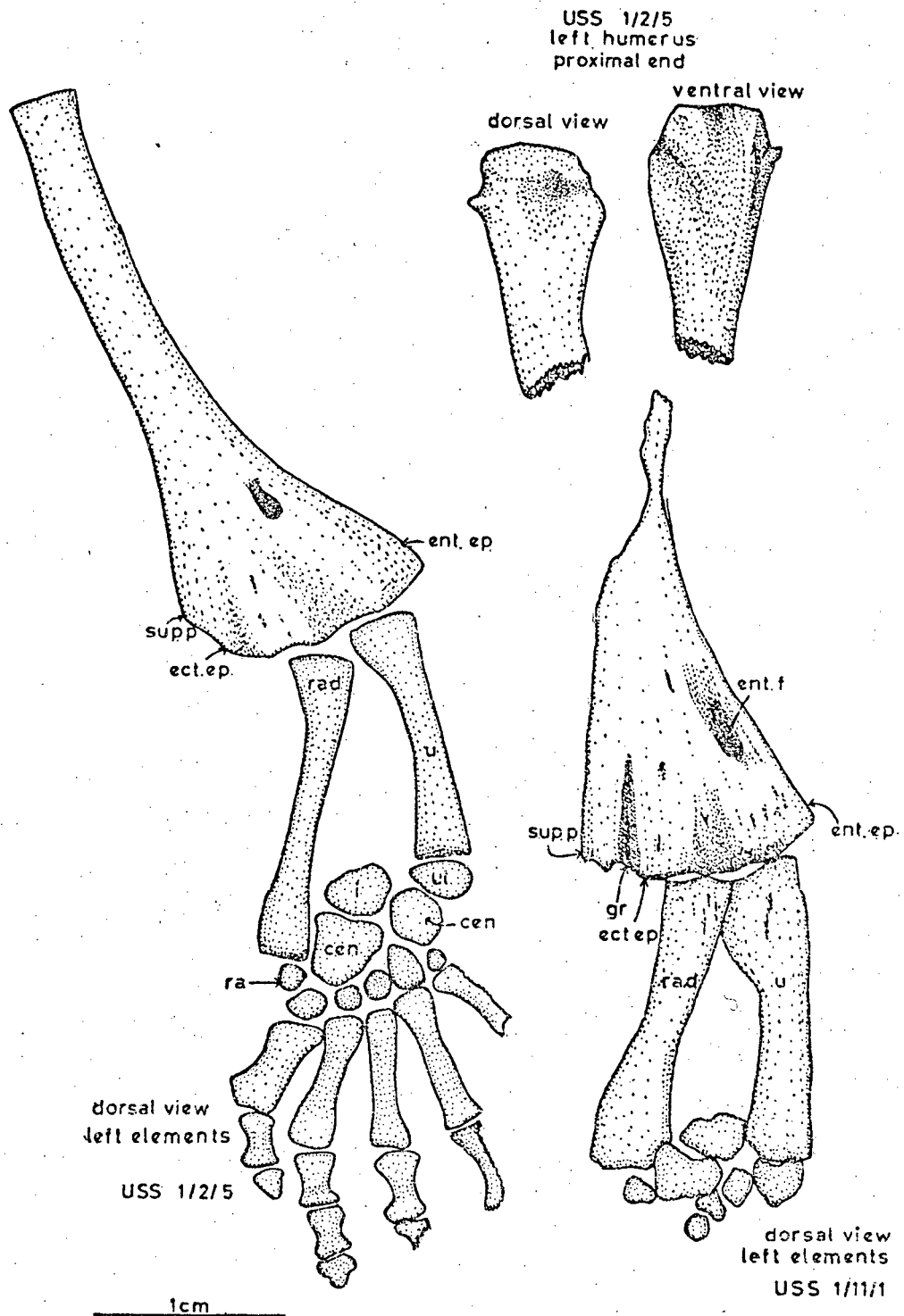
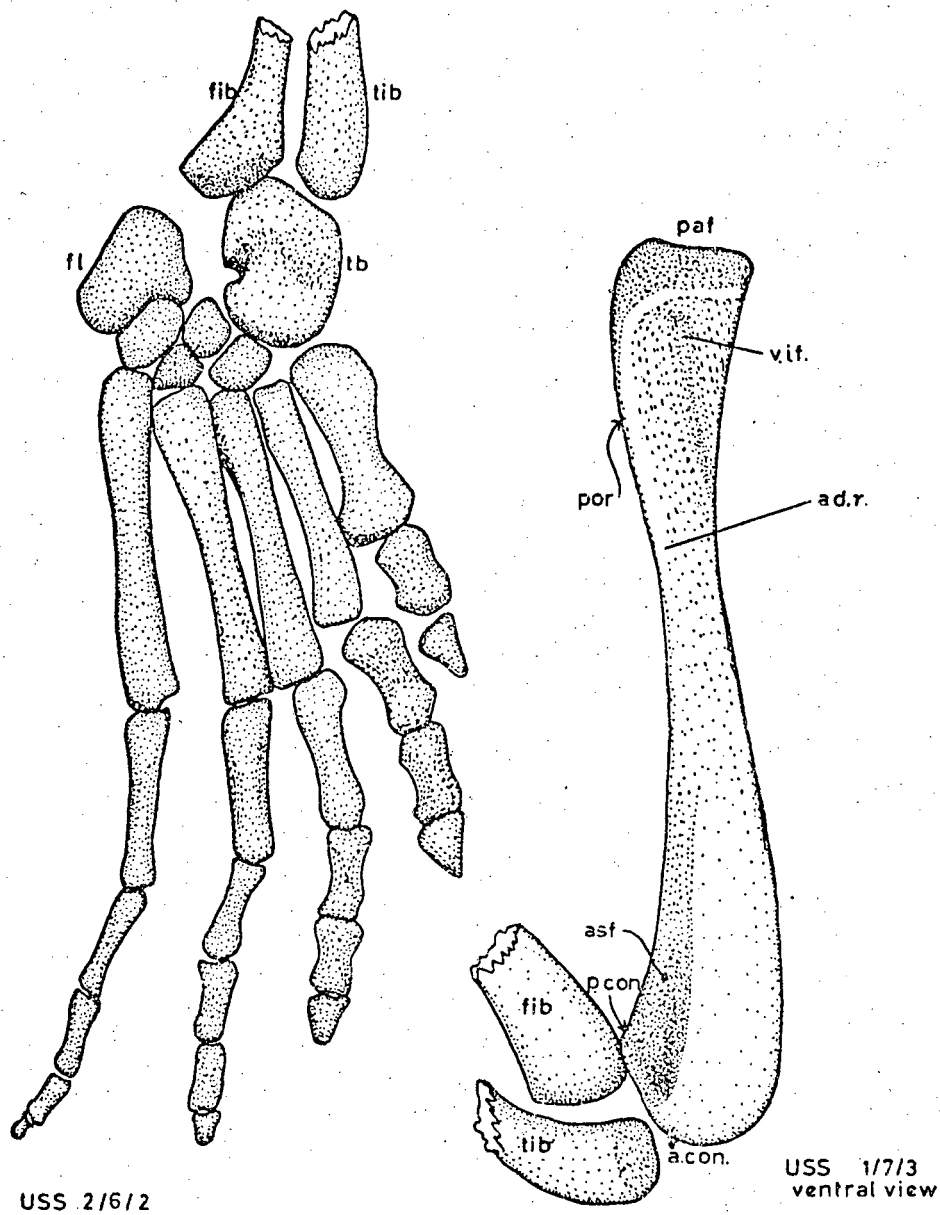


Figure 73: Elements of the hind limb of Mesosaurus.



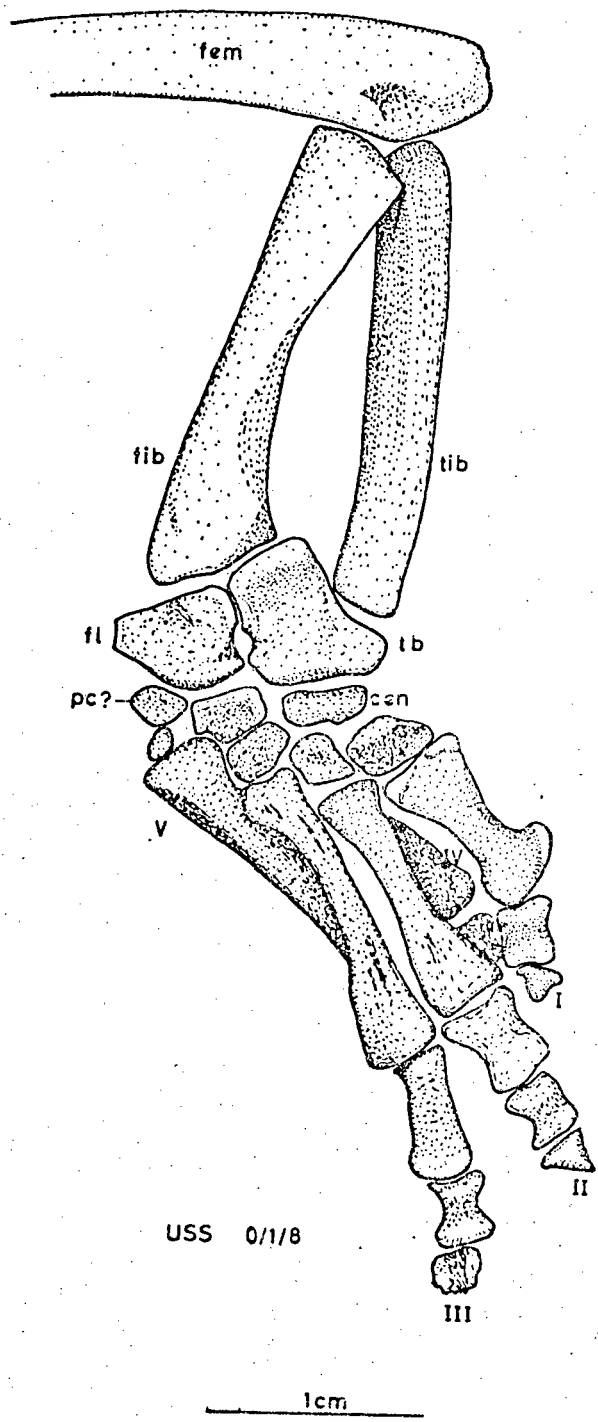


Figure 74: Hind limb of specimen U.S.S. 0/1/8 to illustrate the carpus.

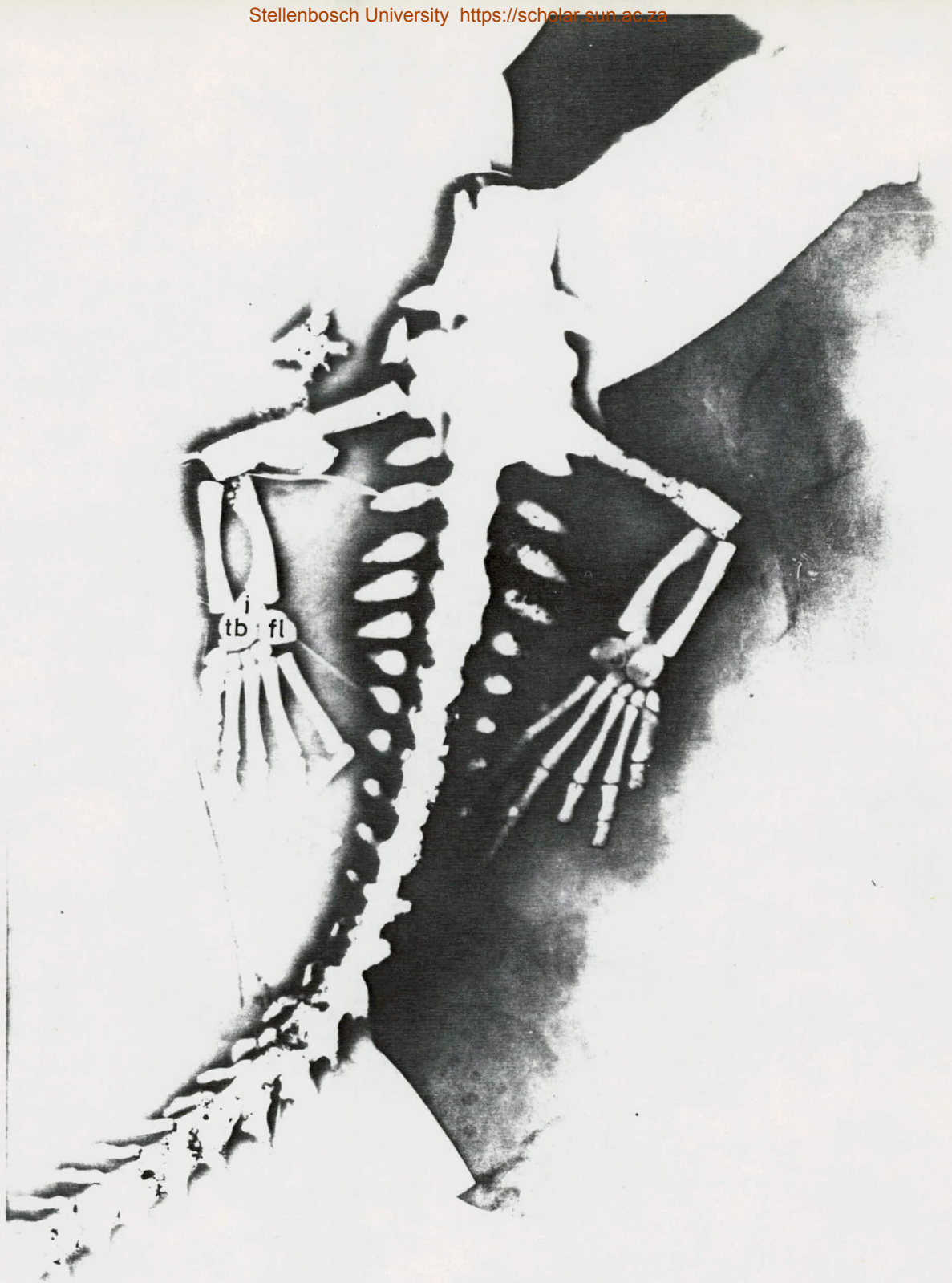


Figure 75: Positive print of X-ray negative. Specimen U.S.S. 3/1/5.

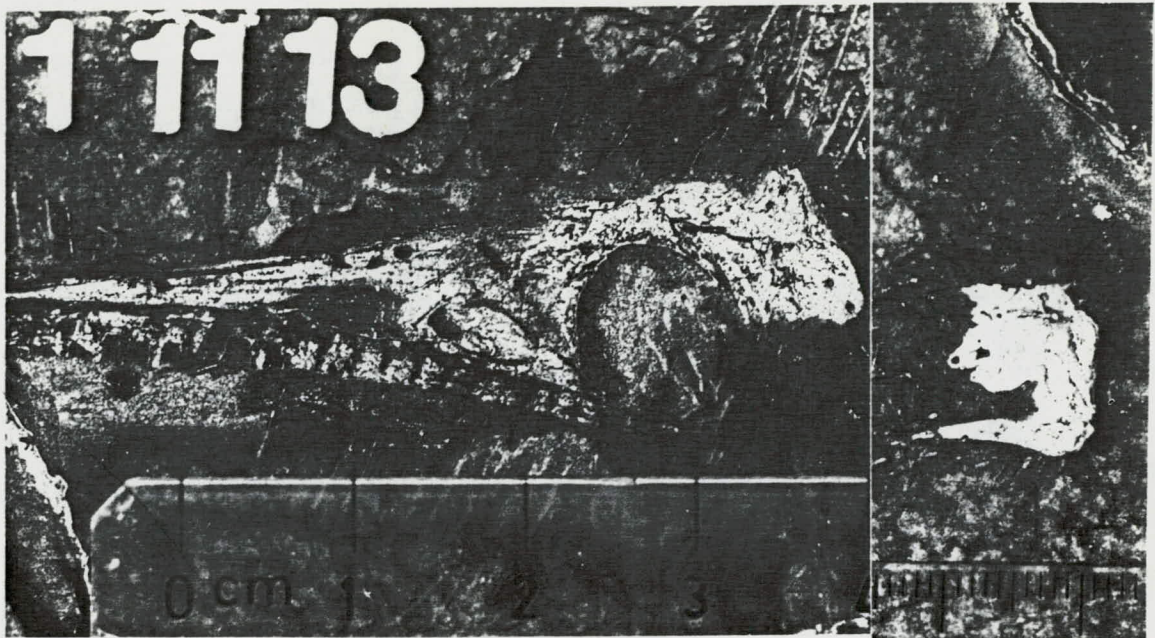


Figure 76: Composite photograph of side wall of skull depicted in Figure 40 B and C.

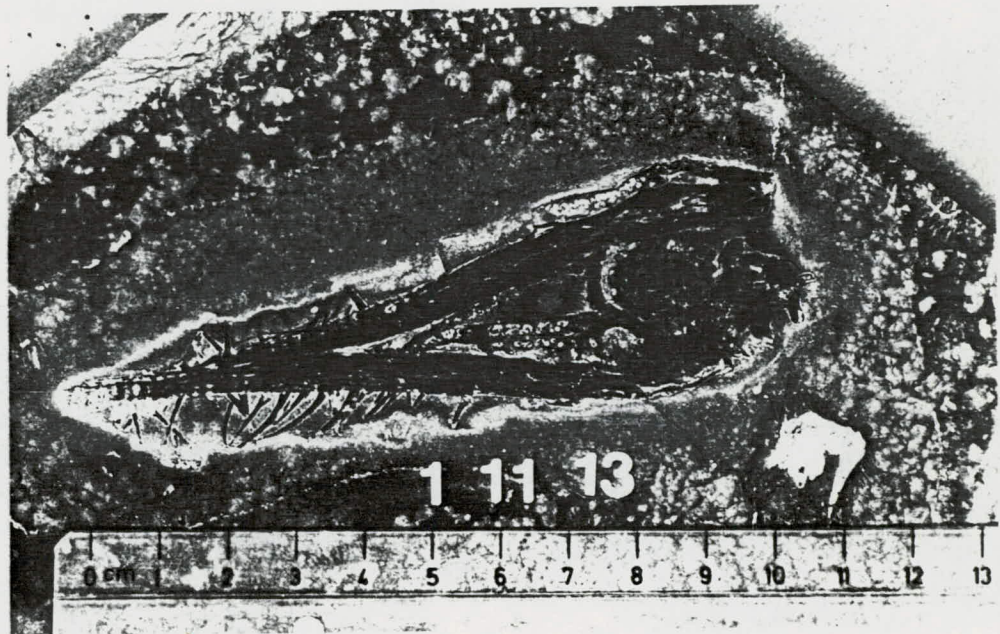


Figure 77: Photograph of ventral view of palate and dislocated jugal-quadratojugal-squamosal portion of sidewall of skull shown in Figs 40 and 76.

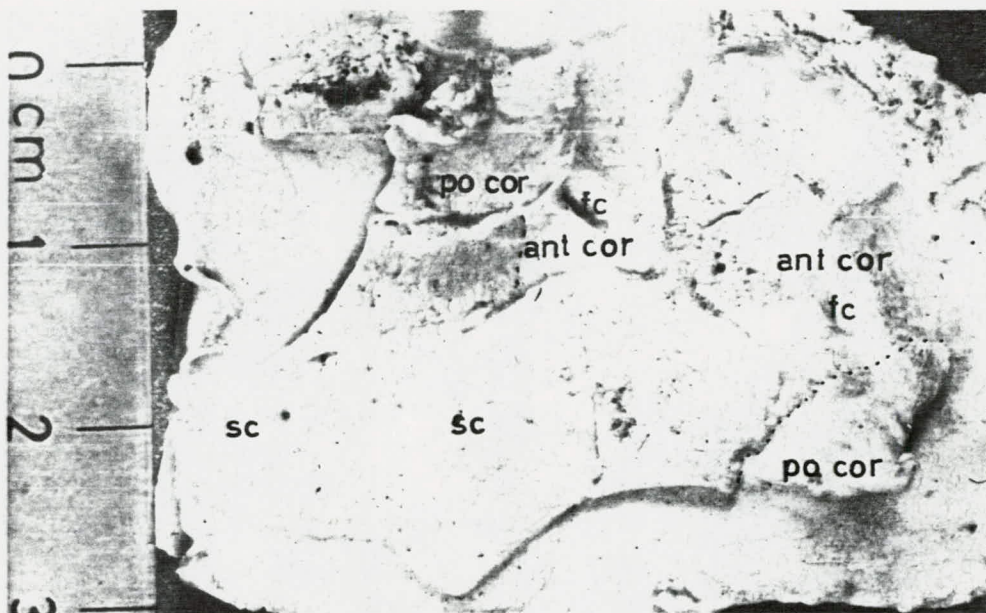


Figure 78: Silicone rubber cast of enchondral elements of pectoral girdle. Specimen U.S.S. 5/4/2.

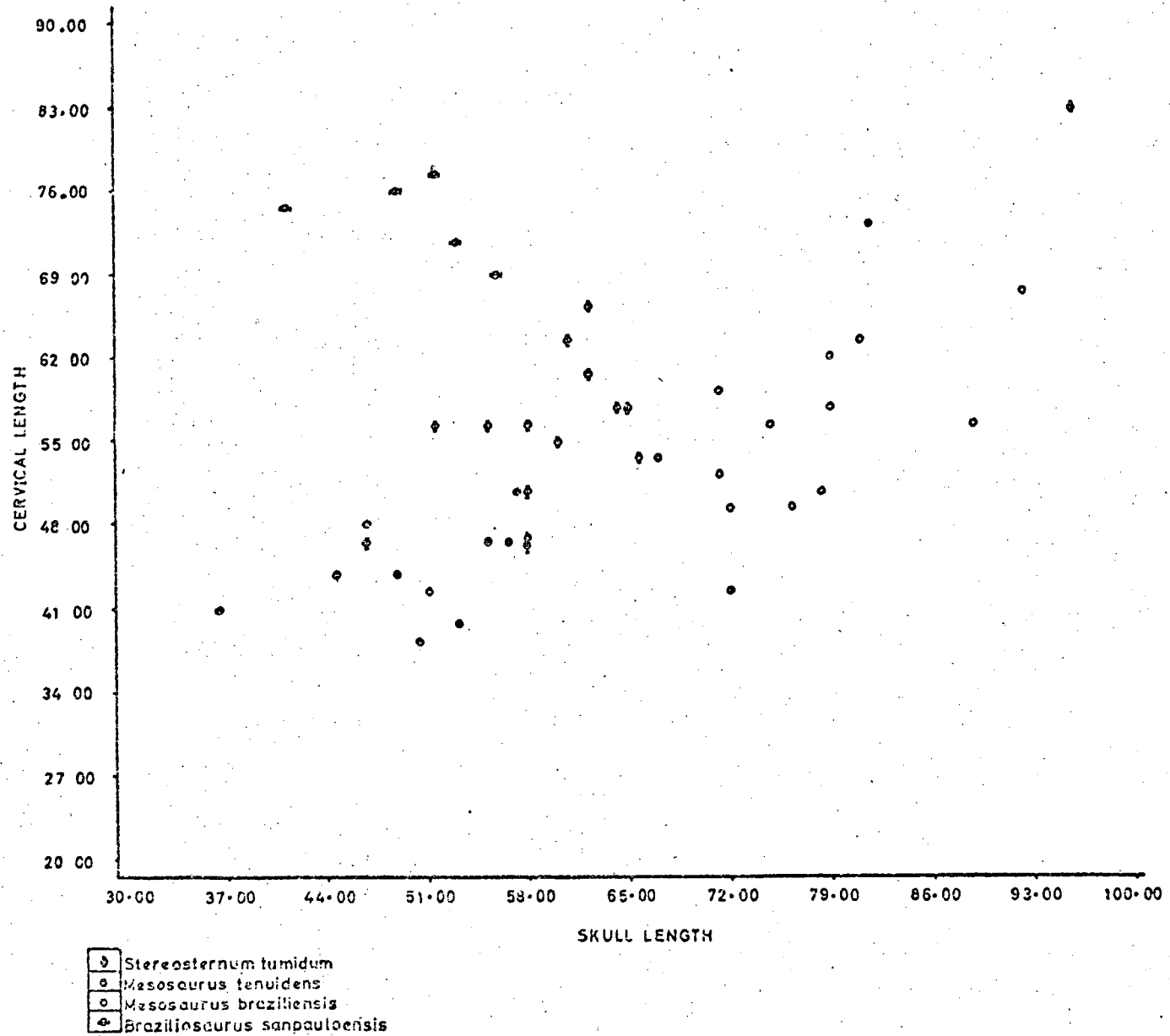


Figure 79: Biplot skull/cervical length; all species of the Mesosauridae.

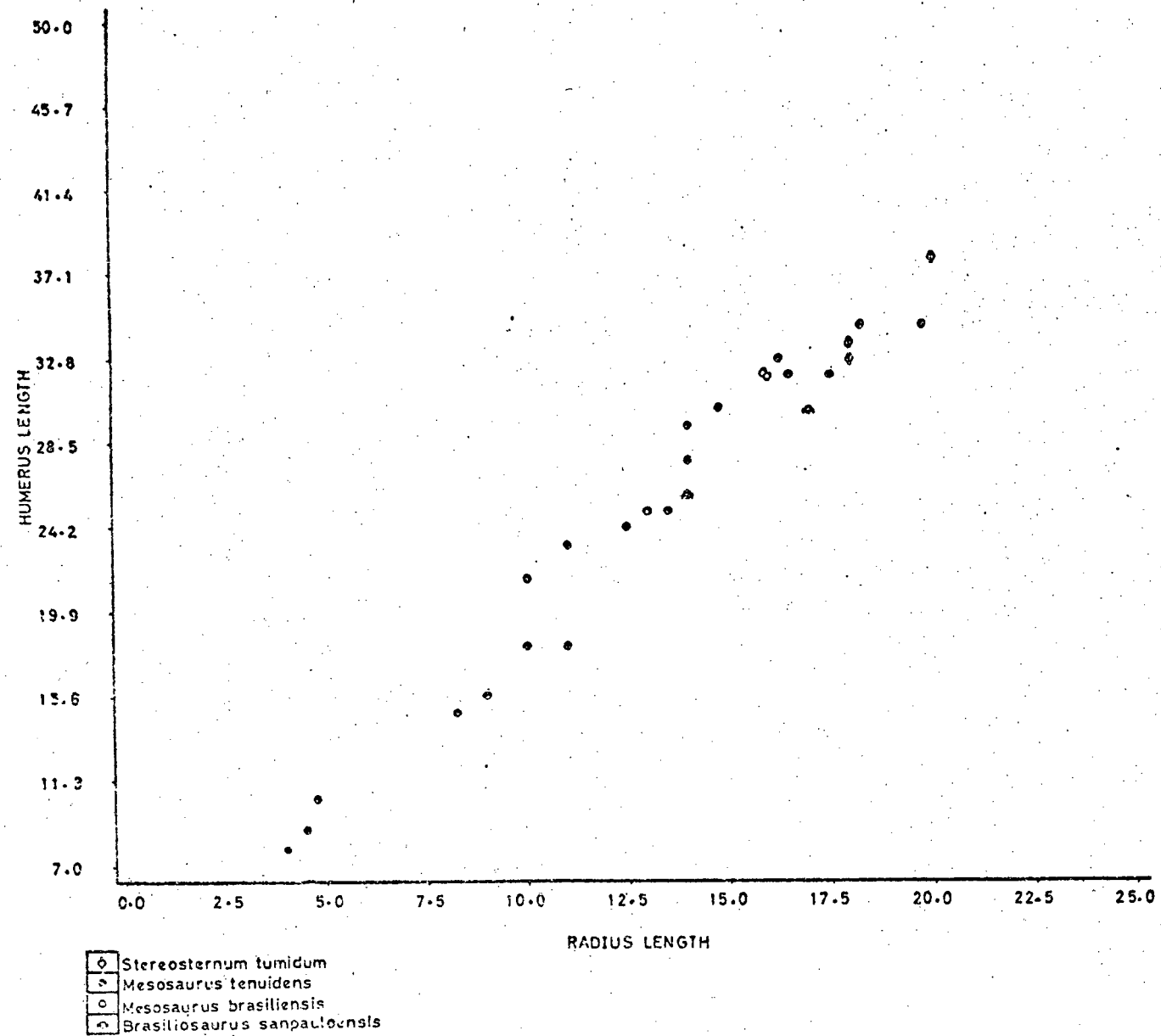
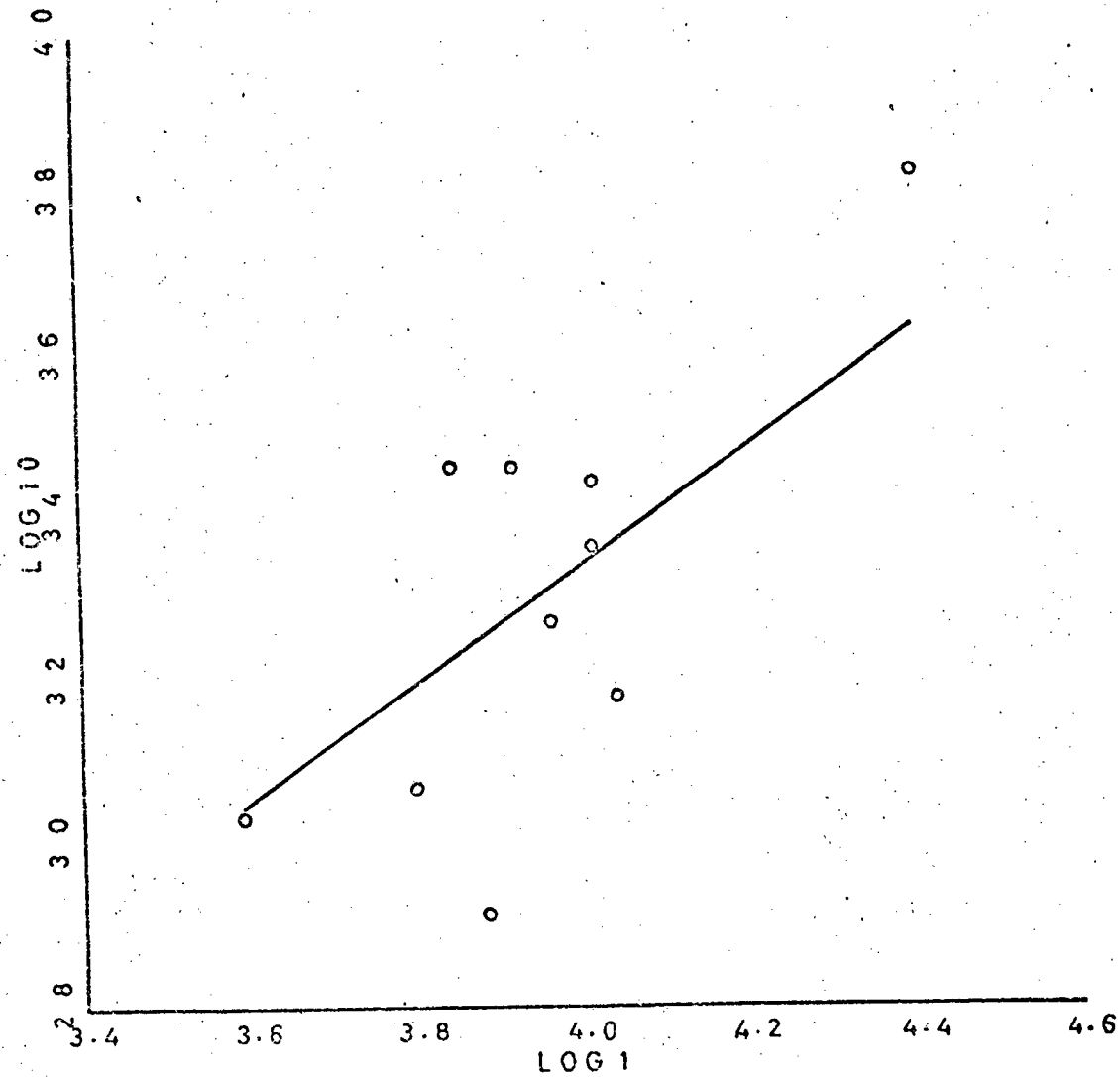


Figure 80: Biplot of radius/humerus length.



<p><i>M. tenuidens</i> x = variable 1 (skull length) y = variable 10 (humerus length) slope = 0.73</p>

Figure 81: Plot illustrating positive allometric growth between skull and humerus.

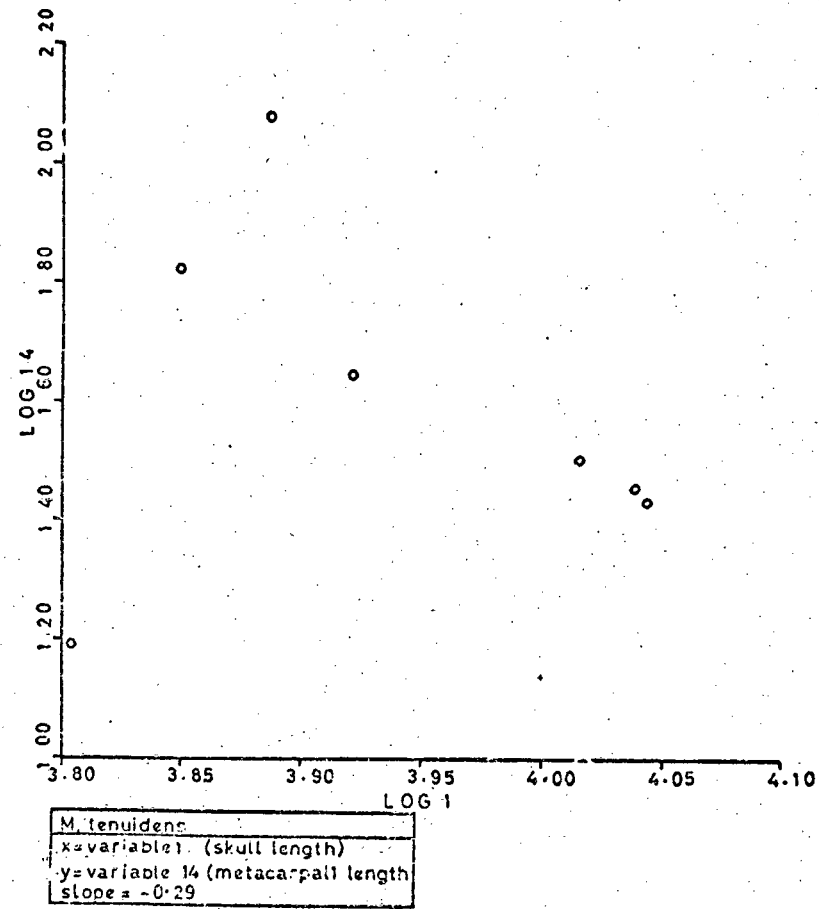


Figure 82: Plot to illustrate negative allometry between skull/metacarpal 1, lengths.

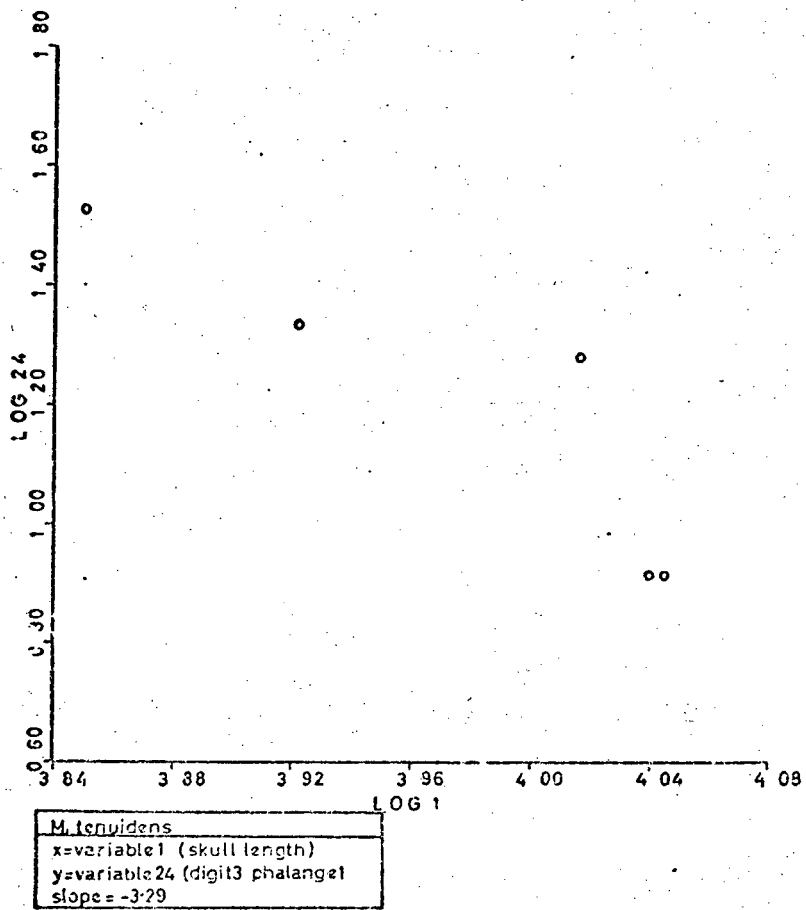


Figure 83: Plot to illustrate negative allometry between skull/digit 3 phalanx 1, lengths

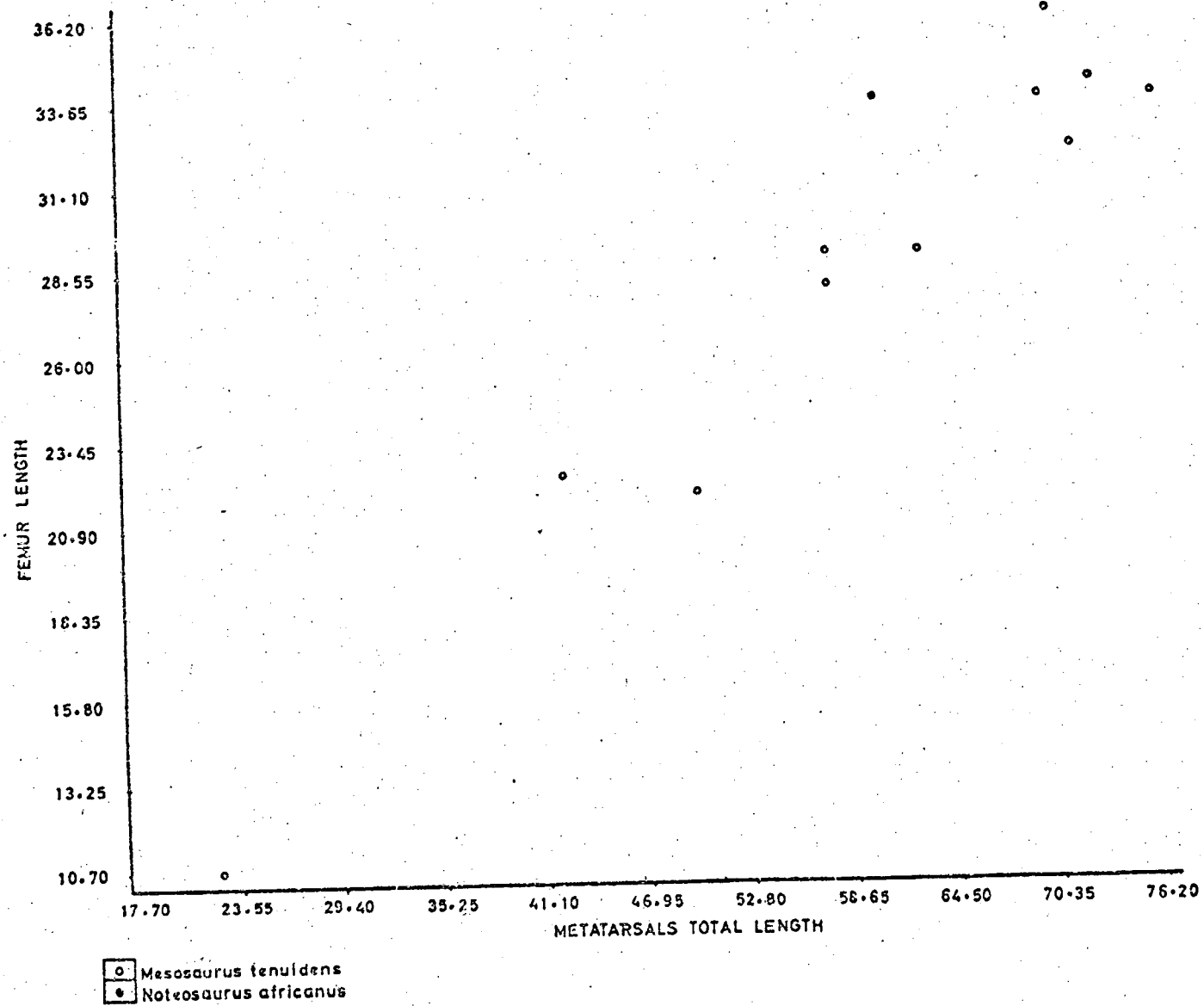


Figure 84: Biplot of femur/metatarsal lengths.

Table 1

Results of Major elements by X. R. F. The first five samples are from Whitehill outcrops. Sample no six from the slab of shale containing Noteosaurus africanus.

Element	1/11/11	1/11/13	2/8/1	2/6/2	6/4/5	Noteosaurus
SiO ₂	73.963	82.994	81.464	76.045	76.869	66.791
TiO ₂	0.870	0.964	0.860	0.837	0.808	0.594
Al ₂ O ₃	18.230	11.134	12.099	15.895	14.131	15.852
Fe ₂ O ₃	0.564	0.446	0.353	0.902	0.789	5.014
MgO	0.025	0.265	0.091	0.308	0.157	1.510
CaO	0.251	0.200	0.83	0.114	0.660	1.035
Na ₂ O	2.927	0.919	1.120	1.708	2.394	2.925
K ₂ O	4.575	3.052	3.269	4.160	4.580	6.090
P ₂ O ₅	0.084	0.120	0.096	0.060	0.100	0.155

K/Al in the Whitehill Samples may indicate Illite as a major clay mineral whilst Illite, Montmorillonite may be the major clay minerals in the Noteosaurus matrix.

1/11/11 and 1/11/13 from Blouputs 33° 44'S, 19° 03'E

2/8/1 from Geelslang 30° 19'S, 20° 54'E

2/6/2 from Klein Tiervlei 31° 10'S, 19° 45'E

6/4/5 from Gellap Ost 26° 12'S, 18° 03'E

Noteosaurus from Victoria West district with the nearest Whitehill outcrops at ± 30° 24'S 22° 59'E

TABLE 2

T-TEST

VARIABLE	GROUP	NUMBER OF CASES	MEAN	STANDARD DIVIATION	STANDARD ERROR	F VALUE	2-TAIL PROB.	<u>POOLED VARIANCE ESTIMATE</u>			<u>SEPARATE VARIANCE ESTIMATE</u>		
								T VALUE	DEGREES OF FREEDOM	2-TAIL PROB.	T VALUE	DEGREES OF FREEDOM	2-TAIL PROB.
Skull length	M.ten.	12	52.108	11.73	3.386	1.29	0.628	-5.78	27	0.000	-5.66	21.86	0.000
	M.bras.	17	75.94	10.34	2.508								
Cervical length	M.ten.	16	46.96	11.94	2.98	1.50	0.429	-2.59	31	0.015	-2.57	29.01	0.016
	M.bras.	17	56.76	9.75	2.36								
Tooth length	M.ten.	7	4.97	2.82	1.067	1.30	0.613	-3.16	24	0.004	-2.97	9.62	0.014
	M.bras	19	8.55	2.47	0.568								
Rib width	M.ten.	27	3.446	1.328	0.256	10.45	0.016	0.13	31	0.898	0.23	27.09	0.817
	M.bras.	6	3.375	0.411	0.168								
Tooth width	M.ten.	7	.6143	0.107	0.040	1.44	0.686	-0.32	24	0.745	-0.35	12.85	0.735
	M.bras.	19	.6316	0.128	0.029								

TABLE 3

T. TEST

VARIABLE	GROUP	NUMBER OF CASES	MEAN	STANDARD DIVIATION	STANDARD ERROR	F VALUE	2-TAIL PROB.	POOLED VARIANCE ESTIMATE			SEPARATE VARIANCE ESTIMATE		
								T VALUE	DEGREES OF FREEDOM	2-TAIL PROB.	T VALUE	DEGREES OF FREEDOM	2-TAIL PROB.
Skull length	M.ten. M.bras.	12 14	52.1083 59.0000	11.731 5.159	3.386 1.379	5.17	.007	-1.99	24	.058	-1.88	14.61	.079
Cervical length	M.ten. M.bras.	16 14	49.9687 55.2143	11.948 6.179	2.987 1.651	3.74	.022	-2.32	28	.028	-2.42	23.08	.024
Tooth length	M.ten. M.bras.	7 12	4.9714 3.4792	2.823 .815	1.067 .235	12.00	.001	1.74	17	.099	1.37	6.59	.214
Tooth width	M.ten. M.bras.	7 12	.6143 .5308	.107 .109	.040 .031	1.04	1.000	1.62	17	.123	1.63	12.89	.127
Rib width	M.ten. M.bras.	27 9	3.4463 2.9722	1.328 .618	.256 .206	4.62	.030	1.03	34	.312	1.44	29.83	.159

Table 4

Summary of data concerning relative growth and variability in mesosaurid material from southern Africa (X = skull length) Y = number of specimens; β - CI = 95% confidence interval for β ; α - CI = 95% confidence interval for α ; r = correlation coefficient; df = degrees of freedom; t = Bartlett's statistics; RL = rejection of linearity in favour of a parabolic relationship.

Y	N	α	β	α - CI	β - CI	r	df	t	RL		
2	11	0.84	-0.59	-0.07	1.94	-0.71	-0.47	0.59	8	0.800	yes
4	8	1.33	-1.33	-5.68	7.62	-4.22	-2.85	0.24	5	1.686	yes
6	11	0.81	0.72	-0.06	1.88	0.62	0.83	0.74	8	0.807	yes
8	10	-0.18	2.53	-3.07	0.91	2.31	2.74	0.20	7	0.069	yes
10	10	0.73	0.43	-1.22	1.61	0.27	0.58	0.75	7	6.683	yes
11	10	0.59	-1.31	-1.42	1.82	-1.49	-1.12	0.59	7	0.028	yes
12	7	-0.35	3.94	-6.91	2.41	3.57	4.20	0.07	4	-0.438	yes
13	7	1.13	-3.90	-3.21	6.48	-4.20	-3.60	0.38	4	0.070	yes
14	7	-0.29	2.74	-4.34	6.17	2.42	3.05	-0.18	4	-1.318	yes
15	7	-0.94	5.61	-4.72	1.36	5.44	5.78	-0.38	4	-2.029	yes
16	7	-1.17	6.41	-7.17	0.30	6.23	6.60	-0.40	4	0.407	yes
17	6	-1.65	8.43	-2.12	1.17	8.37	8.48	-0.72	3	-8.645	yes
18	6	-1.91	9.39	-3.07	0.31	9.32	9.46	-0.91	3	-2.87	yes
19	6	-1.68	7.51	-7.82	-0.15	7.31	7.72	-0.48	3	-2.897	yes
20	6	-2.42	9.84	-9.99	-0.16	9.56	10.12	-0.40	3	-4.118	yes
21	6	-1.00	5.04	-8.62	2.09	4.71	5.37	-0.18	3	-1.595	yes
22	6	-1.87	8.12		1.45	7.66	8.58	-0.33	3	-0.684	yes
63	7	0.28	2.38	-3.45	1.21	2.20	2.55	0.49	4	-2.179	yes
64	8	1.13	3.29	-3.49	2.52	-3.53	-3.05	0.82	5	-0.456	yes

Table 5

Summary of data concerning relative growth and variability;
 Mesosaurid material from southern Africa and South America (x=
 cervical length) Y=variable number; N=number of specimens;
 α - CI = 95% confidence interval for α ; β -CI = 95% con-
 fidence interval for β ; r = correlation coefficient; df =
 degrees of freedom; t = Bartlett's test statisticks; RL =
 reflection of linearity in favour of a parabolic relationship.

Y	N	α	β	α -CI		β -CI		r	df	t	RL
1	47	2.52	.40	2.46	2.58	.06	.76	.30	44	-2.356	yes
2	10	1.01	.44	1.06	1.34	1.03	1.91	.28	7	-1.535	yes
4	37	0.14	.35	.08	.53	-0.95	1.65	-1.05	34	0.000	yes
5	37	-0.88	.08	-0.98	-0.84	-0.31	-.47	.13	34	-0.431	yes
7	16	2.18	.05	2.19	2.25	-0.12	.23	.14	13	-0.464	yes
8	14	-2.11	1.01	-2.39	-2.03	-0.43	2.45	.66	11	-0.784	yes
9	14	1.95	.02	.55	.91	-1.49	1.53	.43	11	-0.628	yes
10	25	0.11	.81	-0.07	.11	.41	1.21	.75	22	-0.232	yes
11	13	-0.30	.33	-0.96	-0.67	-0.36	1.01	.66	10	0.026	yes
12	16	-1.47	1.04	-1.56	-1.29	.37	1.71	.75	13	-0.931	yes
13	11	0.253	-0.56	-1.23	-0.79	-2.99	1.86	.49	8	-0.25	yes
14	10	-8.88	2.71	-3.61	-3.08	-0.80	6.22	.21	7	-0.473	yes
15	10	-3.41	1.37	-0.83	-0.40	-1.33	4.06	.12	7	0.396	yes
16	10	-4.25	1.57	-3.03	-2.70	-0.43	3.57	.56	7	0.625	yes
17	9	-0.19	.52	-0.19	.29	-2.45	3.50	.20	6	1.048	yes
18	8	3.74	-0.54	1.09	1.68	-5.65	4.58	.08	5	0.23	yes
19	9	1.50	-0.17	.60	1.0	-2.59	2.25	.02	6	1.462	yes
20	9	-2.03	.59	-2.10	-1.40	-3.67	4.84	.16	6	0.706	yes
63	9	10.72	-0.201	-0.64	-0.13	-6.28	2.27	.80	6	-0.053	yes
64	26	1.28	-0.08	.69	1.05	-0.94	.77	.24	23	-1.29	yes
65	9	10.41	-1.88	-0.48	.04	-6.08	2.32	.79	6	-0.653	yes

Table 6

Summary of data concerning relative growth and variability in Stereo-
sternum (raw data from Araujo 1976) (X = skull length) Y = variable
number; N = number of specimens; α - CI = 95% confidence interval
for α ; β - CI = 95% confidence interval for β ; r = correlation
coefficient; df = degrees of freedom; t = Bartlett's test statis-
tics; RL = rejection of linearity in favour of a parabolic relation-
ship.

Y	N	α	β	α - CI		β - CI		r	Df	t	RL
4	12	0.49	0.18	-2.06	-1.73	-2.25	2.61	0.50	9	0.231	yes
5	12	1.86	-0.62	0.78	1.06	-2.56	1.33	-0.10	9	0.536	yes
6	14	0.63	0.83	0.94	1.07	-0.16	1.82	0.50	11	0.689	yes
64	8	-9.75	2.65	-7.28	-7.02	-0.41	5.71	0.68	5	2.067	yes

Table 7

Summary of data concerning relative growth and variability in Mesosaurus brasiliensis and Stereosternum tumidum (raw data from Araújo 1976) (X = skull length) Y = variable number; N = number of specimens; α - CI = 95% confidence interval for α ; β - CI = 95% confidence interval for β ; r = correlation coefficient; df = degrees of freedom; t = Bartlett's test statistics; RL = rejection of linearity in favour of a parabolic relationship.

Y	N	α	β	α - CI		β - CI		r	DF	t	RL
4	26	-8.34	2.37	-8.39	-8.13	1.56	3.19	.81	23	-0.316	yes
5	26	-2.50	0.46	-2.64	-2.48	-0.06	0.98	.46	23	0.309	yes
6	31	2.80	0.29	2.66	2.75	-0.02	0.60	.52	28	-0.964	yes
10	9	3.85	-0.08	3.33	3.51	-1.13	0.96	.02	6	-1.286	yes
64	11	-4.77	1.41	-3.44	-3.21	0.23	2.58	.59	8	-1.236	yes

APPENDIX 1

List of variable numbers:

- 1 Skull length
- 2 Skull width
- 3 Number of teeth
- 4 Teeth maximum length
- 5 Teeth maximum diameter
- 6 Cervical region total length
- 7 Cervical region number of vertebrae
- 8 Intergirdle region total length
- 9 Intergirdle region number of vertebrae
- 10 Humerus length
- 11 Humerus width at middle
- 12 Radius length
- 13 Radius width at middle
- 14 Metacarpal 1
- 15 M. carpal 2
- 16 M. carpal 3
- 17 M. carpal 4
- 18 M. carpal 5
- 19 Digit 1 Phalange 1
- 20 Digit 1 Phalange 2
- 21 Digit 2 Phalange 1
- 22 Digit 2 Phalange 2
- 23 Digit 2 Phalange 3
- 24 Digit 3 Phalange 1
- 25 Digit 3 Phalange 2
- 26 Digit 3 Phalange 3
- 27 Digit 3 Phalange 4
- 28 Digit 4 Phalange 1
- 29 Digit 4 Phalange 2
- 30 Digit 4 Phalange 3
- 31 Digit 4 Phalange 4
- 32 Digit 5 Phalange 1
- 33 Digit 5 Phalange 2
- 34 Digit 5 Phalange 3
- 35 Femur length
- 36 Femur width at middle
- 37 Tibia length
- 38 Tibia width at middle
- 39 Metatarsal 1 length
- 40 Metatarsal 2 length

- 41 Metatarsal 3 length
- 42 Metatarsal 4 length
- 43 Metatarsal 5 length
- 44 Digit 1 Phalange 1
- 45 Digit 1 Phalange 2
- 46 Digit 2 Phalange 1
- 47 Digit 2 Phalange 2
- 48 Digit 2 Phalange 3
- 49 Digit 3 Phalange 1
- 50 Digit 3 Phalange 2
- 51 Digit 3 Phalange 3
- 52 Digit 3 Phalange 4
- 53 Digit 4 Phalange 1
- 54 Digit 4 Phalange 2
- 55 Digit 4 Phalange 3
- 56 Digit 4 Phalange 4
- 57 Digit 4 Phalange 5
- 58 Digit 5 Phalange 1
- 59 Digit 5 Phalange 2
- 60 Digit 5 Phalange 3
- 61 Digit 5 Phalange 4
- 62 Digit 5 Phalange 5
- 63 Rib length
- 64 Rib width at middle
- 65 Rib stretched length

APPENDIX 2

LIST OF ABBREVIATIONS

a	=	angular
a ₁	=	arcus of atlas
a con	=	anterior condyle
acr	=	articulation for cervical ribs
add. f.	=	adductor fossa
add. r.	=	adductor ridge
ant cor	=	anterior coracoid
art	=	articular
asf	=	articulation sulcus for fibula
bo	=	basioccipital
bp	=	basipterygoid process
bsf	=	basisphenoid
c	=	coronoid
c ₁	=	pleurocentrum
cap	=	capitulum
cen	=	centrale
cl	=	clavicle
cr	=	cervical rib
d	=	dentary
ds	=	dorsum sellae
ect ep	=	ectepicondyle
ent ep	=	entepicondyle
ent f	=	entepicondylar foramen
ep	=	epipterygoid
ept	=	ectopterygoid
ex	=	exoccipital
f	=	frontal
fc	=	coracoid foramen

fem	=	femur
fg	=	fossa glenoidea
fib	=	fibula
fl	=	fibulare
fm	=	foramen magnum
fno	=	foramen nariale obturatum
gr	=	groove for radial nerve and bloodvessel
h	=	haemal arch
i	=	intermedium
ic	=	intercentrum
icl	=	interclavicle
il	=	ilium
isc	=	ischium
j	=	jugal
l	=	lacrimal
m	=	maxillary
n	=	nasal
na	=	nares
oc	=	occipital condyle
ot	=	otic notch
op	=	opisthotic
p	=	parietal
pa	=	pila antotica
pal	=	palatine
paf	=	proximal articular facet
part	=	prearticular
pc	=	proximal central
p con	=	posterior condyle
po cor	=	posterior coracoid
pf	=	postfrontal

pm	=	premaxillary
po	=	postorbital
por	=	posterior edge of ventral ridge system
pp	=	postparietal
pr	=	proötic
prf	=	prefrontal
psph	=	parasphenoid
pt	=	pterygoid
pub	=	pubis
q	=	quadrate
qj	=	quadratojugal
r	=	rostrum
ra	=	radiale
rad	=	radius
sa	=	surangular
sc	=	scapula
sei t	=	sella turcica
sm	=	septomaxillary
so	=	supraoccipital
spl	=	splenic
sq	=	squamosal
st	=	stapes
sup	=	supratemporal
sup p	=	supinator process
t	=	tabular
tb	=	tibiale
tib	=	tibia
troc	=	trochlea
tub	=	tuberculum
u	=	ulna
ul	=	ulnare

v = vomer

vif = ventral intertrochantric fossa

S.A.M. = South African Museum

U.S.S. = University of Stellenbosch, Zoology Department

APPENDIX 3

Farms and Localities

Aussenkjer	28° 30'S	,	17° 30'E
Blaawboschkolk	32° 25'S	,	19° 42'E
Blouputs	33° 44'S	,	19° 03'E
Brand hoek	31° 36'S	,	19° 33'E
Breeknie	30° 42'S	,	19° 49'E
Buffelbout	30° 17'S	,	22° 28'E
Daberas Ost	25° 30'S	,	18° 20'E
Damascus	33° 16'S	,	21° 57'E
De Bos	31° 58'S	,	19° 42'E
Devondale	29° 33'S	,	24° 17'E
Driekoppen	33° 35'S	,	20° 21'E
Frisgewaagd	33° 47'S	,	21° 48'E
Gannavloer	30° 18'S	,	21° 59'E
Gellap Ost	26° 12'S	,	18° 03'E
Goeie Hoop	28° 20'S	,	17° 00'E
Grasfontein	33° 07'S	,	25° 50'E
Groote Brak	31° 52'S	,	18° 42'E
Gross Daberas.	25° 30'S	,	18° 20'E
Haib	28° 38'S	,	17° 54'E
Hantam Mountains	31° 25'S	,	19° 41'E
Jachtscherm	30° 24'S	,	22° 59'E
Josias de Kocks Kloof	33° 15'S	,	21° 19'E
Kafferdam	30° 48'S	,	19° 22'E
Kirchberg	27° 20'S	,	18° 10'E
Klein Rooiberg	30° 27'S	,	19° 24'E
Klein Spitskop	26° 13'S	,	18° 10'E
Klein Tiervlei	31° 10'S	,	19° 45'E
Kolkop	29° 12'S	,	24° 26'E

Kolegat	33° 12'S	,	22° 38'E
Krantzpoort	33° 02'S	,	24° 03'E
Langberg	30° 44'S	,	19° 00'E
Leeuwergrivier	30° 27'S	,	19° 24'E
Leinster	29° 33'S	,	24° 11'E
Modderdrift	33° 09'S	,	22° 32'E
Narosies	31° 39'S	,	19° 37'E
Patatsfontein	33° 08'S	,	20° 16'E
Roschcommon	29° 12'S	,	24° 26'E
Skimmelkoppe	31° 52'S	,	19° 42'E
Vlakte onder Hangklip	33° 10'S	,	22° 10'E
Waterval (Klein)	33° 59'S	,	22° 20'E
Zwartskraal	33° 05'S	,	22° 31'E