CORRECTIONS

1) The name Megapedetes augaeus should be replaced by the name Megapedetes aegaeus at all points where it occurs.

2) Page 51, line 6 : for "antero-lateral" read "antero-ventral".

3) Page 338 : Delete the paragraph beginning "The second line of evidence ...."

Insert the following :-

The second line of evidence comes from physiological investigations carried out on Pedetes surdaster (Muller et al., 1979). The animals used are actually described as Pedetes capensis but since the work was done in Kenya it was presumably carried out on P. surdaster. In this work a number of physiological parameters believed to be important in adaptation to hot arid environments (e.g. temperature regulation) were investigated. A distinction is made between mammals which are adapted for life in hot desert environments and particularly those which are active above ground during the day and generalised fossorial mammals that may be found in other than desert environments. It is suggested that P. surdaster has physiological characteristics of fossorial mammals rather than of specifically desert-adapted forms. Examples of features in which P. surdaster seems not to be desert-adapted include its inability to regulate its body temperature at high ambient temperatures and its inability to produce highly concentrated

urine. Muller et al. (1979) suggests that the physiological features of P. surdaster help to explain why this animal does not invade desert environments but can survive in semi-arid environments: also, it may be that fossorial activity has been an important aspect of life in pedetids throughout their evolution.

4) Page 367 : insert at top of page "In all Tables measurements are given in mm."

Title : The Recent and Fossil Affinities of the Genus *Pedetes* (Mammalia : Rodentia)

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Degree : Doctor of Philosophy

Term of Submission : Michaelmas Term, 1982

Abstract : An assessment is given of some of the possible relationships of the living rodent genus *Pedetes*, based on a study of the comparative osteology of both living and fossil forms in the Family Pedetidae. A short examination of the views of previous authors on the position of *Pedetes* and the Family Pedetidae is given and the basic methodology, used in this study, is outlined. The view is put forward that, in a group containing a high proportion of fossil members, only osteological characters can be used in assessing relationships as only these characters can potentially be investigated directly in all members of the group.

A description is given of the skeleton of *Pedetes surdaster* and contrasting points in the skeleton of *Pedetes capensis*, the other living species, are listed. Descriptions are also given of fossil material including *Megapedetes pentadactylus*, *Parapedetes namaquensis*, a new species of the genus *Pedetes* from Laetoli and fragmentary material from a number of sites including Rusinga, Fort Ternan, Maboko, Olduvai Gorge, Taung, Arrisdrift and Elisabethfeld. These descriptions are accompanied by figures, illustrating some of the material, and extensive tables, containing measurements.

An analysis, based on cladistic methodology, divides the Family Pedetidae into two subfamilies: one, Subfamily Parapedetinae, contains only the species *Parapedetes namaquensis*: the other, Subfamily Pedetinae, contains all the other named species, four species of *Pedetes* - *surdaster*, *capensis*, *gracilis* (from Taung) and the new species from Laetoli - and *Megapedetes pentadactylus*. Material of *Megapedetes augaeus* has not been examined but on the basis of the published description its validity must remain doubtful. Much of the fragmentary material has not been ascribed to any of the named forms but appears to represent at least two further species. Consideration is also given to possible functional interpretations of some characters.

THE RECENT AND FOSSIL AFFINITIES OF THE GENUS

PEDETES (MAMMALIA : RODENTIA)

Christopher Davies

St. Peter's College

Oxford

Michaelmas Term 1982

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CHAPTER 1

Introduction.

The Order Rodentia Bowdich, 1821 and the position of the Family Pedetidae Owen, 1847.

The Family Pedetidae has always proved something of a problem to rodent taxonomists: it forms a morphologically closely-knit group with no obvious relationships to any other rodent group. Simpson (1945) stated: "... [Pedetids] have been placed in irreconcilably different systematic positions and really are of quite unknown affinities." Likewise Wood (1974) stated: "... there are no rodents known from any part of the world that look to me like possible relatives." The family, at present, is considered to consist of three genera: there are probably seven species although a dedicated splitter might, even on the basis of available evidence, recognise at least an additional three fossil species. There are two living species (see Chapter 2) belonging to the genus Pedetes Illiger, 1811: also ascribed to this genus are three fossil species from the Plio-Pleistocene (see Chapters 5 & 6) of which one is probably not distinguishable from the living species found in southern Africa. Two genera can be recognised in the Lower Miocene (see Chapters 3 & 4); further remains, of this same age, represent a distinct species but are so fragmentary that they must be described as of indeterminate genus (see Chapter 6). Some fragmentary material from the Lower Miocene of

South West Africa, from Elisabethfeld and Arrisdrift, can probably be ascribed to species already described and named but it may be thought to represent new species (see Chapter 6).

From the time of the first description of Pedetes, by J. R. Forster (1778), under the name Yerbua (now suppressed), until 1902 the family was believed to consist of a single living genus and species - Pedetes capensis (Forster, 1778). In 1902 a second living species, Pedetes surdaster Thomas, 1902, was described: this species has, subsequently, often been equated with Pedetes capensis but arguments will be presented below in favour of its status as a separate species. Between the two World Wars a further living species, Pedetes angolae Hinton, 1920, now considered a probable subspecies of P. capensis, was described. Also at this time two fossil species were described and placed in the genus Pedetes: these were Pedetes gracilis Broom, 1930 and Pedetes hagenstadi Lyle, 1931 (in Dreyer & Lyle, 1931). A new genus and species was described from the Lower Miocene deposits at Elisabethfeld and was named Parapedetes namaquensis Stromer, 1924 (in Stromer, 1923). Finally MacInnes (1957) described Megapedetes pentadactylus from the Lower Miocene of Kenya and Sen (1977) described Megapedetes augaeus from the Middle Miocene deposits of Anatolia; the present work describes some fragmentary Lower Miocene material, including some representing a species that is left unnamed, and also describes a new fossil species of the genus Pedetes from Laetoli in Tanzania.

In early classifications of the Rodentia the position of Pedetes was sometimes unassigned as in Waterhouse (1839) in

which a number of genera, including Helamys (Cuvier's junior synonym of Pedetes), are listed after the main classification on the grounds of their uncertain position. In other classifications Pedetes was placed, together with the jerboas and the gerbils, in a single family. This was done by Illiger (1811) in which genera 30 - 32 (Dipus, Pedetes and Meriones) are placed in a single Family Macropoda. As this name suggests the principal reason for this association appears to have been the shared adaptations for saltatorial locomotion, especially the presence of greatly elongated hindlimbs, coupled with the presence of reduced forelimbs.

The grouping with the gerbils does not seem to have persisted for very long and the latter were moved into association with the muroids. However, the grouping of the dipodids and Pedetes did persist for a considerable time and is found in the classifications of Gervais (1849), Brandt (1855), Alston (1876) and Flower & Lydekker (1891). In the last three classifications the genus Pedetes is placed in its own Subfamily Pedetinae within the Family Dipodidae. The first placing of Pedetes in a family of its own actually predates the previous four classifications: Owen (1847) uses the term Pedetidae as a family-group name but claims that he is quoting from Cuvier (1829). The latter uses the generic name Helamys, not Pedetes, and does not place the genus in a separate family. This leads one to wonder whether Owen's designation of a Family Pedetidae was not, in fact, an error.

Thomas (1896), although following Alston (1876) in many respects, moved Pedetes from the Family Dipodidae stating:

"... its differences from all the Dipodidae being infinitely greater than any of theirs from each other." He also moved the genus out of the Myomorph Series of rodents, where it had been placed while in association with the dipodids, and placed it, in its own Family Pedetidae, at the beginning of the Hystricomorph Series. The reasons for this move, although given, are not really adequately explained. Tullberg (1899 & 1900) retained Pedetes within a Subtribe Myomorphi which formed part of the Tribe Sciurognathi. Pedetes was placed in its own family but was now associated, not with the dipodids, but with the anomalurids: the two families, Pedetidae and Anomaluridae, were placed in the Section (= Superfamily) Anomaluroidei. An association between these two families seems to have first been proposed by Winge (1887).

The classification of Miller & Gidley (1918) retained the association of pedetids and anomalurids but also reassociated pedetids and dipodids by placing these three families, together with a number of others, in a single Superfamily Dipodoidae (sic.). Simpson (1945) comments that this superfamily is an artificial grouping and the attempt by the authors to fit awkward groups in, even without good evidence, can be seen in the consideration of the position of Pedetes. Within the Dipodoidae the Family Pedetidae is placed in the "Four-cusped series" in which the cheekteeth are described as: "... based on an underlying quadritubercular structure, the hypocone always entering into the essential mechanical scheme of the crown." A short while later the Family Pedetidae is described as having cheekteeth with: "... all

trace of the original crown structure lost." If this second statement is accurate, which seems to be generally accepted (Wood, 1965a), then there is no basis for placing the Family Pedetidae in any higher taxon defined on the crown structure of the cheekteeth.

Weber (1928) also associated pedetids and anomalurids within a single Superfamily Anomaluroidea. However he was one of the first "modern" authors not to attempt to group superfamilies into suborders. Romer (1933 & 1945) also placed together the Pedetidae and Anomaluridae. In his first classification (Romer, 1933) he placed the resulting Superfamily Anomaluroidea in the Infraorder Sciuromorpha even though one of the characteristics of the infraorder was that the masseter muscle did not pass through the orbit and infraorbital foramen whereas, in every member of the Superfamily Anomaluroidea, the infraorbital foramen is enlarged and m. masseter medialis passes through it. Subsequently, in his second classification (Romer, 1945), the Anomaluroidea was placed in the Suborder Hystricomorpha although, by implication, only because it would not fit anywhere else. Simpson (1945) noted that the grouping of pedetids and anomalurids in a single superfamily appeared to have the support of general consensus but added: "... this is not based on any very strong evidence or reasoning and is at least as likely to be wrong as right." This was apparent in the formal classification in which Pedetidae was placed, incertae sedis, in the Superfamily Anomaluroidea (which, incidently, was placed incertae sedis in the Suborder

Sciuromorpha).

The Family Pedetidae was placed in its own Superfamily Pedetoidae (sic.) by Ellerman (1940). As in Tullberg (1899) this group was placed in the Myomorph Series of the Sciurognathi. Contrary to Simpson (1945) the Superfamily Pedetoidae is placed between the anomaluroids and the ctenodactyloids and not between the ctenodactyloids and muroids. However it seems likely that serial position held no especial phylogenetic significance since it is explicitly stated that there is little basis for supposing a close relationship exists between the pedetids and the anomalurids and a number of characters are quoted in support of this view. By the time Volume III was published (Ellerman, 1949) a slight change in emphasis had occurred and there seems to be an, at least implicit, acceptance of association between the pedetids and the anomalurids although not of the placing of the pedetids in the Sciuromorpha. With regard to the classification at the subordinal level Ellerman (1940) uses key characters which prevent the placing of the pedetids in either the Hystricomorpha or the Sciuromorpha. This only leaves the Myomorpha as a possibility. The claim is made that pedetids are archaic rodents which may be a hint that they do not properly fit in any of the suborders.

Several classifications of rodents have been produced by A.E. Wood and generally the Family Pedetidae has been left unassigned, much in the manner of and for similar reasons to Waterhouse (1839). Wood (1947) lists four African families, including Pedetidae, as unassigned: in Wood (1955) the family

is placed "c.f. Sciuromorpha or Theridomyomorpha inc. sed." which is really no improvement. Wood commented on this classification, as a whole, that it would probably be as well if it were the last attempt, for the present, to produce a subordinal classification of Rodentia and that, should it not receive a reasonable degree of acceptance, "... it would probably be advisable to throw out everything above the level of the superfamily until we know much more about rodent paleontology and evolution." However Wood (1958) returns to associating anomalurids and pedetids which are placed as a new, unnamed, suborder although as a preferred alternative, he leaves the two families unassociated and unassigned in his second classification: this is also done in Wood (1965b) in which it is suggested that the pedetids had a derivation from primitive rodent stock independent of all other rodents. This position was also put forward in Lavocat (1956), in discussing Wood (1955). Romer (1966) also followed Wood (1958) in leaving the pedetids unassigned.

More recently little effort has been made to produce an overall classification of the Order Rodentia presumably because of the magnitude of the task. Various groups have, however, been studied in detail and classifications of these groups produced. Also some workers have studied single or small suites of characters throughout several groups or even the whole order. A number of these studies have looked at the relationships of the pedetids. Work on the cephalic arterial system (Bugge, 1974) supports the association of pedetids and anomalurids which, on this basis, have been

placed in a new Suborder Anomaluromorpha Bugge, 1974 which is the formal designation of the new suborder proposed in classification I of Wood (1958). Parent (1976), working on the structure of the middle ear, also claims that the evidence supports a close relationship between anomalurids and pedetids. Countering this Fischer & Mossman (1969) claim that the structure of the foetal membranes shows no evidence of close relationship between the two groups and Luckett (1971), while stating that there are a number of morphological similarities in the foetal membranes, suggests that these are primitive characters that would, in consequence, have low taxonomic value. Wood (1974 : 48) points out that on the evidence of the foetal membranes the genera Pedetes, Anomalurus and Ctenodactylus are supposed to be closely related yet the fossil history of Ctenodactylus is separate back to the Eocene and that, therefore, the evidence from these structures should not be given too much weight. George (1980) states that studies of the chromosomes of the living species of Pedetes provide no basis for stating possible relationships.

The fossil record has proved of little help in determining the relationships of the pedetids. Relatively unworn lower cheekteeth of Megapedetes pentadactylus, which has the least specialised cheekteeth of any known pedetid, have been examined by Lavocat & Michaux (1966) and are said not to provide any evidence for close relationship between the pedetids and anomalurids. Wood (1974) has criticised the analysis presented by Lavocat & Michaux (1966) on the grounds

that the premolar was interpreted as a permanent tooth when it may, in fact, be a deciduous one: but there does not seem to be much disagreement over the conclusions. The statement by Wood, quoted at the beginning of this chapter, is especially pertinent, coming from a scientist who has spent a lifetime studying rodents from many epochs and many localities, and probably represents one of the best statements of the current state of knowledge of pedetid relationships.

The value of the fossil record:

Up to the present day, as briefly noted above, the fossil record has proved of little value in elucidating the relationships of the Family Pedetidae. The group first appears in the fossil record in the Lower Miocene of East and South West Africa and specimens from that time, ascribed to it, show many of the essential adaptations found in the living forms. There is a relatively long gap, of some 5 - 6 million years, in the Upper Miocene and Lower Pliocene, in which there are no fossil pedetid remains (and, in Africa, relatively little fossil material of any other group) but the evolution and relationships within the family can be hypothesised with some degree of certainty on the basis of the reasonable amount of evidence now available. The time of extinction of the Lower Miocene genera cannot be known until a reasonable fossil record for the Upper Miocene and Lower Pliocene is known. However, the overall evolution of the family, as measured by the degree of morphological change, has been relatively slow since the beginning of

the Miocene.

Particularly with regard to the possible relationships of the family to other rodents the absence of a pre-Miocene fossil record for the pedetids is of great moment. The morphological conservatism of the family since the Lower Miocene means that if the pre-Miocene evolutionary rate were similar to the later one then the history of the family must be extremely long: this would suggest that the pedetids are derived directly from the most primitive rodents. An alternative possibility is that the pre-Miocene evolution of the pedetids was rapid as the family evolved to fill a vacant niche and subsequently, adapted for this niche, selective pressure and, consequently, rate of morphological change have been lower. Since the pre-Miocene fossil record in Africa is not extensive the absence of pedetids in it may mean nothing although it may perhaps be significant that of the known Miocene rodents of Africa the pedetids are the only ones that provide no evidence for invasion or of ancestry in the remains from earlier deposits (Simons & Wood, 1968). Even the anomalurids are now reported to extend back to the Oligocene with a fragment of ulna reported from the Fayum deposits (Lavocat, 1973 : 196).

Since the only records of the family outside Africa are the occurrences of Megapedetes in Greece (Tobien, 1968), Turkey (Sen, 1977) and Israel (Goldsmith et al., 1982) it seems reasonable to assume that the Family Pedetidae evolved within Africa. Presumably the group arose from amongst the early rodents occurring in the continent and such a derivation could well mean that the pedetids are not especially closely

related to any other rodent group. Lavocat (1956), Wood (1965b) and Cooke (1968) assume that the Family Pedetidae is an African endemic family that evolved from the early African rodent stock. Further information on this early stock will, hopefully, enable resolution of the problem of the relationships of the pedetids. An alternative possibility, however, is that the Family Pedetidae evolved outside Africa, migrated in, but subsequently became extinct in its original area of occurrence: such a suggestion was made in Simons & Wood (1968). The evidence against this hypothesis is all negative, being based on the absence of finds, and it cannot therefore be entirely discounted. It would be an extremely speculative hypothesis and on the present evidence it is probably more reasonable to believe that the pedetids are a basically African group and occurrence outside this continent is due to migration out.

Material and Methods:

This research has involved the detailed study of both Recent and fossil pedetid material housed in a number of Research Institutes and Museums in both Europe and Africa. A list of these institutions and an abbreviation for most of them, for use in this work, are given in Appendix I: also listed in this appendix are the species held in each of these collections together with, in the case of the fossils, the site from which the material came. Detailed lists of the material examined are given in Appendices II - VI with each appendix listing the specimens described in one of Chapters

2 - 6.

All the material has been carefully examined and described: much has also been measured using Mitutoyo dial calipers accurate to 0.05mm. For most purposes the measurements have been rounded off to an accuracy of 0.1mm. In calculating mean values for measurements the original values were used with only the final result then being rounded off. Some of the material was sketched, drawn using a Wild M5 binocular microscope with a drawing tube attachment or photographed; this provided the material from which the figures have been largely prepared. Only in the case of the figures of the bones of P. surdaster, based on OUM specimens and accompanying Chapter 2, was the original material available for consultation during the actual preparation of the illustrations: in all other cases, except for the auditory bulla of Megapedetes pentadactylus in which case a cast of Sgr.258'48 was available, only the drawings and photographs of the material were available.

In dealing with the fossil material only a relatively small number of individuals were represented and often only by fragmentary material. This problem is common to much palaeontological work and, while it is to be regretted, it is largely beyond the control of workers in the subject. However an equally serious shortage of material is found if it is desired to examine the post-cranial skeleton or the whole corpse in the living species. There are probably few palaeontologists now who would organise a collecting trip with the intention of only collecting skulls and leaving most

of the post-cranial material behind, although circumstances may ultimately force them to take this action (Attridge et al., 1964). Thus the shortage of fossil material for study is generally related to its original preservation, or lack of it, rather than to the way that it was collected and stored. In the case of Recent material many collections are still being made on the traditional basis of only skulls and skins and often no effort is made to collect post-cranial material or to preserve whole corpses. It is recognised that there are problems in preparing a post-cranial skeleton in the field and that, subsequently, it requires more storage space but it is felt that Recent mammalogists should begin to pay more attention to the post-cranial skeleton as a potential source of taxonomic data and that any modern collecting expedition should preserve the whole skeleton in a proportion of the animals collected, even if, as will often be the case, this results in loss of parts of the skin. The preservation and storage of whole corpses presents even greater problems than the preservation of post-cranial skeletons: nevertheless any expedition should be encouraged to preserve a small number of corpses whole, in anticipation of further study.

In the present study the post-cranial material of the living species that was examined was almost entirely confined to two collections: M.J. Coe's collection (now in the University Museum, Oxford) and the collection in TILLMIAP, which was started by L.S.B. Leakey for the purpose of providing a reference collection of Recent material with which the fossils could be compared. Both of these

collections only contain material of the East African springhare, Pedetes surdaster, and there is very little material of the southern species to compare with it. Material of the latter species is scattered amongst a number of museums, none of which possesses much more than the equivalent of a single skeleton. Thus the comparative work involving the post-cranial skeleton has had to be almost completely restricted to P. surdaster when the living species are considered. No attempt was made to collect further material, either fossil or Recent, because the cost and organisational problems, such as obtaining the required permits, could not be justified when it was only desired to collect material of one species. This is especially true of fossil material, particularly as pedetids do not seem to be especially common fossils, and it would not be sensible to attempt to organise an excavation solely with the aim of collecting pedetid fossils. In the case of the Recent forms, also, it would have proved difficult to arrange for the shooting of numbers of springhares, at the required localities, and their export from the respective countries.

The major part of this work comprises descriptions of the osteology of the forms concerned. In the case of the fossil material it is hoped that, together with the diagrams accompanying them, the descriptions will assist other workers in the identification of isolated bones, especially from the post-cranial skeleton. The osteological description of the living species provides a basis against which the fossil material can be compared. On the basis of the comparative

osteology consideration is given to possible functional interpretations of the fossils by using available information relating form and function both in the living species and in other mammals. Possible ecological interpretations are also considered.

Hypotheses about possible function and ecology in fossil forms involve some consideration of the probable soft anatomy of the form concerned, especially consideration of the muscular system. For the present work much of this interpretation was derived from descriptions of mammalian soft anatomy, and particularly rodent anatomy, in the literature. Dissection of the Recent forms shows that this approach is essentially accurate. Anatomical nomenclature has generally followed that of the 35th Edition of Gray's Anatomy (Warwick & Williams, 1973) but some exceptions occur, such as the use of the name astragalus rather than talus for the tarsal articulating with the distal end of the tibia.

Also using the data of comparative osteology the intra-familial phylogeny of the Family Pedetidae is hypothesised and some discussion is given of the possible relationships with other rodents. The only remains of fossil forms are parts of the hard skeleton so that any classification, or phylogenetic analysis, of a group containing fossil forms can only be made on the basis of the osteology if the fossil representatives are to assume equal importance in the analysis as do the living representatives. In the case of a group such as the pedetids, in which the majority of the members are fossil forms and the group itself is small, a

worthwhile phylogeny can only be produced if information from both fossil and Recent forms is treated as of equal weight. With the Recent forms the soft tissues contain a considerable amount of potential taxonomic information but none of this information is available for comparison in the fossil forms. The soft anatomy hypothesised in considering possible functional anatomy in the fossils contains no taxonomic information because it is derived entirely from the skeletal anatomy and hence merely expresses, in another way, the taxonomic information contained in the latter. It is for this reason that this work has concentrated on osteology since a major aim was to produce a taxonomic assessment of the pedetids.

The taxonomic assessment of the pedetids, especially the more detailed intrafamilial assessment, has been mainly carried out according to cladistic principles (Hennig, 1966; Cracraft, 1974) although this philosophy has not been followed slavishly. Hypotheses of relationship are based on the presence of postulated synapomorphies and where these produce incongruities with the most firmly supported hypothesis the possible occurrence of parallelism is discussed. While the principles of cladistic analysis in some form are rather generally accepted (Griffiths, 1972 : 20 - 21 ; Mayr, 1974 : 97 - 98) and have been, in a less rigorously expressed form, for many years the principle of turning a phylogeny directly into a classification is much more controversial. In the case of the pedetids the group is sufficiently small that one major problem of a cladistic

classification, namely rank proliferation, is not found. However the principles for producing a strictly cladistic classification (Cracraft, 1974; Hennig, 1966; Mayr, 1974) have not been adhered to; entirely fortuitously the classification produced for the genera is indistinguishable from a true cladistic classification but when species are considered this is not the case as it was felt unnecessary to produce extra ranks between genus and species within the genus Pedetes. Discussion of the possible relationships of the pedetids to other rodents is based on the principles of cladistic analysis but in such a way that it more closely resembles what is often termed the evolutionary systematic approach to classification (Mayr, 1974; Cracraft, 1974). A rigorous analysis has not been attempted as it was felt to represent too great a task requiring, as it would, a detailed study of representatives of all the known rodent families and, preferably, of every known genus in order that the correct distribution of character states could be determined. Failure to do this would render the cladistic analysis no more rigorous than any other approach and consequently it was felt to be better not to attempt such an analysis rather than to do one on the basis of partial knowledge and so produce a classification, apparently of great rigour, but which was not, in fact, at all firmly based.

CHAPTER 2

The living species of the genus Pedetes Illiger, 1811.

Synonymies:

1) Genus :-

1778 Yerbua — Forster J.R. K. svenska VetenskAkad. Handl. 39 111
This name has now been suppressed by the International Commission on Zoological Nomenclature (1965 - 66) for the purposes of the Law of Priority, but not for those of the Law of Homonymy, and is placed on the Official Index of Rejected and Invalid Generic Names in Zoology as No. 1758. (Opinion 730 : Bull zool. Nomencl. 22 : 84).

1811 Pedetes — Illiger C. Prodromus Systematis Mammalium et Avium. Genus 31 pp. 81 - 82 Berlin. (N.B. On p.302 Yerbua Forster is synonymised with Dipus (genus 30)).

1817 Helamys — Cuvier G. Le Règne Animal distribué d'après son organisation. 1st. Edition Volume I pp. 202 - 203 Paris. (The name is ascribed to "Fred. Cuv." but no reference is given : it is proposed as an improvement on Pedetes).

1821 Helamis — Cuvier F. In : Levrault F.G. [Ed.] Dictionnaire des Sciences Naturelles. Volume XX pp. 342 - 344 Paris ; Strasbourg.

1843 Pedestes (laps. cal.) — Gray J.E. List of the Specimens of Mammalia in the Collection of the British Museum. p.130 B.M. Trustees : London. (N.B. On p.xxv the genus name is spelt correctly as "Pedetes").

Original generic diagnosis:-

"Genus 31. PEDETES (πηδητης saltator) (Hupfer). Dentes Primores utrinque 2 pagina antica laevigata. Pro Laniariis diastema. Molares abrupti, complicati tritorii utrinsecus supra infraque 4. Rostrum acutum. Auriculae longitudine capitis. Cauda longissima, floccosa. Mammae apertae 4 pectorales. Antipedes breves pentadactyli, digitis aequalibus. Scelides antipedibus triplo longiores fortiores, tetradactylae, digito secundo reliquis majore, extremo illis breviore. Ungues falculares, maniculorum fossorii digitis longiores.
Species. Dipus Cafer LinGmel." Illiger, 1811.

A modified generic diagnosis based on both the Recent and the fossil members of the genus is given in Chapter 7.

2) Species :-

A) Pedetes capensis:

1778 Yerbua capensis — Forster J.R. K. svenska VetenskAkad. Handl. 39 116 - 119

The specific name capensis has now been validated by the International Commission on Zoological Nomenclature (1965 - 66) for this species as No. 2073 (Opinion 730 : Bull. zool. Nomencl. 22 84).

1779 Mus cafer Pallas P.S. Novae Species Quadrupedum e Glirium Ordine. Species 29 pp. 87 - 88 Erlangae.

1834 Pedetes typicus Smith A. S. Afr. Quarterly J. 2nd. ser. 2 169.

Original species diagnosis:-

"Cauda floccosa, palmis pentadactylis, plantis tetradactylis. CORPUS magnitudine circiter Leporis timidi, pilis mollibus consitum, colore e fusco fulvo, subtus helvo.

CAPUT lateribus compressum seu subcuneatum, antice fronte extrorsum arcuata.

ORE infero, supra mystacibus elongatis plurium ordinum cincto.

DENTES Incisores in maxilla utraque duo, validi, exserti, contigui, occursantes, paralleli, incurvati, quadrati, apice oblique scissi. Superiores ex maxilla superiore exserti, labium superius perforantes, & habent inter se foramen saccatum, nullo orificio, quod sciam, in os interius exeunte. Inferiores quoque e maxilla inferiore exserti.

Canini nulli.

Molares, ab incisoribus remotissimi, 4 utrinque.

OS exiguum, longitudinale. Inter os & foramen, ex quo dentes superiores prodeunt, membrana musculosa, transversa, labium superius format infra incisores.

LINGUA exigua, teres.

PALATUM rugosum.

NARES oblongae, rostrum rubicundum, nudum.

OCULI laterales, amplissimi, protuberantes, nocturni.

AURICULAE longitudine fere capitis, amplae, patulae, cochleatae, apice & intus nudae, venosae.

TRUNCUS thorace compresso, abdomine & femoribus pro reliqua corporis proportione dilatatis.

MAMMAE 4, duae utrinque, pectorales, vicinae, sub pedibus anticis, at in feminis paulo retrorsum.

FORAMEN amplum, saccatum, prominulum, rotundum, rugosum, contractile, inter clunes situm, intra quod anus & genitalia.

ANUS posticus.

PENIS in postica directus, glande reticulata, verrucosa.

PEDES, PALMAE quinquedactylae, brevissimae, exiles, subcylindricae.

DIGITIS tribus mediis subaequalibus, lateralibus brevioribus. Subtus callus torosus, nudus, parti interiori substratus: parti exteriori lobus lateralis, profunde divisus, extus nudus, intus pilosus, adhaeret. UNGUES validi, subincurvi, subsolidi, fere longitudine digitorum.

PLANTAE longissimae, validae, tetradactylae. FEMORA & TIBIAE validae, musculosae, elongatae, pilosae, hirtae (versus tarsos minus hirtae).

METATARSI TARSIQUE longissimi, vestiti. DIGITI medio longiore, lateralibus brevioribus, extimo magis breviore.

CALLUS sub calcaneo oblongus.

UNGUES mediocres, validi, subsolidi.

CAUDA longissima, (Corpore longior) pilis densis, longis, fulvis, vestita. Apex caudae incrassatus, floccosus, pilis elongatis nigris." Forster, 1778.

B) Pedetes surdaster:

1902 Pedetes surdaster Thomas O. Ann. Mag. nat. Hist. Lond. 7th series 9 440 - 441

Original species diagnosis:-

A short diagnosis was not given, the main description is as follows : "Size, as judged by skull, rather less than in P. caffer, but part of this difference is due more to the smaller nasals and bullae than to a real reduction in general size. Nasals conspicuously smaller both in length and breadth, not reaching back to the level of the hinder margin of the anteorbital fossa. Premaxillary processes on each side of nasals very narrow, barely 1 millim. broad at the broadest part instead of about 3 millim. Top of braincase more vaulted than usual. Interparietal broad, short antero-posteriorly, its anterior margin projected angularly forward instead of being evenly convex. Bullae conspicuously smaller in every dimension than in P. caffer, the visible surface above barely two thirds that in the allied species; the distance from the most anterior upper corner to the level of the most projecting point behind is 13.3 millim., as compared with 18.5, 19 and 19.5 in three skulls of P. caffer, while below the antero-posterior diameter of the inflated bulla is 11.5 as compared with over 14 in P. caffer. Key-shaped process across bulla from back of squamosal shorter (9.7 millim.) and narrower. Anterior palate much less deeply concave, the region of the palatine foramina much less sunk below the general palatal level. Palatine foramina shorter, their septum much narrower. Basicranial region with only one mesial vacuity, the usual opening in the basisphenoid connecting with the floor of the brain-case absent, that in the basioccipital alone present.

Incisors comparatively weak, both narrower and less deep than in P. caffer. Molars also rather smaller and narrower; the two laminae of each tooth more parallel with each other, less opened out externally than in P. caffer."

Type : Skull. BM(NH)2.4.5.5

Loc. : Morendat; mile 365 of Uganda Railway, British East Africa. Altitude 2000m.

C) Pedetes angolae:

1920 Pedetes angolae — Hinton M.A.C. Ann. Mag. nat. Hist. Lond. 9th series 6 102 - 104

Original species diagnosis:-

A short diagnosis was not given but only the main description: the section of this description referring to the skull is as follows: "Skull longer and relatively narrower than in P. caffer, the zygomatic arches being considerably less expanded; zygomatic and greatest squamosal breadths respectively equal to 69.6% and 56% of the condylo-basal length; in caffer (fourteen skulls belonging to three subspecies examined) the zygomatic breadth varies between 72.3 and 78.3%, the greatest squamosal breadth between 56.7 and 63.2% of the condylo-basal length. The petro-mastoid is rather more inflated than in caffer, for the least distance between the bullae upon the upper surface of the skull amounts to no more than 26.6% of the greatest squamosal breadth; the average value of this dimension in all forms of caffer is 31.7%, the range being 28.5 to 34.7%. The anterior border of the interparietal is but slightly convex, almost straight, not thrown forwards as a strong process intercalated between the parietals, as is the case in caffer and surdaster. On the ventral surface the lateral flanges of the basioccipital, abutting against the median surfaces of the auditory bullae, are much less developed than in caffer; there are two small foramina — one behind the other — in the middle line of the basisphenoid, and a larger irregular vacuity in the basi-occipital. The fossa containing the anterior palatal foramina is as deep and extensive as in caffer. In profile the maxillary portion of the outer wall of the infraorbital canal is considerably broader antero-posteriorly than in any other Pedetes before me. In caffer and in surdaster the hinder part of the jugal bears a well-marked impression for

the origin of the "postero-superior almost horizontal" portion of the masseter lateralis muscle (figured by Tullberg, Taf.x.fig.8), and the ventral border of the bone is produced downwards and backwards to form a well-marked angular process; in angolae the muscular impression in question is very feebly developed, while the angular process is lacking. The cheek-teeth offer no tangible differences. The upper incisors are a little less opisthodont than in caffer, but, owing to the irregular form of the incisive alveolus in this genus, the incisive angle is difficult to measure satisfactorily."

Type : Adult female. BM(NH)19.12.19.1

Loc. : Cholinde, 20 miles N.E. of Bihé, Angola.

This species is relegated to the status of a subspecies in Hill & Carter (1941).

Modified species diagnoses are given in Chapter 7.

3) Subspecies :-

All the named subspecies are listed below together with the type locality and the original reference. In the references only the relevant page numbers are quoted, full references are given in the Bibliography. The possible validity and taxonomic status of these subspecies is discussed in Chapter 7.

Pedetes capensis capensis (Forster, 1778)

Cape of Good Hope (probably around Stellenbosch, see p. 114 [Forster, 1778]).

Forster J.R. (1778) K. svenska VetenskAkad. Handl. 39 116 - 119

Pedetes capensis orangiae Wroughton, 1907

Aberfeldy District, Orange River Colony.

Wroughton R.C. (1907) Ann. Mag. nat. Hist. Lond. 7th series 20 32 - 33

Pedetes capensis salinae Wroughton, 1907

Woodbush, Zoutpansberg District, N.W. Transvaal.

Wroughton R.C. (1907) Ann. Mag. nat. Hist. Lond. 7th series 20 33

Pedetes capensis damarensis Roberts, 1926

Quickborn, Okahandja, South West Africa.

Roberts A. (1926) Ann. Transvl. Mus. 11 261 - 262

Pedetes capensis dentatus Miller, 1927

Dodoma, Tanganyika.

Miller G.S. (1927) Proc. biol. Soc. Washington 40 113 - 114

Pedetes capensis taborae Allen & Loveridge, 1927

Tabora, Tanganyika Territory.

Allen G.M. & A. Loveridge (1927) Proc. Boston nat. Hist. Soc. 38 438 - 439

Pedetes capensis fouriei Roberts, 1938

Itota Pan, 40 miles S. of Ondonga, Ovamboland, South West Africa. (Lat. 18°26'S : Long. 15°58'E Skead (1973)).

Roberts A. (1938) Ann. Transvl. Mus. 19 242

Pedetes capensis albaniensis Roberts, 1946

Committees Drift, Great Fish River, Albany District.

Roberts A. (1946) Ann. Transvl. Mus. 20 313 - 314

Pedetes capensis angolae Hinton, 1920

Cholinde, 20 miles N.E. of Bihé, Angola.

Hinton M.A.C. (1920) Ann. Mag. nat. Hist. Lond. 9th series 6 102 - 104

Pedetes capensis bradfieldi Ellerman, 1940 [Nom. nud.]

Ellerman J.R. (1940) The Families and Genera of Living Rodents. Volume 1 p.552 BM(NH) : London.

Pedetes surdaster surdaster Thomas, 1902

Morendat, mile 365 of Uganda Railway, British East Africa.

Thomas O. (1902) Ann. Mag. nat. Hist. Lond. 7th series 9 440 - 441

Pedetes surdaster larvalis Hollister, 1918

Ulukenia Hills, Athi Plains, British East Africa.

Hollister N. (1918) Smithsonian Misc. Collections 68 No. 10 p.2

Pedetes surdaster currax Hollister, 1918

Kabalolot Hill, Sotik, British East Africa.

Hollister N. (1918) Smithsonian Misc. Collections 68 No. 10 p.3

Introduction:

I believe that there are two living species of the genus Pedetes - Pedetes capensis and Pedetes surdaster - although, in recent years, many authors have stated that there is only a single species, namely P. capensis, (Butynski, 1979; Dorst & Dandelot, 1970; Misonne, 1971; Morris, 1965; Kingdon, 1974). In this chapter material of the East African form, Pedetes surdaster, is described and, at the end, the principal features in which P. capensis differs from it are given. Discussion of the taxonomic implications of these differences and the arguments in favour of the recognition of two species will be deferred to Chapter 7 in which the relationships of all the pedetids are discussed.

The principal description of the anatomy of Pedetes is Parsons (1898) which deals briefly with the osteology and also with the anatomy of the soft parts. Despite the assertion in Parsons (1898) that the osteology of Pedetes is well known there is, in fact, no detailed, bone by bone, description of the osteology available in the literature. Both Brandt (1855) and Tullberg (1899) describe the genus; a number of other authors, in the context of general works that include rodents, also describe Pedetes but most of such descriptions are brief (Owen, 1866; Fitzsimons, 1920; Haagner, 1920; Sclater, 1901).

Various aspects of the anatomy of Pedetes have been described in more detail, especially in the last 20 years. These include the brain and skull (Dräseke, 1929); the reproductive system (Coe, 1969); the cephalic arterial

system (Bugge, 1974); some other aspects of the blood vascular system (George, 1981); the foetal membranes (Fischer & Mossman, 1969; Mossman & Fischer, 1969); the middle ear region (Parent, 1976); the dentition (Wood, 1962a and 1965a); the laryngeal region (Kupper, 1970). Other work on Pedetes includes ecological studies, to date largely restricted to Botswana (Smithers, 1971; Butynski, 1972, 1973 and 1975); investigation of the reproductive cycle (Butynski, 1979; van der Merwe et al., 1980) and chromosome mapping (Bogart et al., 1976; George, 1980). Yet, in all this, the gross anatomy has been fully investigated in only one individual of the southern African species, P. capensis, (Parsons, 1898): the external characters are, however, well described (Pocock, 1922; Jones, 1940).

The following description is intended to remedy this situation, at least as far as osteology is concerned. 50 skulls and 27 post-cranial skeletons of P. surdaster have been examined in detail and measured so that some idea of potential individual variation has been obtained: in addition a further 385 skulls of P. capensis have been examined and measured. In the case of both species, however, only adult material has been used to calculate mean values of measurements and for giving an observed range. A brief outline of the material used is given in Appendix II. Work on the living species has concentrated on osteology because only in the skeletal system can direct comparisons be made with fossil forms.

DESCRIPTION:

Cranium (Table 2.I ; Fig. 2.1A, B ; Fig. 2.2A, B ; Plates 1 & 2):

Dorsal aspect:- (Fig. 2.1A). The nasals are relatively short (77% of frontal length and 31% of cranial length) with the naso-frontal suture, which may have a median anterior salient, generally anterior to the preorbital bar. They widen from the front back, reaching their widest between one-half and two-thirds of the way back then narrowing slightly (their maximum width is 78% of their length), the anterior tips are slightly depressed. The premaxillae edge the nasals for much of the latters' length and at the level of the naso-frontal suture are overlain by the maxillae: they terminate just behind this point. Immediately beyond the end of the premaxilla the maxilla turns out quite sharply into the preorbital bar (upper maxillary root of the zygoma) forming an anterior angle of 90° or slightly more with the rostrum.

In the anterior half of the frontals there is a median depression, the development of which is variable; it is generally quite pronounced. The upper rims of the orbits converge very slightly in their anterior halves then diverge more strongly in their posterior halves: the frontals are consequently broad without a distinct interorbital constriction. The parietals are pentagonal with the fronto-parietal suture at the same level as the post-orbital bar, which is reduced to a tubercle. This suture is often almost straight but sometimes has a pronounced median, anterior salient. Just lateral to the parietals the squamosal forms the edge of the

dorsal surface of the cranium. There is some upward vaulting of the cranium at the level of the post-orbital tubercle.

The postero-lateral corners of the cranium are occupied by the inflated mastoid bullae (see below). There is a distinct interparietal, even in adults, which lies between the bullae; it is pentagonal in outline with the apex, which is either rounded or pointed, forward. The supraoccipital forms the posterior edge of the dorsal surface of the cranium behind the interparietal. There is no lambdoidal crest; the bullae extend a little way behind the supraoccipital.

Profile:- (Fig. 2.1B ; Plate 1). The outline of the dorsal surface is even in some specimens but, due to a lesser development of the frontal sinuses, it is uneven in others: from the middle of the parietals, posteriorly, it curves down slightly. The incisors are strongly opisthodont and the incisive alveolus forms a broad, curved ridge across the anteorbital region, reaching two-thirds up the rostrum at its highest point and ending at the level of the infraorbital foramen. Beginning at the zygomatic root and running antero-dorsally to the level of the base of the nasal opening, then along the dorsal edge of the premaxilla, there is a ridge marking the edge of the origin of m. masseter medialis. Finally this ridge continues onto the maxilla and turns out onto the preorbital bar. The premaxilla-maxilla suture forms an S-shaped curve aligned postero-dorsally across the anteorbital area. Anterior to the premaxilla the nasal overhangs and has a very pronounced lateral wing.

Immediately behind the incisive alveolus the lower

maxillary root of the zygoma originates. It is slightly upcurved and broadened where it meets the rostrum and it passes back almost horizontally; it is fairly robust. The preorbital bar is formed by the maxilla anteriorly and by the lachrymal and jugal, which have retained their contact, behind. The lachrymal does not form a preorbital process and hardly interrupts the smooth curve of the anterior edge of the orbit. Below the jugal, which is a robust bone, and merging with it at the level of m^1 - m^2 there is a short back process of the maxilla. The lower edge of the zygoma slopes slightly postero-ventrally but does not pass below the occlusal level of the cheekteeth. About two-thirds of the way back along the orbit the lower edge of the jugal bears a tubercle or has a smoothly rounded corner; this is the inferior process of the zygoma. From this point the jugal curves up to meet the squamosal. On the lateral surface of the zygoma, divided into several, usually three, conchoidal depressions, there is the origin of m. masseter lateralis. The upper edge of this origin forms a curved ridge across the zygoma and is at the same level as the horizontal suture between the jugal and squamosal.

The large lachrymal foramen is hidden by the preorbital bar and opens at the posterior edge of the greatly enlarged infraorbital foramen. In the orbital plate of the frontal there are two ethmoid foramina; the superior just below the upper rim of the orbit, the inferior, lower down and further forward, near the suture with the lachrymal. In the floor of the orbit the maxilla slopes antero-dorsally and bears

three thin-walled tubercles, one for each of the molars. Opening internally to the tubercle of m^1, at the junction of the maxilla and palatine, there is the sphenopalatine foramen: there may also be a small foramen anterior to m^1. The dorsal palatine foramen is just internal to the posterior edge of the tubercle of m^2, on the suture of the maxilla and palatine. The elliptical optic foramen is relatively large; in many specimens there is a shallow fossa, into which opens a small interorbital foramen, by its postero-ventral corner. The sphenoidal fissure is usually simple but occasionally a thin bony strut divides it into a smaller ventral and a larger dorsal opening.

The post-orbital bar is usually reduced to a tubercle but it is quite long in some specimens. Behind it the groove for m. temporalis is generally very small and indistinct: the muscle is a thin slip and does not reach the midline. It originates on the squamosal and the lateral part of the parietal. There is a process of the squamosal, passing back over the mastoid bulla: this process is simple, expanding at its distal end into a small triangular plate. Where the process meets the main part of the squamosal, usually between the bulla and the squamosal but sometimes completely within the squamosal, there is a temporal foramen opening into a canal between the parietal and the mastoid. The internal pterygoid flange is visible in profile with the hamulus reaching to or just below the occlusal level of the cheek-teeth. The cranium behind the orbit is made up largely by the bullae (see below).

Ventral aspect:- (Fig. 2.2A). The relatively short incisive foramina, separated by a thin bony interforaminal septum, are confluent at their posterior ends and are set immediately posterior to the incisors in a shallow palatal groove. Their mean length is 29% of the mean diastemal length. From their postero-lateral corners the premaxilla-maxilla suture passes posteriorly for a short distance, then turns laterally, across the lower maxillary root of the zygoma just anterior to the origin of m. masseter superficialis, and finally turns forward. The origin of m. masseter superficialis extends along the ventral edge of the zygoma to the level of the preorbital bar. At its medial end there may be a small tubercle. The palatal groove extends back to the anterior edge of pm^4 and at this point a distinct median ridge is formed on the palate and this continues back to the posterior termination of the palate, at the level of m^2, where it may then form a slight posterior process. Between the cheekteeth the palate is arched ventrally. On the maxilla-palatine suture, at the level of the middle of m^1, there are the posterior palatal foramina, which are very occasionally wholely within the palatine. Passing forward from each foramen, in the maxilla, there is a groove or partially enclosed canal that opens by an anterior foramen; posteriorly there may also be additional foramina, wholely within the palatine, associated with the posterior palatal foramina. The canals to the dorsal palatine foramina are open to the nasal passage although covered by a membrane in life. Posterior maxillary foramina are usually absent. The

toothrows are straight and diverge posteriorly; the zygomata almost parallel them but actually diverge slightly more.

On either side of the presphenoid and basisphenoid there is a large fenestra connecting the orbit with the meso-pterygoid fossa. Very rarely a thin bony arch may create a small canal running antero-posteriorly in the angle between the basisphenoid and the base of the medial lamina of the pterygoid. In the anterior angle between the basisphenoid and the medial pterygoid lamina there may be a small foramen: this is just below the antero-lateral foramen from the basi-sphenoid into the orbit. Opening through the basisphenoid to the sella turcica there is usually a small foramen although this may be absent; Parsons (1898) stated that the opening did not enter the cranial cavity. Further posteriorly, in the midline of the basioccipital, there is a larger opening to the cranial cavity which is sometimes divided longitudinally into two halves. The lateral edges of the anterior half of the basioccipital form wings although these are rather flat. Between the ends of these and the condyles, on either side, there is a groove in which is situated the hypoglossal foramen. A small canal may run from the internal part of the hypoglossal foramen, within the exoccipital, to emerge from the foramina in the external face of this bone above the condyle. Just lateral to the hypoglossal foramen, between the basioccipital and the tympanic bulla, there is the elongated jugular foramen.

The pterygoid fossae are well developed and the palatine may just contribute to the anterior wall along the ventral

edge. There is a large transverse canal through the basisphenoid connecting the pterygoid fossae: this canal also connects with the vertical canal to the sella turcica and to two antero-laterally directed canals that are wholely within the basisphenoid and open, one on either side, into the orbit at the level of the sphenoidal fissure. Parsons (1898) appears to be referring to these foramina when he describes the foramina rotunda but they occupy a different position to that of the foramina rotunda in other rodents. Also connecting to the transverse canal there is a vertical canal, passing ventrally, against the lateral face of the medial pterygoid lamina.

Between the auditory bullae and the pterygoid fossae there are two foramina: medially, adjacent to the basisphenoid, is the middle lacerate foramen which forms the anterior end of the canal that runs between the bulla and the basioccipital and that terminates posteriorly between the condyle and the styloid process. The large lateral foramen is separated from the middle lacerate foramen by a thin bony bar and occupies almost the whole of the surface between the bulla and the pterygoid fossa. It seems to represent a very enlarged foramen ovale. From the antero-lateral corner a short canal passes antero-laterally in the alisphenoid, under the poorly developed lateral pterygoid lamina; this represents the combined buccinator and masticatory nerve canal. There is no alisphenoid or sphenopterygoid canal and the whole of this region of the cranium seems to have been simplified.

The glenoid fossa is formed entirely by the squamosal;

the sutures with the jugal and the alisphenoid are along the edges of the fossa but neither of these bones contributes to the articular surface.

Anterior aspect:- The cranium takes the form of an inverted triangle with the dorsal surface rather flat. The preorbital bars parallel the sides of the rostrum. Along the ventral edge of the nasal opening the premaxillae send up thin vertical crests continuous with the external and internal surfaces and separated by a deep groove. There are numerous small nutritive foramina in the premaxillae.

Posterior aspect:- The supraoccipital has a pronounced external occipital crest and shows very clearly the origins of the neck muscles. The foramen magnum is the shape of a flattened triangle with very rounded ventro-lateral corners against which the occipital condyles lie: it opens postero-ventrally. There is a clear lateral nuchal crest that is continuous with the styloid process: this is at the level of the condyle. Above the condyle, in the exoccipital, there are a number of nutritive foramina. The auditory bullae form the lateral portions of this aspect.

Auditory bulla:- The auditory bulla is very much enlarged, with the mastoid portion much more inflated than the tympanic portion, and occupies the whole of the postero-lateral corner of the cranium. Running back across the mastoid, above the opening of the external acoustic meatus, there is a shallow groove that expands at its distal end: this groove is for the process of the squamosal. Along the middle of the groove

there is a slight ridge. The opening of the external acoustic meatus is directed dorsally and the meatal tube is well ossified. Along its anterior edge it bears a ridge that continues until it almost reaches the lower edge of the tympanic bulla. Between the meatal tube and the mastoid flange there is a groove, at the top of which is the stylo-mastoid foramen, about 3mm below the upper edge of the bone of the meatal tube. The mastoid flange overlaps the tympanic and has a slight backward projection overlapping the base of the styloid process.

The posterior surface of the bulla is quite clear in posterior view of the cranium. Immediately above the junction with the exoccipital, passing ventro-laterally and curving round onto the mastoid flange is the insertion of mm. sternomastoideus and cleidomastoideus. In posterior view the tympanic bulla is somewhat obscured by the styloid process. The sutures of the petrosal to mastoid and tympanic can be made out on the internal surface. When the bulla is in position there is a foramen situated just inside the jugular foramen. This is in the position of a stapedial foramen but according to Bugge (1974) there is no stapedial artery in Pedetes. Just by this foramen and running dorsally from it there is a ridge and a groove; at the dorsal end of the ridge there is an opening into the bulla. At this level the groove curves slightly and continues across the bulla above the floccular fossa before turning ventrally, continuing to the level of the floccular fossa, then passing out to the antero-medial ridge where it ends. The floccular

fossa is large and central; just below it there is another fossa containing the foramina for cranial nerves VII and VIII. The petrosal continues ventrally over the upper part of the ventro-medial flange of the tympanic, which fits into a groove in the lateral edge of the basioccipital thus helping to lock the bulla in place. At the anterior edge of this flange there is the opening of the Eustachian tube. The tympanic forms a process here so that the lateral side of the tube is ossified for a longer distance than is the medial. At the level of the fossa for cranial nerves VII and VIII there is a short antero-medial ridge.

The medial part of the anterior surface of the bulla is smooth. A small ridge on the tympanic marks the level of the squamosal and is continued on the mastoid as a groove into which the squamosal fits. Just at the junction of the ridge and the groove there is the opening of the canal of Huguier. Medially at this level a slight crest overlaps the squamosal.

Internal aspect:- (Fig. 2.2B ; Plate 2). Specimen OUM13561 was sectioned parasagitally just to the right of the mid-line. Additional information was provided by specimens in which damage had exposed parts of the internal aspect.

The nasal cavity occupies almost half the length of the cranium. Immediately inside the external nares, which are floored by the premaxillae, there is a channel, on either side, passing postero-ventrally to the incisive foramina. Separating the two channels is a posterior median process of the premaxillae; this forms the interforaminal septum and

then continues back above the maxilla, being separated from the latter by an open channel, to lie below the anterior end of the vomer which it supports. The vomer supports a thin cartilaginous median nasal septum which is ossified in its posterior pcrtion where it joins the cribriform plate. In its posterior part the vomer is suspended, on either side, from the turbinals and, at its posterior end, it bifurcates and sutures, on either side, to the dorsal wing of the palatine. At no point does the vomer contact the maxillae. There is an opening from the braincase to the nasal cavity between the presphenoid and the cribriform plate, just above the posterior end of the vomer; the bifurcation of the vomer also produces a small opening, between the main nasal cavity and the nasal passage, just anterior to the presphenoid.

Pm^4 curves anteriorly and slightly medially in the maxilla below the root of the incisor.

The optic foramen is elliptical; just medial to it, about three-quarters of the way back, there is an opening that represents the internal opening of the canal from the interorbital foramen. The two openings, one coming from either side, are very close together. The optic foramen is separated from the sphenoidal fissure by a relatively thin area of bone. This region of the cranium is very simplified. The foramen rotundum, orbital fissure and sphenoidal fissure are combined in a single large opening from the braincase to the orbit. There is no alisphenoid canal; it is probably represented by a slight groove in the floor of the braincase that runs antero-medially from the foramen ovale to the sphenoidal fissure. The large foramen ovale together with

the middle lacerate foramen leave a relatively large section of the floor of the braincase open. Occupying the postero-lateral corners of the braincase are the auditory bullae.

In the midline bones the internal openings of the inter-orbital foramina in the presphenoid have been mentioned above. Posterior to these in the basisphenoid there are two large openings which connect to the transverse canal, the small foramen in the ventral surface and the two canals that open at the level of the sphenoidal fissure. The median opening in the basioccipital is, in this specimen, divided into two by a thin bony bar. The hypoglossal foramen is single, on either side; just inside it there is a canal that runs vertically within the exoccipital and opens to the external surface by a number of small foramina above the condyle.

Upper dentition:- (Fig. 2.4A, B, E, F). The incisors are strongly opisthodont and arise in the maxilla at the level of the interorbital foramen: the alveolus forms a distinct curved ridge across the lateral surface of the rostrum. They are about as broad transversely as they are deep antero-posteriorly. The enamel is white or slightly yellow and extends about halfway back on either side. Transversely the anterior surface is slightly convex. There are no grooves or ridges on the anterior face; the antero-medial corner is more sharply curved than the antero-lateral. The bevelled surface is pierced by a small central hole that represents the end of the pulp-cavity.

The four cheekteeth are hypsodont and have persistent

pulps, the pulp cavities remaining open throughout the life of the animal: the teeth are generally interpreted as $pm^4 - m^3$ although Smith (1965) tentatively suggests that, in P. capensis, they may be $pm^3 - m^2$. In adults the occlusal pattern consists of two simple lobes, each consisting of an incomplete, dentine-filled, enamel ring, that join on the lingual side to give a U-shaped tooth with a cement-filled buccal infold. This infold extends through the whole height of the tooth so that, once established, the typical occlusal pattern remains unchanged throughout the remainder of the animal's life. In $pm^4 - m^1$ the anterior lobe is sometimes slightly larger than the posterior; in $m^2 - m^3$ both lobes are about the same size: in a number of animals the anterior lobe is slightly the larger in all the cheekteeth. The apex of pm^4 curves very sharply anteriorly; the apices of $m^1 - m^3$ curve slightly posteriorly.

The typical pattern appears to be established relatively early in the life of the animal. In the stage immediately preceding it the tooth pattern consists of two separate lobes, each a complete dentine-filled enamel ring, which are separated buccally by the main infold and on the lingual side by a shallow groove in the occlusal surface. With wear the occlusal surface comes below the bottom of this groove, obliterating it and resulting in the two lobes joining on the lingual side.

Only in very young animals is there any clear evidence of cusps in the cheekteeth. Wood (1962a and 1965a) describe the pattern in juvenile cheekteeth of the southern African

species, Pedetes capensis. In the BM(NH) there is a juvenile specimen of P. surdaster (BM(NH)1.8.9.107) in which m3 have not erupted: even in this animal the anterior lobe of pm^4 has been worn down so that no cusp structure is apparent. The posterior lobe of pm^4 has a single large cusp in the buccal half and in the lingual half there is an antero-lingual cusp and a crest or row of cuspules along the edge of the tooth, curving round onto the lingual side and joining to the anterior lobe. M^1 and m^2 have both been subjected to slight wear and are similar to each other. The anterior lobe consists of a large buccal cusp; an antero-lingual crest and a postero-lingual cusp. The posterior lobe also has a large buccal cusp but the lingual half consists of two relatively small anterior cusps and a posterior crest. M^3 is unworn: both lobes seem to be completely covered by enamel and probably consist of a large buccal cusp with one or two lingual cusps and a crest, anterior in the anterior lobe and posterior in the posterior lobe. The infold between the two lobes is not filled with cement in any of the teeth. This specimen shows the least worn teeth observed in P. surdaster but they are difficult to interpret and as in the case of P. capensis (Wood, 1965a), which they quite closely resemble, they seem to provide little useful information.

Mandible (Table 2.II ; Fig. 2.3A, B, C, D):

Just antero-lateral to pm_4 there is a small tubercle, the lower masseteric tubercle, that marks the anterior end of the insertion of m. masseter medialis. This muscle insertion runs

back as an approximately horizontal ridge to the base of the coronoid process, which arises laterally to the toothrow at the level of m_2. The coronoid process is thickened along the anterior and dorsal edges but the centre is very thin. The condyle stands above and behind the dorsal edge of the coronoid plate, it overhangs both laterally and medially but more on the former. Just below the condyle on the medial surface of the ascending ramus there is the insertion of m. pterygoideus externus. The incisive alveolus curves up high into the ascending ramus and forms a tubercle in the lateral wall of the ramus where it ends. On the medial face, just above the end of the incisive alveolus, there is the inferior dental foramen; the posterior surface of the alveolus is formed by an open network of bone.

The jaw is sciurognath with the angle arising from the postero-lateral edge of the alveolus. The anterior and posterior processes of the angle are usually poorly developed. Along the ventral edge of the angle the medial side bears the insertion of m. pterygoideus internus. On the lateral side the lower edge of the angle is continuous with the relatively poorly developed masseteric crest. This begins at the lower masseteric tubercle and curves down the face of the ramus and around the incisive alveolus into the angle. The masseteric crest forms the anterior edge of the insertion of m. masseter lateralis which also spreads onto the lateral face of the angle. M. masseter superficialis inserts onto the extreme ventral edge of the angle.

The lateral face of the ramus is marked by the tubercles

of the apices of the cheekteeth. There are two openings of the foramen mentale: a dorsal one in the diastema and a ventral one just above the incisive alveolus. The symphysis is relatively robust and may be prolonged slightly, back and below the incisive alveolus, in the midline. There are many nutritive foramina on the medial surface of the ramus.

Lower dentition:- (Fig. 2.4C, D, G, H). The lower incisors are just like the uppers but, originating high in the ascending ramus of the mandible, they have a greater radius of curvature.

In the cheekteeth, of which there are four, as in the upper jaw, the typical adult occlusal pattern is like that of the upper cheekteeth except that the infold penetrates from the lingual and not from the buccal side. In pm_4 the anterior lobe is distinctly smaller than the posterior; in m_1 the anterior lobe may be slightly smaller than the posterior while in m_{2-3} the posterior lobe may be slightly the smaller but in each of the three molars the two lobes are of very similar size.

Development of the occlusal pattern occurs from two separate lobes much as in the upper cheekteeth except that the groove between the lobes is shallower on the buccal side. In BM(NH)1.8.9.107 the lower cheekteeth are relatively unworn. The infold in pm_4 forks at the buccal end to leave a cuspule in the middle of the buccal side: the anterior lobe consists of two large and two small cusps forming an arc that is convex anteriorly; there is a postero-buccal cuspule, an antero-buccal cusp, an antero-lingual cuspule and a postero-

lingual cusp. The posterior lobe of pm_4 comprises a large central cusp with crests running buccally and lingually from it, there is also an antero-buccal cuspule. In m_1 the anterior lobe appears to be made up of three cusps in a transverse row but this may also, possibly, be interpreted as buccal and lingual cusps joined by a crest: on the anterior face of the tooth there is an abrupt change of slope a little way down that may represent the remains of an anterior cingulum. The posterior lobe of m_1 consists of a central cusp with buccal and lingual crests. There is little pattern visible in either m_2 or m_3: in the former the anterior lobe may be made up of two cusps, one buccal and one lingual, but the division between the two is hardly visible: the posterior lobe of m_2 is probably made up of a large central cusp with buccal and lingual crests. Both lobes of m_3 consist of a large lingual cusp and a buccal crest or elongated cusp: the tips of the lobes are completely covered with enamel. On the posterior surface of m_3 there is a slight shelf which may represent the remains of a posterior cingulum. As in the upper cheekteeth the median infold is not filled with cement in any of these teeth.

Vertebral column:

Cervical vertebrae:- (Table 2.III ; Table 2.IV ; Table 2.V ; Fig. 2.5A - E ; Fig. 2.6A, B). The dorsal arch of the atlas is broad, relatively thick and strong with the laminae inclined dorso-medially. There is a low dorsal, median tubercle that represents the remains of the neural spine.

Large oval facets occupy the whole of the anterior face of the lateral portions of the arch and articulate with the occipital condyles. The ventral arch is less broad than the dorsal and has a low ventral, median tubercle: on the dorsal surface this arch bears a median facet for articulation with the dens of the axis. Posteriorly, on either side, there is a large facet articulating with the antero-lateral facets of the axis; these two facets are slightly more medially placed than are the anterior facets for the condyles.

The transverse process of the atlas is large, wing-like and directed postero-laterally: it is pierced at the base by the vertebrarterial canal. The suboccipital foramen, at the lateral edge of the lamina of the dorsal arch, connects with the vertebrarterial canal and may be quite complex. It opens through the lamina into the vertebral foramen immediately above the facet for the occipital condyle. A groove runs postero-laterally from the suboccipital foramen into the vertebrarterial canal. This groove may be bridged by a bony strut as it joins with the vertebrarterial canal thus giving rise to two anterior foramina (Fig. 2.5D).

The axis (Table 2.IV) is fused to Ce3 (cervical 3) (Fig. 2.5E) except occasionally in juvenile animals. The spinous process of the axis is large, vertical and fused at the dorsal tip with the neural spine of Ce3; from examination of juvenile specimens it appears that fusion first occurs between the neural spines. The transverse process of the axis is reduced to a thin, delicate bony ring around the vertebrarterial canal. There is a thin centrum with the line

of fusion to Ce3 still visible on the ventral surface: in the dorsal surface of the centrum there are two foramina, one on either side of the midline. The dens projects well forward and on the dorsal surface there is a pronounced groove separating it from the rest of the axis. Two large antero-lateral facets articulate with the atlas.

The remaining cervicals (Ce3 - 7) (Table 2.V) are all basically similar; although the anterior part of Ce3 shows no features as it is fused to the axis. Cervical 4 may occasionally be fused to Ce3 although this is not common: there may also be some fusion between other cervical vertebrae. The neural spines in Ce4 - 7 are shorter than in Th1 but are more robust and are vertical. The laminae of the neural arch are broad and straight and the arch itself is low. In the more anterior vertebrae the neural arches are almost in contact but they are more separated further back. Both pre- and postzygapophyses arise at the junction of the lamina and pedicle of the neural arch: they are vertical except for the postzygapophyses of Ce7 which are horizontal. The anterior and posterior vertebral notches are about the same size.

Transverse processes arise from the junction of the pedicle of the neural arch and the centrum and are pierced at the base by a large vertebrarterial canal except in Ce7 in which the vertebrarterial canal is small or, sometimes, absent. In Ce5 - 7 the transverse processes may approach very closely at their tips and sometimes touch and fuse. The centra are broader than they are long or deep and may

have two foramina in the dorsal surface especially in the more anterior members of the series. In Ce7 the centrum bears small hemi-facets for rib 1 on its postero-lateral corners. Ventral processes are present from Ce3 - 6 but are not normally present in Ce7. They begin in Ce3 as small antero-laterally directed processes on the lateral edges of the ventral surface of the centrum and are best developed in Ce6 (Fig. 2.6A, B) in which they extend anteriorly and posteriorly below the centra of Ce5 and Ce7.

Thoracic vertebrae:- (Table 2.VI ; Fig. 2.6C, D, E ; Fig. 2.7A - F). There are twelve thoracic vertebrae and the anticlinal vertebra is Th10 or Th11. Anteriorly in the series the ventral surface of the centrum is flattened and has two antero-lateral tubercles: from Th5 or Th6 posteriorly the ventral surface becomes convex transversely and slightly concave longitudinally. Occasionally Th12 may show a slight trace of a ventral median keel. The dorsal surface of the centrum is flat in the anterior vertebrae but is concave transversely in the more posterior ones. There are two foramina in the dorsal surface of each centrum but only in the last four vertebrae are there usually foramina in the ventral surface as well. All the centra are wider than they are long or deep; the anterior centra are shallow but they become deeper posteriorly. Rib 1 articulates mainly with Th1 which consequently bears a large anterior hemi-facet for the rib capitulum. More posteriorly the hemi-facets on the posterior ends of the centra become dominant and the anterior hemi-facets are reduced in size.

The pedicle of the neural arch arises from the lateral edge of the centrum in the anterior half of the vertebra – this makes the posterior vertebral notch much larger than the anterior which may be hardly apparent. In Th11 and Th12 the lateral wall of the pedicle bears a fossa that probably forms part of the origin of m. psoas. The laminae of the neural arch lie back over the posterior half of the centrum. The neural arch is relatively flat and low in the more anterior members of the series but becomes higher and more rounded posteriorly. Neural spines are thin, relatively short and vertical in Th1 - 3 but further back they are longer, more slender and angled sharply posteriorly as far as the anticlinal vertebra in which the neural spine is vertical. Posterior to this vertebra the spines slope anteriorly and more resemble the spines of the lumbar vertebrae although they are not so long or strong as in the latter.

The zygapophyses are horizontal as far as the pre-zygapophyses of the anticlinal vertebra; the postzygapophyses of this vertebra are more vertical. In the vertebrae posterior to the anticlinal vertebra the zygapophyses are vertical.

The transverse process arises at the junction of the pedicle and lamina of the neural arch; it passes out laterally. At the distal end there is an antero-laterally directed facet for the tuberculum of the rib. Anapophyses may be present from Th7 back but normally are first apparent in Th9. In this vertebra the transverse process bears a

slight posterior tubercle just proximal to the distal facet: in more posterior vertebrae this tubercle elongates to form a distinct anapophysis. It may bear a small ventrally directed tubercle about halfway along its length and this is best developed in Th11. The metapophyses develop in a similar way beginning, in Th9, as a tubercle on the transverse process just proximal to the distal end and directed anteriorly. More posteriorly in the series this process elongates and moves medially to become more closely associated with the prezygapophysis. By Th12 it has come to resemble the metapophyses in the lumbar vertebrae and lies adjacent to the prezygapophysis. The distal end of the transverse process, bearing the facet for the rib, appears to move antero-ventrally relative to the metapophysis and becomes reduced in size and closely associated with the anterior hemi-facet of the centrum. In Th12 it is reduced to a small tubercle. Parsons (1898) also describes the development of the transverse process in the thoracic vertebrae. This description appears to describe four processes on the transverse process (although only three are present in these specimens) and states that the meta-pophysis is not associated with the transverse process which it is in the early stages in this material.

Lumbar vertebrae:- (Table 2.VII ; Table 2.VIII ; Fig. 2.8A, B, C). There are seven vertebrae in the lumbar series. The centra are broader than they are long or deep with a transversely concave dorsal surface that becomes less pronounced in the more posterior members of the series. The ventral surface is convex transversely and concave longitudinally

with a slight median ridge in the anterior half of the centrum. This ridge increases in size back to Lu3 - 4 and then becomes less pronounced further posteriorly. There are two large foramina in the dorsal surface of the centrum that open into canals passing through the centrum and emerging, each by a single foramen, on either side of the midline. One of these two ventral foramina may be absent.

The neural arch is broader than it is high in all members of the series but the two dimensions are more equal in the anterior members. In Lu1 - 5 the lateral surface of the pedicle bears a fossa providing part of the origin of m. psoas. In all the vertebrae the posterior vertebral notch is larger than the anterior. The neural spines are well developed and become increasingly long posteriorly. They slope anteriorly but become more vertical in more posterior members and there is often a particularly distinct change in alignment between Lu6 and Lu7. The posterior face of the spine forms a shallow groove but this becomes less pronounced posteriorly and is usually lost between Lu5 and Lu7. The edges of the groove may form well developed wings especially in Lu1 - 2.

The zygapophyses are predominantly vertical: the pre-zygapophyses originate at the junction of the pedicle and lamina of the neural arch; the postzygapophyses from the posterior surface of the lamina. Metapophyses are present and well developed in Lu1 - 5 but are best developed in Lu2 or Lu3. They then decrease in size posteriorly and are minute or absent in Lu7.

The anapophyses are well developed in Lu1 - 4 and normally project back beyond the posterior edge of the post-zygapophyses. Their greatest development is reached in Lu2 or Lu3 and they are generally small in Lu5, reduced to a tubercle in Lu6 and absent in Lu7. The transverse processes arise from the dorso-lateral portion of the centrum. They become larger posteriorly reaching their maximum development in Lu5 or Lu6. The process on Lu1 usually projects laterally or even slightly posteriorly but from Lu2 back they project antero-laterally and ventrally. The transverse processes are bowed and the ventral ends expand longitudinally in the posterior members of the series: this expansion is greatest in Lu5 or Lu6. These processes are broad and flat.

Sacrum:- (Table 2.IX ; Fig. 2.9A, B ; Fig. 2.10A). The sacrum is composed of three fused vertebrae although only the anterior two provide support for the ilium and the majority of this support is provided by the most anterior vertebra. Parsons (1898) states that there are four vertebrae in the sacrum: this has only been found in one specimen (OUM 13551) in which Ca1 was beginning to fuse to the end of the sacrum. MacInnes (1957), on the other hand, states that there are only two sacral vertebrae: this has not been found in any specimen but might be expected to occur in a few juveniles as fusion of the separate sacral vertebrae occurs. In a single specimen in TILLMIAP (OM 5348) the sacrum is composed of what would normally be Lu7 - Sa2 and in this specimen Sa3 forms an additional free caudal vertebra whilst there are only six lumbar vertebrae: the

sacro-iliac expansion is formed by both Lu7 and Sa1.

In the normal sacrum the sacro-iliac expansion extends anteriorly to lie laterally to Lu7. The auricular surface is J-shaped with the horizontal stroke longer than the vertical. The anterior end of the sacro-iliac expansion provides an origin for a bundle of ligaments to the ilium and ligaments also arise from the sacro-iliac expansion above the horizontal portion of the auricular surface.

At the posterior end of the sacrum the ventral surface bears two small tubercles that provide the bases for the first chevron bone. This bone is often composed of two separate splints, that are not fused at their tips, and is inclined sharply posteriorly. The splint mentioned by Parsons (1898 : 861) is probably only one half of this bone.

The neural spine of Sa2 is the stoutest: that of Sa1 is thinner but is often slightly taller while the neural spine of Sa3 is generally the thinnest, although it may be as thick as that of Sa1, and is always the shortest. The spines may fuse at the tips although in a number of specimens only two are fused: either Sa1 or Sa3 may be the spine that is not fused to another. In juvenile specimens there may not be any fusion of the spines.

Caudal vertebrae:- (Table 2.X ; Fig. 2.10B, C, D ; Fig. 2.11A, B, C). The caudal series appears to consist of 31 vertebrae, this being the maximum number found in any specimen. The absence of the tiny vertebrae at the tip of the tail in some specimens may not, however, be an artefact due to preparation.

The first few caudal vertebrae have a similar basic

appearance to more anterior vertebrae. In the anterior caudals the centra have a wide ventral surface between two ventro-lateral ridges. More posteriorly these ridges come closer together, narrowing the ventral surface, and, between Ca7 and Ca11, they meet and form a single median ventral ridge. The transverse process in the more anterior caudal vertebrae is positioned just below the junction of the pedicle of the neural arch and the centrum; it forms a horizontal plate with the postero-lateral corner thickened to form a bifid tubercle. In more posterior vertebrae, from around Ca7 back, the edge of the transverse process becomes indented in the middle and this indentation increases in size and divides the process into separate anterior and posterior processes. The neural arch in the anterior caudal vertebrae is well formed and there is a relatively short neural spine that is either vertical or slopes slightly posteriorly. Functional zygapophyses are also found in these vertebrae.

From about Ca6 the form of the vertebrae begins to change: the centra and neural arch elongate and the latter becomes less high. The neural spine is usually lost around Ca7 - 8 having gradually been reduced in size from the anterior end of the series, the articulation between the zygapophyses is lost at about the same point. In Ca10 or thereabouts the neural arch becomes open dorsally forming a groove and finally becomes reduced to a small tubercle at the posterior end of the dorsal surface of the centrum. Metapophyses are present in the anterior vertebrae and increase in size posteriorly to reach their maximum development

in the last vertebra with functional prezygapophyses; the metapophyses are then continued as a pair of anterior processes on the dorsal surface of the centrum. They decrease in size posteriorly and are finally lost around Ca29.

Thus for about two-thirds of the tail the vertebrae consist of an elongated centrum with six anterior and four posterior processes. Two of the anterior processes are the continuation of the metapophyses mentioned above. There are also two anterior processes on the ventral surface; these are very close together and appear to represent the remains of the chevron bones, fused to the centrum, as is discussed below. The remaining two anterior processes are the anterior portions of the divided transverse processes (see above). From these lateral processes a ridge runs along the side of the centrum to the posterior lateral processes that are the remains of the posterior portions of the transverse processes. The lateral processes decrease in size posteriorly and disappear between Ca18 and Ca23, but usually after Ca20. At the posterior end the other two processes consist of a dorsal and ventral median process. The paired anterior dorsal processes are connected by tough ligaments that run the length of the tail from about Ca7 where the processes first become important: the paired anterior ventral tubercles are similarly connected by longitudinal ligaments. The general trend down the tail is for the processes to be reduced and the vertebrae to become increasingly simplified and cylindrical.

The chevron bones are found from the junction of Ca3 and

Ca1 back to the region of Ca8 - 9. They reach their greatest development between Ca3 and Ca5. Anterior to this region they are thin, short and slope posteriorly; in the region of Ca3 - 5 they are longer, stronger and vertical. Posteriorly they become even thicker but are much shorter and slope anteriorly. Towards the posterior end of the series they have an increasing tendency to fuse to the posterior of the two vertebrae between which they lie. Under the more posterior chevron bones the anterior end of the more posterior vertebra developes two tubercles and it is to these that the chevron bone sometimes fuses. These last few chevron bones may be incomplete and not fused at the tip but consist of two splints of bone. Beyond the last free chevron bone the anterior ventral tubercles continue down the tail as described above.

Ribs:

The ribs are quite normal. The first eight articulate with the sternum; ribs 9 and 10 are attached ventrally to the costal cartilage of the next anterior rib; ribs 11 and 12 are floating. The longest ossified rib is rib 6. Each rib has the normal two articulations although in the more posterior ribs these come very close together. The main shaft of the ribs is usually rounded with a slightly flattened posterior surface ventrally and both anterior and posterior surfaces somewhat flattened dorsally.

Sternum (Table 2.XI ; Fig. 2.11D - H):

The sternum is composed of six elements: a manubrium

sterni, four sternebrae comprising the mesosternum and the xiphoid process.

Manubrium sterni:- (Fig. 2.11D, E). This is expanded anteriorly to form a plate with the points of attachment of the clavicles at the antero-lateral corners of the dorsal surface. On the postero-lateral corners of the anterior plate, also on the dorsal surface, there are the attachment points of rib 1. Between the two attachments on either side there is a low tubercle. Behind the anterior plate a short posterior process connects to the mesosternum. The ventral surface of the manubrium bears a slight median ridge and in anterior aspect the plate forms a very flattened V-shape.

Mesosternum:- (Fig. 2.11F, G). The sternebrae are of rectangular form with a distinct waist. They have wide, flat, dorsal surfaces; the ventral surfaces are narrower and have, at either end of each sternebra, two small tubercles, which may be indistinct. The first two sternebrae are about the same length, the other two are progressively shorter. In a number of specimens there is a relatively large ossification in the cartilage between the last sternebra and the xiphoid process. This ossification may fuse to the last sternebra and is usually only visible in dorsal view. Centres of ossification are also associated with the ventral ends of the costal cartilages and, in a number of specimens, small ones occur, one on either side, in the cartilages between the sternebrae.

Xiphoid process:- (Fig. 2.11H). The xiphoid process is

long, thin and spatulate: it narrows distinctly in the anterior half. A slight ventral median ridge may be present but often the ventral surface is flat. Beyond the posterior end of the process the xiphoid cartilage, which is generally longer in young animals than in older ones, may include a small ossification.

Clavicle (Table 2.XII ; Fig. 2.12B, C):

The clavicle is J-shaped with the long arm bearing the sternal end at which the bone expands, especially anteriorly, and has a rounded cross-section. The sternal epiphysial line is clearly visible in most of the specimens examined. There is no distinct articular surface on the sternal end and any mobility of the joint would appear to have been dependent on the presence of a large pad of clear cartilage between the clavicle and the manubrium sterni.

The acromial end of the bone is flattened antero-posteriorly and is positioned just anterior to the acromion: it is attached to the acromion by cartilage, which forms a quite substantial mass ventrally. At the medial end of this cartilage, about 5mm from the acromial end of the bone, there is a small tubercle on the ventral surface. Usually there is no conoid tubercle on the dorsal surface and the coraco-clavicular ligament inserts in a shallow fossa, occasionally a small tubercle may be present adjacent to the fossa.

Scapula (Table 2.XIII ; Fig. 2.12A):

The supraspinous fossa is relatively small and D-shaped

and the infraspinous fossa forms most of the scapular plate. At the postero-dorsal corner there is a distinct teres major process. Along the posterior edge the scapular plate is thickened to form a ridge from the teres major process to the infraglenoid tubercle which is quite pronounced. In some specimens there may be an additional small tubercle just dorsal to the infraglenoid tubercle.

The spine is well developed and reaches to the dorsal edge of the blade. It may overhang slightly posteriorly. The acromion is slightly flattened latero-medially and projects a short way beyond the glenoid. There is a pronounced acromial angle but no metacromion. The glenoid is drop-shaped with the long axis antero-posteriorly: it narrows toward the coracoid process which is not especially well developed.

Humerus (Table 2.XIV ; Fig. 2.13A, B, C):

The head is rounded with the antero-lateral surface covered by the greater tuberosity and the pronounced lesser tuberosity on the antero-medial edge. Between the two tuberosities the bicipital groove is usually well developed.

From the anterior edge of the greater tuberosity a pronounced pectoral ridge runs down the shaft. About half-way down the shaft this joins with the less well developed tricipital ridge that runs down the shaft from the posterior edge of the greater tuberosity to form a pronounced deltoid tubercle. Below the lesser tuberosity and nearly halfway down the shaft there is a low ovoid tubercle for the

insertion of m. teres major. In some juveniles this is replaced by a fossa.

The supinator crest is well developed, reaching about one-third of the way up the shaft; its lateral edge is thickened to form a ridge. Between the supinator crest and the deltoid tubercle the radial nerve sulcus can be distinguished. There is no supratrochlear foramen but an entepicondylar foramen is always present. The medial epicondyle is better developed than the lateral epicondyle and usually has a pronounced dorsal hook-like process. The olecranon fossa is deeper than the anterior supratrochlear fossa.

Ulna (Table 2.XVI ; Fig. 2.13D, E):

The olecranon process has a pronounced medial process, a less pronounced anterior process, both at the free end of the bone, and a small postero-lateral tubercle. All three are joined together by a ridge. The olecranon face of the trochlear notch projects laterally forming a slight process while the coronoid process is truncated laterally by the radial notch. At the bottom of the trochlear notch there is a non-articular area passing in from the radial side: it does not quite reach the opposite edge. Immediately distal of the coronoid process there is a small fossa.

The shaft is quadrangular in cross-section with a curved postero-medial face. Along the antero-lateral edge there is a very sharp ridge and below this the lateral face forms a groove. On the anterior face, toward the distal end, there

is a shallow groove aligned proximo-laterally to disto-medially. This groove passes on the medial side of a tubercle on the disto-lateral corner of the anterior face; this tubercle fits against the distal end of the radius. On the posterior surface there is also a distal tubercle. The distal epiphysial line is visible in many specimens and the styloid process is hamulate and articulates with the cuneiform and pisiform.

Radius (Table 2.XV ; Fig. 2.14A, B, C):

The radius is described in the position of full pronation. The proximal facet articulating with the humerus is round. There is a narrow facet around the edge of the head articulating with the ulna on one side and the sesamoid in the radial collateral ligament on the other side. The bicipital tuberosity is relatively well developed and there is generally a distinct oblique line running from it.

The shaft is flattened antero-posteriorly toward its distal end and the interosseus border forms a sharp, thin edge. The antero-medial edge is thickened and the ridge so formed curves slightly laterally at the distal end of the bone and finishes in a tubercle. This leaves a distinct groove on the lateral side of the tubercle. In the lateral side of the shaft at the distal end there is a slight ulnar notch. There does not appear to be a facet present suggesting that free rotation of the forearm is restricted. Distally there is an oval facet articulating with the scapho-lunar and adjacent to this laterally there is a small facet for the

cuneiform. The styloid process is not long and bears a facet on its medial face for a tendon.

Manus (Fig. 2.15A):

This is described in the normal quadruped position with the palmar surface ventral. In the case of each bone the terms proximal and distal refer to the manus as a whole and not necessarily to the bone as normally orientated: this distinction is especially important with the pisiform and the radial ossicle in which the long axes of the bones are dorso-ventral and not proximo-distal with respect to the manus as a whole.

Scapho-lunar:- (Fig. 2.15B, C). The main feature of this bone is the large, dorso-ventrally convex proximal facet for the radius: the medial edge of the facet may form a slight fossa to fit the styloid process of the radius. On the ventral surface of the bone there is a flange projecting distally and, medially, a bar aligned proximo-distally. This bar has a ventro-medial facet about which the radial ossicle articulates (the radial ossicle is described after the phalanges). At the proximo-medial corner of the scapho-lunar, separated from the facet on the bar by a groove, there is a facet for the process of the radial ossicle. Immediately distal to this there is a roughened area where the ligaments attaching to the process of the radial ossicle are attached.

The magnum, centrale, trapezium and trapezoid all articulate with the distal surface of the main part of the scapho-lunar. Except for the trapezium they are all

supported along their proximal edges by the ventral flange, although there are distinct facets only for the magnum and centrale. The trapezium is wholely medial to the ventral flange but articulates with the distal end of the ventral bar.

Laterally to the magnum the unciform just meets the scapho-lunar to articulate with the main body of the bone and the lateral edge of the ventral flange. The cuneiform articulates with the scapho-lunar laterally to the unciform. On the ventral surface, in the corner where the ventral flange arises, there is a small fossa providing the origin for the ligaments to the cuneiform and the pisiform. The distal half of the lateral edge is roughened for the attachment of ligaments to the dorsal surface of the cuneiform while the more proximal portion bears a small facet for a muscle tendon.

Cuneiform:- (Fig. 2.16A, B, C, D). The cuneiform consists of a central body with proximo-medial and disto-ventral processes. The deeply concave facet for the styloid process of the ulna is on the lateral face of the body, while the proximal face of the body articulates with the lateral part of the distal end of the radius. There is a retinaculum from the anterior tubercle of the radius to the dorsal surface of the central body which is, in consequence, roughened. On the ventral surface, along the edge of the facet for the ulna, there is a facet for the pisiform and this continues onto the proximal face of the ventral process. The distal face at the end of the ventral process makes contact with Mc.V but the

facet formed is continuous with the facet for the unciform.

The medial process articulates with the scapho-lunar laterally to the unciform. On the distal surface of this process, continuing onto the medial and distal surfaces of the central body, there is a single large facet for the unciform. Along the dorso-distal edge of the process there is a slight ridge where ligaments to the unciform and magnum attach.

Pisiform:- (Fig. 2.16E, F). This bone is found on the lateral side of the carpus and projects ventrally: its ventral end projects medially. The dorsal end of the bone is expanded and bears a facet, convex latero-medially and concave proximo-distally, that articulates with the styloid process of the ulna. Along the medial edge of the dorsal end of the bone there is a facet for the cuneiform continuous with a facet, on the dorsal part of the distal face, which articulates with the ventral process of the cuneiform.

On the medial surface, near the ventral end, there is a pronounced transverse groove, apparently covered by a sheet of connective tissue in life. Ventrally to this the bone projects medially. The dorsal edge of this projection is continuous around the proximal edge of the bone with a ridge on the lateral surface that becomes less pronounced distally. The whole length of the distal edge of the bone gives rise to ligaments: at the dorsal end there is a pronounced disto-lateral tubercle and at the ventral end a pronounced fossa.

Centrale:- This bone is ovoid and is only visible in dorsal

aspect. The proximal surface forms a convex facet articulating with the scapho-lunar. Disto-laterally there is a dorso-ventrally convex facet for the magnum and disto-medially there is a slightly larger facet for the trapezoid. These two facets meet to produce a distal ridge which, rarely, may just articulate with the proximo-lateral corner of Mc.II. The dorsal surface is triangular with the apex distally and usually has a slight central tubercle.

Unciform:- (Fig. 2.17A, B). The unciform is L-shaped with one arm directed proximo-medially to form a process. On the distal face there are two facets, inclined slightly palmar-medially, separated by a ridge. The medial facet is large, transversely concave, articulating with Mc.IV; the lateral facet is also slightly concave, narrows dorsally and articulates with Mc.V.

There are two facets on the medial wall of the proximal process. The distal facet is flat and articulates with Mc.III. Between this facet and the proximal one there is a shallow groove into which the lateral ridge of the magnum fits: the proximal facet is rounded and articulates with the magnum. On the proximal end of the process, and extending just onto the ventral surface, there is a facet articulating with the scapho-lunar.

The proximal face of the bone and the lateral face of the proximal process bear a large, continuous facet articulating with the cuneiform. On the lateral end of the unciform there is a small tubercle from which ligaments extend to the proximo-lateral tubercle of Mc.V. The ventral surface of the

bone has a pronounced disto-medial tubercle and a proximo-medial facet for the scapho-lunar: along the lateral edge there is a ledge from which ligaments originate. On the dorsal surface the central area forms a slight fossa surrounded by ridges on the edges of the bone.

Magnum:- (Fig. 2.17C, D, E). The dorsal surface of the magnum is trapezoidal in shape. The longest side is the disto-lateral and this face forms a facet for Mc.III. At its proximal end it meets the proximo-lateral face at an acute angle thus forming the lateral ridge that fits into the groove on the medial surface of the unciform. The proximo-lateral surface articulates with the unciform by a relatively small and slightly concave facet.

The second longest side is the disto-medial and this face articulates, by a relatively large, quadrilateral facet, with the long axis dorso-ventrally, with the proximo-lateral facet of Mc.II. In the dorsal half the facet is convex dorso-ventrally; in the ventral half, concave.

Proximally the magnum articulates with the scapho-lunar by a triangular facet with the apex ventrally. Occasionally this facet may be divided into two. Facing proximo-medially there is a dorso-ventrally concave facet for the centrale.

The dorsal surface has a ledge along the medial edge that does not quite reach the distal end of the bone. Laterally there is a slight ridge separating the ledge from the shallow fossa that occupies most of the rest of the dorsal surface. On the lateral corner there is another small ledge while proximally and distally there are low tubercles.

On the ventral surface proximo-laterally there is a facet for the scapho-lunar that is inclined disto-ventrally and is usually continuous with the proximal facet for the same bone. At its distal end there is a pronounced tubercle. The remaining third of the ventral surface is occupied by a fossa or ledge which has a marginal groove where it meets the proximo-medial facet.

Trapezoid:- (Fig. 2.15D, E). The trapezoid is relatively small and somewhat elongated dorso-ventrally. There is a disto-lateral face bearing a facet for Mc.II. Most of this face is occupied by the lateral part of the facet, which is concave transversely, but along the medial edge there is a narrow part that is convex transversely. Immediately below the facet for Mc.II, against the disto-medial edge, there is a fossa.

The proximo-lateral face articulates with the centrale and along the proximal edge there is a small facet for the scapho-lunar. On the medial surface there is a convex facet for the trapezium. Along the medial edge of the dorsal surface there is a distinct ledge, while along the distal and lateral edges there is a low rounded ridge providing an origin for ligaments.

Trapezium:- (Fig. 2.16G, H). On the proximal face of the trapezium there is a convex facet for the scapho-lunar in the lateral half while the medial half forms a non-articular surface with a pronounced fossa. Much of the medial face is occupied by a facet for Mc.I. The distal end of the bone

forms a ridge between Mc.I and Mc.II.

There is a relatively large facet for the trapezoid proximally on the lateral face. In the distal half there are two facets: a very small disto-ventral one and a larger proximo-dorsal one. Both of these facets articulate with Mc.II but in addition there is a ligamentous attachment arising from the roughened area between the two facets. On the dorsal surface there is a slight proximo-lateral tubercle and, distally, a slight ridge, convex distally, terminating in a disto-medial tubercle.

Metacarpal I (Mc.I):- (Table 2.XVII ; Fig. 2.17F, G). Metacarpal I is very short and effectively lacks a shaft, appearing to be composed of just proximal and distal ends. The proximal end is expanded transversely and on the medial surface there is a large tubercle which extends ventrally as a flange. This forms the insertion for the tendon of m. abductor pollicis and other ligaments. Centrally on the proximal end there is a slight tubercle and laterally a transversely concave facet, facing proximo-laterally, for the trapezium. Ventro-laterally the proximal end bears a tubercle that passes below the proximal end of Mc.II and articulates with it. Above this, along the dorso-lateral edge of the facet for the trapezium, there is sometimes a very small facet for Mc.II.

Beyond the proximal end, the lateral side of the bone is much better developed than the medial. The distal articulation takes the form of a central groove separating two ridges, of which the lateral is the much better developed. On the dorsal

surface proximo-medially of the distal articulation there is a very slight fossa.

Metacarpal II (Mc.II):- (Table 2.XVII ; Fig. 2.18A, B). The proximal end forms a large facet for the trapezoid that is transversely concave in the medial part. On the medial side of the bone there is a proximo-palmar facet for Mc.I and, immediately adjacent and proximo-dorsal, there is a facet for the lower part of the trapezium. There is a further facet for the trapezium, as well as a ligamentous connection, at the proximo-dorsal corner.

The proximo-lateral edge forms a flange, extending into the carpus between the trapezoid and the magnum, that may bear a facet on its end for the centrale. There is a facet, shaped like a reversed C, for the magnum on the lateral surface of this flange proximally while distally there is a slight vertical groove where Mc.III touches the bone. A very slight proximal palmar process is present.

On the sides of the shaft there are roughened areas providing points of insertion for ligaments and tendons: there is an especially well developed fossa on the medial side. The distal end is at a slight angle to the shaft and the articulation is barrel-shaped with a keel that is median or slightly lateral to the midline. This keel is developed distally and ventrally and is clearly visible in dorsal aspect: ventrally it terminates sharply at the end of the facet. The articular surface extends back a short distance on the dorsal surface of the bone to articulate with the extensor tendon sesamoid. There is a slight fossa in the

dorsal surface immediately proximal to the articular surface and a fossa in each side wall from which ligaments originate.

Metacarpal III (Mc.III):- (Table 2.XVII ; Fig. 2.18C, D).

The proximal end of Mc.III is oblique to the shaft so that the most proximal point is in line with the lateral side of the shaft. This point is the corner of the proximo-lateral process. On the proximo-medial face of the process and extending across the whole width of the bone there is a large flat facet for the magnum. On the medial side this facet protrudes beyond the shaft forming a slight ridge at the end of which there is a facet articulating with Mc.II. The proximo-lateral face of the process articulates with the unciform by a flat or slightly concave facet and the distal face bears a facet for Mc.IV that truncates the distal dorso-lateral corner. There is a slight proximal palmar process present with, on its ventral end, a proximal fossa and a distal tubercle.

Along the sides of the shaft there are areas of attachment for ligaments: on the medial side there is a pronounced fossa with distinct distal and ventral ridges bordering it. The distal articulation is as in Mc.II except that the keel is median and the fossa on the dorsal surface is deeper.

Metacarpal IV (Mc.IV):- (Table 2.XVII ; Fig. 2.19A, B).

The proximal end is set obliquely, disto-medially, to the shaft and the proximo-lateral corner projects to form a process. There are two facets, separated by a groove, on the proximal face. The lateral facet is the larger, it is

slightly convex transversely and articulates with the unciform: the medial facet is flat and articulates with Mc.III, it projects slightly beyond the medial surface of the shaft forming a low ridge with the articular surface curving round onto the ridge especially in the dorsal half. Beyond the slight proximo-lateral process the lateral surface is slightly hollowed out with a facet in the proximal part of the hollow. This facet extends through the whole depth of the bone and expands distally at its dorsal end; it articulates with Mc.V. There are also strong ligaments connecting the medial side of the proximal end to Mc.III.

There is a proximal palmar process with a proximal fossa and a distal tubercle on the palmar end. The distal end of the bone is as in Mc.II except that the keel is median or slightly medial of the midline and the fossa on the dorsal surface is very large.

Metacarpal V (Mc.V):- (Table 2.XVII ; Fig. 2.19C, D). This metacarpal is relatively short. At the proximal end there is a single, large facet, facing proximo-dorsally, extending onto the dorso-medial edge of the bone, and articulating with Mc.IV, the unciform and the ventral process of the cuneiform. There may be a slight ridge separating the proximal portion, for the unciform and cuneiform, from the medial portion for Mc.IV. Generally the palmar process is well developed and there is also a very well developed proximo-lateral tubercle from which ligaments attach to the unciform. Proximo-dorsal to this tubercle there is a small fossa. On the medial surface of the bone there is a well

developed tubercle near the proximal end from which ligaments attach to Mc.IV.

The distal end is basically as in Mc.II but the keel is set somewhat obliquely passing from the dorso-medial side of the bone down to the midline position on the palmar side. The fossa on the dorsal surface is not especially well developed: medial to it the distal facet is extended for the sesamoid bone found in the extensor tendon on this side. Generally the medial side of the shaft and distal end is better developed than is the lateral.

Phalanx I (Ph.I):- (Table 2.XVIII ; Table 2.XIX ; Fig. 2.20A, B ; Fig. 2.19E). The proximal facet for the metacarpal consists of two articular surfaces separated by a deep median groove for the keel on the metacarpal. The two articular surfaces are not usually confluent dorsally above the groove. Proximo-ventrally there is a process, divided by the midline groove, onto which the facets extend: the facet is thus slightly oblique, dorso-distally, to the shaft. On the proximo-ventral end of this process there is a facet for the flexor sesamoid. In the midline the dorsal surface forms a tubercle on the proximal edge for the insertion of the extensor tendons.

In digit 5 the proximal end is expanded on the lateral side. To a lesser degree this is also the case in digit 4 and, on the medial side, in digit 2.

At the distal end the facet for Ph.II consists of a deep median groove, extending onto the ventral surface, and a pronounced ridge on either side. Just proximal to the facet,

on the dorsal surface, there is a smooth area for the tendon or sesamoid, when present, of the extensor muscle. On either side at the distal end there is a ring-shaped groove, from which the joint ligaments originate, rather than a fossa as in the metacarpals.

In digit 1 the distal articulation of the metacarpal is just like that of Ph.I in the other digits and the Ph.I shows all the characteristics of a Ph.II. For ease of description, and without implications on the homology of the bones, the phalanges of the pollex are described in the two sections below as Ph.II and Ph.III although they appear in Tables 2.XVIII and 2.XIX as Ph.I and Ph.II.

Phalanx II (Ph.II):- (Table 2.XVIII ; Table 2.XIX ; Fig. 2.20E). At the proximal end the facet is concave dorso-ventrally and there is a pronounced median ridge fitting the groove in the distal facet of Ph.I. The facet continues onto both the dorsal and ventral processes: the former is pointed and lies along the dorsal surface of Ph.I for a short distance while the latter is rounded and bears, on its proximal end, an indistinct facet for the flexor sesamoid. On the dorsal surface there is a distally directed tubercle at the base of the dorsal process.

In the pollex the dorsal process is usually slightly less well developed than in the other digits while the ventral process is usually better developed, notched in the midline at the end, and on the medial side forms a very slight tubercle. This bone also bears a ventral flange of cartilage, aligned proximo-distally, that articulates with the second

segment of the radial ossicle.

The dorsal surfaces of the shafts are slightly concave proximo-distally. At the distal end the articulation is as in Ph.I except that the median groove is less pronounced. On the ventral surface, immediately proximal to the facet, there is a slight fossa into which the flexor sesamoid fits in flexion of Ph.III. In either side wall there is a fossa providing the origin for the joint ligaments.

Phalanx III (Ph.III):- (Table 2.XVIII ; Table 2.XIX ; Fig. 2.18E). This is long, transversely compressed, with an elongated proximal palmar process. The proximal end is like that of Ph.II but there is a longer dorsal process that lies back over Ph.II. The proximo-ventral edge bears a facet for the flexor sesamoid.

The palmar process is wide proximally, narrows to a waist about two-thirds of the way distally, then expands so that the distal third forms a wide tubercle the ventral surface of which overhangs the sides of the process and to which the flexor tendons attach. Just distal to the waist, on either side of the process, there is a foramen into the bone. Distally the process is rounded and curves down gradually to merge with the palmar surface of the bone.

Beyond the palmar process the phalanx curves ventrally and comes to a point. The whole bone is covered by the claw which projects well beyond the end. Ventrally the sides of the claw project, usually leaving a pronounced subunguis, although sometimes in digits 2, 3 and 4 the sides may curve under and meet in the midline. In digits 3 and 4 this

ventral projection is about equal on the two sides whereas in digits 1 and 2 the medial side projects more and in digit 5 the lateral side projects the greater amount.

Radial ossicle:- (Table 2.XVIII ; Table 2.XIX ; Fig. 2.20D, E). The facet articulating with the ventral bar of the scapho-lunar is on the lateral face of the bone and its ventral edge forms a ridge. Above the facet, dorsally, there is a short process with a facet on its lateral face that articulates with the medial surface of the scapho-lunar. On the disto-medial edge, at the level of the main articulation, there is a tubercle from which ligaments go to Mc.I. A straight ridge runs dorsally from this tubercle while ventrally there is a ridge that curves round the medial edge of the bone, immediately before the attachment of the second segment, onto the proximal surface and down to the slight tubercle found on this surface near the ventral end. On the proximal surface, about halfway down the bone, there is a low rounded tubercle which is attached by a short tendon to the palmar aponeurosis.

The ventral end of the bone is flattened proximo-distally and spatulate, expanding slightly in width over the shaft. In addition to the tubercle on the proximal surface mentioned above there is often also one on the distal surface which may be extended into a ridge.

The second segment of the radial ossicle attaches to the medial edge of the first segment in the ventral half. It is directed dorsally and distally towards the proximal end of the middle phalanx of the pollex. The proximal part of the segment is often composed of a light spongy bone but much of

the structure is keratin and nail-like. The proximo-dorsal corner of this segment bears a small cartilaginous pad that articulates with the cartilagincus flange which passes ventrally from the midline of the proximal half of the middle phalanx of the pollex.

Innominate bone (Table 2.XX ; Fig. 2.21A ; Fig. 2.22A):

The acetabulum is set just over halfway back and the acetabular notch is pronounced. Immediately anterior to the acetabulum there is a large roughened fossa where m. rectus femoris originates. Running anteriorly from this there is a pronounced ridge that continues to the anterior end of the bone and divides the ilium into a broad dorsal plate and a narrower ventral one. The anterior and antero-dorsal edges of the ilium are thickened producing a distinct iliac crest and the anterior end of the ilium curves out laterally. Proceding antero-ventrally from the origin of m. rectus femoris, on the ventral plate of the ilium, there is a second smaller ridge. On the medial surface of the ilium, just at the midpoint, there is an area of attachment for the ligaments of the sacro-iliac joint with, at its posterior end, an L-shaped auricular surface.

The pubis is relatively thin with a strengthening ridge running along the middle and at the postero-ventral corner of the bone there is a pronounced pubic tubercle. The ischium is thick and strong, expanding posteriorly and forming a very large ischial tuberosity. Level with the posterior edge of the acetabulum, on the internal surface, there is a small ischial spine. The obturator foramen is

pear-shaped.

Femur (Table 2.XXI ; Fig. 2.21B, C):

The head is hemispherical and set on a short neck the dorsal surface of which is overlain by a flange of the articular surface. There is a distinct fovea for the ligamentum teres. There is a very well developed trochanter major, set slightly laterally to the line of the shaft; its upper edge overhangs medially. At the level of the head the anterior face of the trochanter major bears two tubercles: the medial tubercle is a little further dorsal than the lateral, neither is particularly large. The trochanter minor is well developed; there is a high intertrochanteric crest and a deep trochanteric fossa. There is no trochanter tertius.

The shaft is slightly flattened antero-posteriorly and is distinctly bowed forwards. On the lateral surface, extending almost down to the condyles, there is a slight ridge. Except in certain young individuals, in which the proximal end leans outward slightly, the bone is vertical when stood on the two distal condyles. In the proximal half of the femur, on the posterior face, there is a short linea aspera that, proximally, joins with the lateral ridge. Distally the lateral and medial supracondylar lines are not apparent but the posterior face of the shaft is roughened for the attachment of muscles.

The patellar groove is aligned disto-medially and is bounded by two well developed ridges. Posteriorly above both the lateral and medial condyle there is a facet for the

sesamoid bone found in the tendon of origin of the respective head of m. gastrocnemius. The sesamoid above the lateral condyle is the larger. The articular surfaces of the condyles do not join anteriorly. There is a relatively deep intercondylar notch and the lateral face of the lateral condyle bears a number of fossae, usually three.

Patella (Table 2.XXII ; Fig. 2.14D, E):

This is triangular with a straight lateral edge and an angular proximo-lateral corner. The proximo-medial corner is rounded and there is a shallow groove along the medial edge. Most of the posterior surface is taken up by the facet that articulates with the femur.

Tibia (Table 2.XXIII ; Fig. 2.22B, C):

The cnemial crest is well developed and is visible for about half the length of the bone. There are ridges down the postero-lateral and postero-medial edges that are apparent for the whole length of the bone although these are only just visible in the middle section of the bone. On the medial surface of the postero-lateral crest, in the upper half, there is a groove with a nutritive foramen at its distal end. The two proximal articular surfaces are separate, convex antero-posteriorly and slightly concave transversely: between their anterior ends and the proximal tuberosity on the cnemial crest there is a transverse groove. There is a facet for the head of the fibula on the postero-lateral corner of the head.

The shaft thins in the middle and expands again slightly

at the distal end. The distal articulation for the astragalus consists of two grooves aligned antero-laterally, separated by a slight ridge posteriorly and, anteriorly, by a groove passing in from the anterior edge of the bone. There is a pronounced postero-medial flange with a well developed ridge down each side: there is also a small antero-lateral flange the medial edge of which is continuous with a ridge on the anterior face of the shaft. On the edge of the lateral facet there is a small facet for the fibula.

Fibula (Fig. 2.22C):

The fibula is reduced to a very thin bone. The head is expanded anteriorly and articulates with a facet on the edge of the lateral condyle of the tibia. The anterior part of the head ends in a rounded knob with a facet for the tendon of m. extensor digitorum longus on the anterior face. At the distal end the fibula is also expanded and projects beyond the tibia, articulating by a small facet with the latter's distal end; it articulates, by a small antero-medial facet, with the lateral condyle of the astragalus: there is no contact with the calcaneum. Except in old animals the fibula does not fuse to the tibia and even in the old individuals resorption of bone does not occur and the fibula remains visible. Thus the fusion is of a different kind to that found in the "Myomorpha".

Pes:

Astragalus:- (Table 2.XXV ; Fig. 2.23A - D). The trochlear

surface for the tibia on the body of the astragalus consists of two ridges separated by a groove. The lateral ridge is larger than the medial and the groove separating the two is deepest midway between them. On the lateral surface of the lateral condyle there is a facet for the distal end of the fibula. On the ventral surface, running disto-medially from the lateral edge and gradually becoming shallower, there is a groove that articulates with the primary articulation on the calcaneum. This groove almost reaches the medial edge of the bone and in so doing prevents any contact between the groove of the trochlear surface and the sulcus tali. On the plantar surface of the lateral condyle, along the distal edge of the main groove, there is a small facet articulating with the distal, dorsally facing portion of the primary articulation on the calcaneum. The secondary articulation for the calcaneum is on the proximo-lateral corner of the plantar ridge that runs the length of the head of the bone on the medial side. Along the medial surface of this ridge there is a long facet for a tendon.

The head is expanded slightly and bears a small dorso-lateral ridge. The distal facet is convex dorso-ventrally and usually extends onto the plantar surface medial to the end of the plantar ridge. This facet is usually single and articulates with the navicular and the proximal process of the cuboid; sometimes the small facet for the cuboid may be separated off by a slight ridge. There is no contact between the head of the astragalus and the calcaneum. On the medial edge of the distal end there is a very small facet for the proximal end of the first cuneiform.

Calcaneum:- (Table 2.XXIV ; Fig. 2.24A - D). The tuber calcis comprises about 45% of the bone and has a small flat process projecting back on the medial edge at its free end. In the ventral third of the free end of the tuber calcis there is the insertion of the Tendo Achilles: the dorsal extent of this is marked by a transverse, horizontal groove. The primary articulation for the astragalus forms a central dorsal eminence with the facets on the distal and medial faces and a small dorsal facet extending distally. The sustentaculum is small and does not project much medially, being in line with the medial edge of the primary articulation. There is a small sulcus calcanei and a long facet on the ventral surface of the sustentaculum for the tendon of m. flexor hallucis longus. Distally the facet for the cuboid curves round onto the medial surface to articulate with the base of the cuboid process. On the dorsal surface distally there is a small tubercle with a facet on the medial surface and a groove just lateral to it in which the peroneal tendons lie. The medial surface of the calcaneum, distal to the primary articulation, is roughened for attachment of the ligaments to the astragalus.

Navicular:- (Table 2.XXVI ; Fig. 2.25E - H). A deep, cup-shaped proximal facet articulates with the astragalus. On the lateral side this bone bears a deep notch into which fits the proximal process of the cuboid. Within this notch there are two facets for the cuboid – a long dorsal one and a ventral one situated on a small tubercle. On the lateral wall, facing disto-laterally, there is a third facet for the

cuboid while at a slightly more proximal level, on the medial wall, there is a facet for the second cuneiform which is often continuous with the main distal facet for the latter bone. Distally there are two facets separated by a thin ridge: the lateral facet, concave dorso-ventrally, is for the third cuneiform; the medial facet, convex dorso-ventrally, is for the second cuneiform. On the medial surface, at its distal edge, there is a small facet for the first cuneiform. The very pronounced plantar ridge projects distally and almost makes contact with Mt.III. The tendon running distally from this process contains a sesamoid bone at its beginning.

Cuboid:- (Table 2.XXVII ; Fig. 2.25A - D). The proximal process fits into the lateral notch in the navicular and bears two facets: the proximal end has a facet articulating with the astragalus; the medial and ventral faces bear a single facet articulating with the two separate facets on the navicular. Laterally of the process there is a facet for the calcaneum which extends onto the lateral face of the proximal process.

On the medial wall of the bone there are two facets for the third cuneiform: a dorsal, oval facet and a vertical one below it; these two sometimes meet to form a single L-shaped facet. The dorsal facet is separated by a slight ridge from the dorsal part of the main facet for the navicular; immediately proximal to the vertical facet for the third cuneiform there is a third facet for the navicular. Just proximal to this level there is a small fossa on the ventral

surface.

The distal end of the cuboid is occupied by a triangular facet for Mt.IV which is truncated at the dorso-medial corner by a small facet for Mt.III. Generally Mt.V does not seem to articulate with the cuboid but occasionally a very thin facet is found along the lateral edge of the distal end.

The dorsal edge of the lateral side forms a ridge terminating about three-quarters of the way along the bone in a ventro-laterally directed process. Just medial to this ridge there is a slight groove.

First cuneiform (C1):- (Table 2.XXVIII ; Fig. 2.26A, C). With the complete suppression of the hallux this bone has become reduced to a thin splint with a central dorsal process and the distal end of the bone does not form an articular surface. The development of the bone is rather variable. On the lateral face there is a distal facet for Mt.II and a facet on the central, dorsal process for C2; a small facet on the proximal end for the astragalus is usually present. The medial face bears a facet for the medial sesamoid on the distal edge of the central process, there is sometimes a second facet for the sesamoid on the proximal edge of this process.

Second cuneiform (C2):- (Table 2.XXIX ; Fig. 2.26B, D). The basic shape of this bone is that of a segment of a circle with the arc medially. The proximal end forms a facet for the navicular that is concave dorso-ventrally. Just below and separated from this by a slight groove there is a second

facet for the navicular that faces more laterally. This second facet is sometimes confluent with the main proximal facet. On the lateral surface there are two facets, near the dorsal edge, for the third cuneiform and, sometimes, a minute facet near the disto-ventral corner. The medial face bears a small facet for the first cuneiform and above this a small tubercle. The distal facet for Mt.II is triangular and curved; it is concave dorso-ventrally and slightly convex transversely. There is a small tubercle on the ventro-distal corner of the medial face.

Third cuneiform (C3):- (Table 2.XXX ; Fig. 2.26E, F, G). This bone has a basically rectangular form with a slight disto-medial process. The proximal end forms a facet for the navicular that is convex dorso-ventrally. On the medial face there are, proximally, two small dorsal facets for the second cuneiform which may be joined to form a single facet; very occasionally there may be another very small facet for the second cuneiform near the ventral edge. Distally on the medial surface there is a dorsal and a ventral facet, both for Mt.II, separated by a fossa. On the lateral face there are two facets for the cuboid which may be joined into a single L-shaped facet with the join marked by a slight ridge. This joining seems to be more common in juveniles. The distal end is occupied by the large triangular facet for Mt.III which has a concave medial edge.

Metatarsal II (Mt.II):- (Table 2.XXXI ; Fig. 2.26H, I ; Fig. 2.27A, B). Proximally there is a distinct plantar

process and the proximal end of the bone forms a curved, triangular facet for C2 that is concave transversely and slightly convex dorso-ventrally. The proximal part of the medial face forms a slightly roughened area against which C1 lies. At the distal end of this area there is a small facet articulating with C1; on the dorso-proximal corner there is a small tubercle with a facet for the anterior edge of the dorsal process of C1. On the lateral face, proximally, there is a dorsal and a ventral facet, both for C3. Beyond these the proximal third of the shaft is roughened for attachment of the ligaments that form the connection between Mt.II and Mt.III.

The shaft is cylindrical with a flattened lateral face where it lies against Mt.III. It curves out from the axis of the foot medially and has an axial twist of about 35°

The distal end is expanded slightly and the articular surface is barrel-shaped. There is a pronounced plantar keel which continues onto the shaft for a short distance proximal to the facet. In either side there is a fossa where the extensive joint ligaments originate. On the dorsal surface the proximal end of the facet is marked by a shallow transverse fossa.

Mt.II extends some distance proximally of Mt.III and so, although longer than Mt.IV, it extends distally only to the same level as the latter bone.

Metatarsal III (Mt.III):- (Table 2.XXXII ; Fig. 2.27C - F). This is the longest of the metatarsals; it is straight and the axis of the foot runs down it. At the proximal end there

is a well developed plantar process and the proximal facet for C3 is flat, triangular and aligned slightly obliquely, disto-medially, to the shaft. It does not extend down to the ventral tip of the proximal plantar process. On the medial surface the proximal part is roughened for the attachment of the ligaments to Mt.II and there is often a small low tubercle in the dorsal half. There may also be a small facet between the tip of the plantar process and the proximal end of the bone. The lateral surface has a large hollow proximally where Mt.IV articulates. There is also a facet on the lateral surface of the plantar process articulating with the plantar process of Mt.IV. The form of the articulation implies that more movement is possible between Mt.III and Mt.IV than there is between Mt.III and Mt.II. The proximal dorso-lateral corner projects and bears a small facet that articulates with the dorso-distal corner of the cuboid.

The shaft is almost square in cross-section, with rounded corners. In the ventral surface, just over one quarter of the way distally, there are two foramina into the interior of the bone; further distally, on the medial wall, there is a very shallow fossa at the level of the distal end of Mt.II. The distal end of this bone is of the same form as in Mt.II.

Metatarsal IV (Mt.IV):- (Table 2.XXXIII ; Fig. 2.28A - D). The proximal plantar process curves medially and has a facet on its medial side for Mt.III. On the proximal end of the bone the facet for the cuboid follows the line of the plantar process and hence is also curved medially: it is slightly

convex both dorso-ventrally and transversely. Proximally on the medial side there is a large tubercle that articulates with Mt.III. The proximal edge of this tubercle may be confluent with the cuboid facet but it is often slightly more distal so that the two are distinctly separated; below the tubercle the medial surface is hollowed out. On the lateral side, proximally, the surface is hollowed out where Mt.V articulates. The lateral face of the plantar process has a slight tubercle that articulates with the plantar process of Mt.V; a little more distally there is a second small tubercle.

The shaft is cylindrical with the medial surface flattened. It has an axial twist of 30° - 34°. The distal end is of the same basic form as in Mt.II but is a little more asymmetrical with the medial side better developed than the lateral.

Metatarsal V (Mt.V):- (Table 2.XXXIV ; Fig. 2.28E - H). This bone is reduced. Proximally a slight tubercle on the medial surface fits the hollow in Mt.IV and has facets on the proximal and dorsal surfaces. The well developed proximal plantar process sometimes has a small medial facet for Mt.IV and one on its disto-lateral corner, presumably for a sesamoid. On the lateral side there is a slight tubercle with a shallow fossa below it; between the medial and lateral tubercles the proximal end consists of a low ridge medially and a broad shallow groove, that continues onto the dorsal surface, laterally. The low ridge may bear a thin facet. In its normal position Mt.V does not generally

articulate with the cuboid although it may just do so in some individuals. If the toes were splayed out, as the articulations suggest they can be, then the proximal ridge of Mt.V would contact the cuboid.

The shaft is very flattened transversely and has an axial twist; it curves out laterally. The distal articulation is based on the same form as in Mt.II but is compressed so as to appear almost triangular in distal aspect; the plantar keel is less pronounced.

Phalanx I (Ph.I):- (Table 2.XXXV ; Table 2.XXXVI ; Table 2.XXXVII ; Table 2.XXXVIII ; Fig. 2.29A - F). The proximal end is saucer-shaped with a ventral groove, fitting the head of the metatarsal with its ventral keel. The articular facet within this saucer is in the shape of an inverted U. In digits 2, 4 and 5 it is set obliquely to the shaft – more distally on the side nearest digit 3. On either side of the groove the ventral edge forms a tubercle with a small facet on the proximal face for the flexor sesamoid. There are roughened areas on the side of the phalanx proximally where the joint ligaments insert. In digits 2 and 4 the proximal ends differ slightly: the medial side projects slightly proximally compared with the lateral side in digit 2 whereas in digit 4 the two sides of the bone terminate proximally at the same level. On the dorsal surface at the proximal end there is a small tubercle.

The shafts are cylindrical with flattened plantar surfaces and all, except in digit 3, are compressed transversely – slightly in digits 2 and 4, pronouncedly in

digit 5. In digits 2 and 4 the shafts curve slightly toward digit 3; in digit 5 this curve is pronounced. The bone is usually slightly longer in digit 2 than in digit 4. On the ventral surface of the shaft, just proximal to the distal articulation, there is a small tubercle on either side - these tubercles are not apparent in digit 5.

The distal articulation is convex dorso-ventrally and does not have a ventral keel. It extends onto the dorsal surface of the bone which is narrower transversely than the ventral surface. On the dorsal surface there is a shallow transverse fossa along the proximal edge of the facet. There is a fossa in either side wall for the origin of the joint ligaments.

Phalanx II (Ph.II):- (Table 2.XXXIX ; Table 2.XL ; Table 2.XLI ; Table 2.XLII ; Fig. 2.30A - F). The proximal end is concave dorso-ventrally to articulate with Ph.I. The ventral edge projects proximo-ventrally and has two small tubercles, one on either side (these are not distinguishable in digit 5), and a continuous transverse facet on the proximal edge for the flexor sesamoid. This facet may occasionally be divided into two. The dorsal edge of the bone forms a slight process projecting horizontally back above the facet except in digit 5 where it is inclined sharply upward.

The shaft is straight, somewhat quadrate in cross-section and thins slightly distally. It has a slight axial twist in digits 2, 4 and 5. The distal end is as in Ph.I but in digits 2 and 4 the distal facet is sometimes set slightly obliquely with the side away from the axis of the

foot more proximal so that, within a given foot, the isolated phalanges of digits 2 and 4 can sometimes be distinguished.

Phalanx III (Ph.III):- (Table 2.XLIII ; Fig. 2.30G, H, I). Viewed proximally the bone appears to be triangular with the apex dorsally and rounded. The proximal end forms a facet, concave dorso-ventrally, for Ph.II. On either side there is a small tubercle and ventro-distal to this there is a groove passing dorso-distally across the side face.

The proximal part of the plantar surface forms a process that is usually not pronounced. This is separated from the rest of the plantar surface on either side by a groove passing distally and toward the midline of the bone. The groove cuts the slight flange around the basal edge in a conspicuous manner. These two grooves do not reach the midline. At each of the proximal corners of the plantar process there is a foramen into the bone. Beyond the plantar process the ventral surface is flat.

The apex of the triangle forms a dorsal ridge that flattens distally; the whole bone narrows to a point at its distal end. In digits 2 and 4 the bone is asymmetrical and the two bones are mirror-images. The side toward the axis of the foot is more vertical so that the dorsal ridge is displaced to this side. The proximal facet is set slightly obliquely rather than vertically. In digit 5 this bone is a more pronounced but much smaller version of the Ph.III in digit 4.

Sesamoid bones of the pes:- Some of the principal sesamoid bones in the pes are described here: these bones are often

not preserved with the remainder of the skeletal material.

The medial sesamoid lies on the medial side of the first cuneiform and has a similar shape to the latter bone but is less elongated with only a short process. There may be a small facet on the dorsal end of the bone. The function of the medial sesamoid has been discussed in Hildebrand (1978).

There are two sesamoid bones on the ventral surface of the distal end of each metatarsal. These bones are kidney-shaped with a dorsal facet for the metatarsal; this facet extends onto the side of the bone to articulate with the distal keel of the metatarsal. The ventral edge forms a sharp ridge and the sesamoids are deepest dorso-ventrally at the proximal end except in digit 5 where the distal end is generally deepest. In the dorsal half of the distal end there is a facet articulating with the proximo-ventral edge of Ph.I. These sesamoids are connected to the sides of the proximal end of Ph.I by ligaments running from the dorso-distal corner; ligaments also connect the sesamoid to the hollow in the side of the metatarsal.

The sesamoid bones below the ventral surface of the distal end of Ph.I and Ph.II are single bony bars although that at the end of Ph.II is not usually ossified in the centre.

Pedetes capensis:

Pedetes capensis differs from Pedetes surdaster in a number of characters. Some of these differences are more

clear cut than others: in the case of the material examined for this study the separation involved varies from unambiguous through to characters which might prove to show clines if large collections are obtained from the key areas, especially southern Tanzania. The principal character differences are listed below.

Cranium (Table 2.XLIV):

1) The nasals are longer in P. capensis and comprise 37% of the cranial length (based on the means for a sample of 300 crania). The naso-frontal suture is positioned further posteriorly, level with the preorbital bar.

2) The palatal groove is deeper in P. capensis: the measurements in the two species show no overlap.

3) The incisive foramina are longer (37% of the diastemal length) and the interforaminal septum is more robust in P. capensis.

4) A large median foramen is normally present in the basisphenoid in P. capensis.

5) The lateral wings of the basioccipital are better developed in P. capensis except in juveniles in which the wings are flatter as in P. surdaster.

6) The depression in the anterior half of the frontals is only slight in P. capensis.

7) Small posterior maxillary foramina are often present in P. capensis.

8) The anterior angle between the preorbital bar and the rostrum tends to be more acute in P. capensis and is often less than a right-angle.

9) The combined buccinator and masticatory nerve canal is generally a little longer in P. capensis.

Mandible (Table 2.XLV):

10) In pm_4 the posterior enamel ridge of the anterior lobe has an infold directed anteriorly in P. capensis. This feature is occasionally absent in P. capensis specimens but has not been found in any P. surdaster specimen.

11) The incisive alveolus curves up into the ascending ramus and becomes more vertical in P. capensis: in P. surdaster it is aligned more obliquely.

Post-cranial:

12) In all 8 specimens in which the axis is preserved there is no evidence to show that it had been fused to Ce3 and where Ce3 is also preserved this was found to be the case. In the single specimen of P. capensis in which all seven cervical vertebrae are present there is no evidence of fusion between any of them.

13) Where the thoracic vertebrae are preserved the transverse processes in the posterior half of the series develop as in P. surdaster and not as described in Parsons (1898).

14) In the two specimens in which lumbar vertebrae are preserved there is no groove in the posterior surface of the neural spine.

15) The coracoid process of the scapula is better developed in the two specimens of P. capensis available for study.

16) The measurements suggest that P. capensis is larger in some of the post-cranial bones. However more material is essential before the measurements of the post-cranial bones of P. capensis can be properly analysed. On the basis of the available specimens there is some evidence of slightly different proportions between the skeletons of P. capensis and P. surdaster: in a few cases the measurements of P. capensis bones fall outside the range that has been found in P. surdaster.

CHAPTER 3

Megapedetes pentadactylus MacInnes, 1957.

Sub-family Megapedetinae MacInnes, 1957.

Diagnosis:- "Medium to large pedetids in which the cheek-teeth were of limited growth. Fibula reduced, but not necessarily fused with tibia. No reduction of digits in manus or pes." (MacInnes, 1957)

Genus Megapedetes MacInnes, 1957.

Diagnosis:- "A large pedetid in which the cheekteeth were of limited growth, each with a median transverse fold not extending throughout the whole vertical height of the crown; hind foot with fully developed hallux." (MacInnes, 1957)

Type species:- Megapedetes pentadactylus MacInnes, 1957

Megapedetes pentadactylus MacInnes, 1957

Diagnosis:- "As for the genus." (MacInnes, 1957)

Introduction:

The available material of Megapedetes pentadactylus is rather limited although some of it is very well preserved. In the original description of the species (MacInnes, 1957) most of the material that had been excavated up to that date was utilised. Since then only a relatively small amount of

additional material has been added to the sample known. A thorough examination of the small mammal material housed at TILLMIAP has revealed the presence of a few pieces that were collected prior to 1957 but were not described in MacInnes (1957). In addition to this some extra material has also been collected. This material includes many fragments; some juvenile mandibles from Songhor, described in Lavocat & Michaux (1966), and an almost complete right leg and foot, part of the left foot, part of the tail and some other fragments, apparently from a single individual, that were collected by M. Pickford in 1977 at Legetet.

The original description of the species was based on two individuals, the holotype from Songhor and the main paratype from Rusinga, together with a number of fragments. All the specimens were identified by their field catalogue numbers: the holotype is Sgr.420'48 and the main paratype is R.982'47. Both these specimens are now housed in the Department of Palaeontology at the BM(NH) where the holotype is accessioned as M21571 - M21598 inclusive and R.982'47 as M21599 - M21619. Lavocat (1973) states that the holotype is KNM-So 808 thus implying that the specimen is housed at TILLMIAP in Nairobi. Following this allocation the holotype has been placed on the accessions catalogue at TILLMIAP. Presumably Lavocat was unaware that the holotype and main paratype were both donated to the BM(NH) in 1961. In addition to these two individuals the BM(NH) also has in its possession a fragment of right mandible with incisor (M16355) from Rusinga. All the other material examined is housed in TILLMIAP and comes

from sites in Kenya. A detailed list of all this material is given in Appendix III.

Geological range:

Lower Miocene - Middle Miocene (9 - 22 million years b.p.)

The earliest known record of M. pentadactylus is from the Bukwa site in Uganda where the fossiliferous beds are capped by a lava dated at 22 million years b.p. (Walker, 1969). The species is also found in Uganda in the Napak volcanics, dated at 19±2 million years b.p. (Bishop, 1964). Remains have been found at the following sites in Kenya:-

Rusinga	16.5 - 23 million years b.p. (Van Couvering & Van Couvering, 1976).
Songhor	c 19.8 million years b.p. (Van Couvering & Van Couvering, 1976).
Mfwangano	18.5 - 21 million years b.p. (Van Couvering & Van Couvering, 1976).
Legetet	c 19.6 million years b.p. (Van Couvering & Van Couvering, 1976).
Fort Ternan	12.5 - 14 million years b.p. (Andrews & Walker, 1976).

Remains of a possible pedetid have been recorded from Lower Member B of the Ngorora Formation in the Kenyan Rift Valley, dated 9 - 12 million years b.p. (Bishop & Pickford, 1975). On the basis of the age of the deposit these remains may well represent M. pentadactylus.

Outside East Africa Megapedetes has been recorded at Beni-Mellal, one of the earliest deposits of rodents in the Maghreb of Morocco, which is believed to be about the same age as Fort Ternan. The species found may be M. pentadactylus and it is not found in the later deposits in the Maghreb (Lavocat, 1961 & 1978). Material ascribed to the genus Megapedetes has been described from Greece (Tobien, 1968); Israel (Goldsmith et al., 1982) and Turkey (Sen, 1977): these are the only records of the Family Pedetidae outside Africa.

DESCRIPTION:

The original description (MacInnes, 1957) was generally fairly accurate. However there are a number of points where MacInnes' interpretation of the specimens can be questioned or where further information can be added. For ease of comparison with the other pedetids described a complete description of M. pentadactylus is given. This is based on an examination of the material listed in Appendix III although much of it is the same as MacInnes (1957). Throughout the description a comparison with Pedetes implies comparison only with the Recent species of that genus and not with any of the fossil forms that have been ascribed to it.

Cranium (Table 3.I ; Fig. 3.1A , B , C ; Plate 3):

The only relatively complete cranium is that of the holotype (M21571). The main paratype includes an incomplete cranium (M21604) and an isolated portion of maxilla: there are also a number of cranial fragments and a complete,

relatively undamaged, right bulla (Sgr.258'48) in TILLMIAP.

Dorsal aspect:- (Fig. 3.1A). In the holotype the nasals comprise 40% of the total cranial length and are relatively narrow with their greatest width 37% of their length. They are not inflated and for much of their length their edges are overlapped by the premaxillae which have a lateral ridge between the vertical wall and the horizontal section. The naso-frontal suture is posterior to the line of the maxilla-lachrymal suture whereas in Pedetes it is generally level with or anterior to this line. At its posterior end the premaxilla curves out to join the preorbital bar much more gently than in Pedetes and the angle between the preorbital bar and the rostrum is much less sharp. The dorsal expanse of the premaxilla at its posterior end is much greater than in the living genus and the maxilla does not overlap it laterally to the same extent.

The frontals are estimated to comprise 33% of the total cranial length in the holotype but at their posterior end they are damaged so that it is impossible to obtain an accurate length for them. There is a distinct median depression in the frontals that probably stretched the full length of these bones rather than being restricted to the anterior half as in Pedetes; it did not extend out to the lateral edge of the cranium. Although the interorbital constriction is relatively narrower than in the living genus it is not any more pronounced. The upper edges of the orbits diverge posteriorly in a shallow curve but MacInnes is incorrect in saying that this is different from Pedetes as

is shown in his diagram (MacInnes, 1957 : 3 Fig. 2). In the posterior half of the orbit there is a distinct supraorbital ridge with a shallow groove medial to it. The post-orbital process is reduced to a tubercle, although this is more pronounced than in Pedetes, and the fronto-parietal suture is level with it. In the main paratype this suture is straight, without a posterior embayment on either side.

The groove in which m. temporalis lay is marked anteriorly by a ridge running postero-medially across the parietal from the post-orbital tubercle. The muscle seems to have been narrow but relatively thick and probably originated on the posterior part of the parietal and/or on the bulla. It did not extend to the midline. Although this region is damaged it appears that the interparietal was pentagonal with an anterior salient between the parietals. It was not sunk below the general level of the surface of the cranium and its posterior edge had a small median salient into the supra-occipital. The latter bone appears to have curved over onto the dorsal surface of the cranium posterior to the inter-parietal. It formed a slight ridge, along the posterior edge of the dorsal surface, marking the edge of the origin of the neck muscles. The postero-lateral corners of the cranium are occupied by the expanded mastoid bullae.

Profile:- (Fig. 3.1B ; Plate 3). The upper surface of the cranium is relatively flat with only a slight rather than a pronounced downward curve of the posterior half of the parietals and the interparietal. The rostrum is relatively a little less deep than in Pedetes.

In contrast to Pedetes there are no lateral nasal wings anterior to the premaxilla. The lower maxillary root of the zygoma arises further posteriorly than in Pedetes and is more robust. It slopes quite sharply postero-ventrally but remains above the level of the toothrow until behind the preorbital bar. The ridge marking the anterior and dorsal edges of the origin of m. masseter medialis is less pronounced than in the living genus: it begins at the anterior junction of the premaxilla and nasal rather than at the base of the lower root of the zygoma, it then runs along the dorsal edge of the premaxilla and curves out onto the antero-lateral edge of the preorbital bar. The incisive alveolus arises at the level of the infra-orbital foramen and forms a broad curved ridge across the rostrum: it reaches relatively further dorsally than in Pedetes and may reach, or at least almost reach, the dorsal edge of the premaxilla at the most dorsal point of the curve.

The preorbital bar has a slightly curved anterior edge not a straight one as in Pedetes: it is composed of the maxilla anteriorly and the jugal and lachrymal posteriorly. The latter two bones are in contact and are not separated by the maxilla. There is a pronounced preorbital process of the lachrymal. In the holotype the preorbital bar is 4.9mm wide antero-posteriorly which is somewhat wider than is commonly found in Pedetes although not as wide as the widest found in the latter genus (5.5 - 6.0mm). The maxilla sends a process back postero-ventrally below the jugal: it passes below the occlusal level of the cheekteeth opposite m^1 and

terminates opposite m^2 in a rounded point. The whole lower edge of the zygoma is thus inclined postero-ventrally up to this point rather than horizontally as in Pedetes. However, from this point the lower edge of the zygoma curves up dorsally. There is a ridge, aligned very slightly postero-dorsally, running across the main body of the zygomatic arch from the lower maxillary root and the zygoma is thickest at the level of this ridge. Below the ridge the jugal curves ventro-medially and provides the origin for m. masseter lateralis, which, in contrast with the Recent genus, is not subdivided into a series of conchoidal fossae. The squamosal root of the zygoma is very robust and a well developed, rounded, inferior process of the jugal is present in the main paratype. The squamoso-jugal suture is horizontal.

The orbit is large and relatively circular. In its anterior edge there is a large lachrymal foramen. A superior ethmoid foramen is visible in the orbital plate of the frontal just below the upper rim of the orbit; the inferior ethmoid foramen cannot be found although the portion of the inner wall of the orbit in which it is found in Pedetes is preserved. The rooted cheekteeth of Megapedetes did not apparently rise so high in the floor of the orbit as do the rootless cheekteeth in Pedetes and consequently the floor is flatter. All of the posterior part of the orbit has been destroyed.

Behind the orbit the groove for m. temporalis is much better developed than in Pedetes. Its lateral edge is formed by a pronounced ridge that begins at the base of the

squamosal process onto the bulla and runs across the squamosal and down onto the zygoma. The antero-medial edge of the groove has been described above. In all the specimens the squamosal process onto the bulla is broken off. At the base of the squamosal process there is a temporal foramen either in the squamosal or between the squamosal and bulla, as in Pedetes. Damage to the posterior part of the cranium makes it difficult to say much about it but most of the cranium behind the orbit is occupied by the enlarged auditory bulla. The bulla is described in detail below, based on Sgr.258'48.

Ventral aspect:- (Fig. 3.1C). The incisive foramina are set further behind the incisive alveolus than in Pedetes. Their length is 31% of the diastemal length in the holotype. They are not set in a palatal groove but on either side a slight ridge runs forward from the edge of the incisive foramina to the posterior surface of the incisive alveolus. The premaxilla-maxilla suture leaves the incisive foramen about halfway down its length and passes out laterally before curving anteriorly: it remains well anterior of the inner rim of the zygomatic arch.

The palate is slightly arched, although less than in the Recent genus, and the median suture is raised as a slight ridge. On the basis of KNM-Ru 4074A, a fragment of palate with pm^4 - m^1, the posterior end of the palate is probably at the level of m^2 as it is in Pedetes. As the palate is damaged in all the specimens it is difficult to interpret the palatal foramina but there appear to have been two sets

of foramina: the main posterior palatal foramina are opposite the anterior lobe of m^1, as described in MacInnes (1957), and lay on the maxilla-palatine suture which is at this level; in the holotype, on the left side, there appears to be a second foramen opposite the middle of m^2.

The only evidence of what the ventral aspect of the basicranium was like comes from the fragment of the basi-occipital associated with the main paratype. At least in this specimen the principal opening in the basioccipital seems to have taken the form of a foramen on either side of the midline as is sometimes found in Pedetes. The lateral wings are very pronounced and tend to converge anteriorly; there is also a median ridge. The portion of the basi-occipital attached to the cranium (M21604) shows that the hypoglossal foramen is single and positioned as in the living genus in the groove between the occipital condyle and the lateral wing. The styloid process is massive and set well behind the condyle; the origin of m. digastricus is on its antero-lateral and antero-medial faces.

The toothrows diverge posteriorly, although less than in Pedetes, and almost parallel the zygomata. The lower maxillary root of the zygoma is set further posteriorly than in Pedetes and curves more gently into the rostrum to produce a larger oblique angle anteriorly. The inner rim forms a ventral ridge as it turns into the palate; it is relatively straight between sharp lateral and medial angles and the ridge continues along the edge of the palate in line with the lingual edge of the alveolus of pm^4. At the posterior

end of the zygoma the jugal contributes to the articular surface of the glenoid fossa. The greatest width of the cranium is further posterior than in the Recent genus.

Anterior aspect:- The premaxillae are more vertical than in Pedetes and the nasal aperture is larger. Below the nasal aperture there is a pronounced median ridge. The infra-orbital foramen is large and the preorbital bar is inclined a little more ventro-laterally than in the living animal. The downward extension of the zygoma is very clear.

Posterior aspect:- This is very badly damaged. The foramen magnum is flatter and more oval than in Pedetes. There does not appear to be an external occipital ridge on the supra-occipital but the dorsal ridge is continuous with the pronounced lateral nuchal crests. The bullae were probably less conspicuous in posterior view than in Pedetes.

Auditory bulla:- (Fig. 3.12G , H). Superficially the bulla is quite similar to Pedetes. However in the intact cranium it was probably less vertically orientated than in the Recent genus. This is associated with the generally less inflated form of the posterior part of the cranium in Megapedetes. The bulla is not so well developed as in the living animal: the tympanic bulla is not so full but is more pointed ventrally, it possesses an anterior ventro-medial process that is larger than but similar to Pedetes; the mastoid bulla is relatively less inflated.

As in the Recent animal a groove runs backward across the mastoid for the posterior process of the squamosal; this

groove is quite shallow. At its distal end it has a triangular expansion like that in the modern genus but the groove itself is more complex being deeper along the edges with a pronounced median ridge. It also extends further across the mastoid, almost reaching the posterior edge of the bulla. The mastoid flange does not extend so far ventrally as in Pedetes and barely overlies any of the tympanic; the posterior portion is very pronounced and projects well behind the bulla to cover the base of the styloid process. There is a distinct groove between this posterior portion and the main part of the mastoid flange. The external acoustic meatus is not so extensively ossified and so appears more open and the mastoid flange contributes to the edge of the opening. There is a well developed ridge along the antero-lateral edge of the external acoustic meatus. A distinct vertical groove separates the mastoid flange and the external acoustic meatus but the exact position of the stylomastoid foramen is difficult to determine. It seems to be in the corner formed between the mastoid flange and the main part of the mastoid bulla and is nearer to the external acoustic meatus than in Pedetes.

In posterior view of the cranium more of the dorsal surface was probably visible than in Pedetes but it seems that little of the posterior surface was exposed as it was almost completely overlain by the exoccipitals. The sutures between the petrous and the mastoid portions of the periotic and between the periotic and the tympanic are still visible on the postero-internal surface of the bulla in Sgr.258'48.

On the internal surface the floccular fossa is of about the same size as in Pedetes. Below it there is another hollow in which the foramina for cranial nerves VII and VIII are found. In Pedetes this hollow is quite complex but in Sgr.258'48 there is a small amount of matrix trapped in it, this proved impossible to remove without the risk of damage to the bulla and it obscures some of the detail. The stapedial foramen is in the same position as in the modern genus but appears smaller as it does not lie in the base of a small hollow. Immediately anterior to the foramen for cranial nerve VII there is a pronounced ridge and a fossa facing anteriorly; these features are absent in Pedetes. The hollow and overhang of the mastoid above the floccular fossa is also better developed in Megapedetes. It seems that the roof of the Eustachian tube was not ossified so far down as it is in Pedetes and consequently the tube forms a groove in its ventral part. It is in the same position as in the Recent animal.

In the anterior face there are three distinct fossae with the ridges separating them meeting to form a small central tubercle. These are not developed in Pedetes. The canal of Huguier opens in the ventro-lateral fossa which is in the same relative position as in the Recent genus.

Upper dentition:- The incisors are strongly opisthodont and much deeper, antero-posteriorly, than they are wide, transversely (Table 3.II). Their anterior face is not grooved and the antero-medial corner is more sharply curved than is the antero-lateral. There is a ridge on the lateral

side of the anterior face and there may also be a slight one on the medial side. The enamel covers just less than half of the side walls and the incisor tip may or may not be stepped.

MacInnes (1957) claimed that the incisors were sorted into upper and lower on the basis of their radius of curvature. However for many fragments this is not possible as the pieces are too short for their radii of curvature to be determined. There are 21 fragments that can be described as upper incisors, including fragments associated with premaxillae and the holotype cranium.

The cheekteeth are brachyodont and rooted, not with persistent pulps. In many specimens the occlusal pattern consists of two separate and sub-equal lobes separated by a transverse infold of the occlusal enamel. This infold tends to be widest in the centre of the tooth and to narrow toward both buccal and lingual edges, more so on the latter side: it is also shallowest on the lingual side. The lobes comprise simple enamel rings filled with dentine and show no other structure in either the holotype or the main paratype. With wear the lobes would evidently unite on the lingual side to produce an occlusal pattern similar to that in Pedetes; this state is found in KNM-Ru 4069 and KNM-Ru 4074A. This pattern is also found in a few of the isolated cheek-teeth but it is impossible to determine whether these teeth are from the upper or the lower dentition.

The crown is expanded over a pronounced neck and the teeth possess two or three roots. MacInnes (1957) notes the

presence of two maxillary fragments from Rusinga (ibid. p. 11). In his table their numbers are transposed: specimen R.1 (= KNM-Ru 4068) has $pm^4 - m^1$ and R.110 (= KNM-Ru 4069) has $pm^4 - m^2$.

Mandible (Table 3.III ; Fig. 3.2A , B):

There is a pronounced lower masseteric tubercle antero-lateral to pm_4. The insertion of m. masseter medialis begins at this tubercle: it is relatively pronounced and runs back almost horizontally just below the cheekteeth. It merges with the anterior edge of the coronoid process which arises at the level of the posterior edge of m_1. The coronoid plate is missing in all specimens but it appears to have been relatively thin with a thick base. Between the base and the toothrow there is a distinct groove. The coronoid process completely obscures m_3 in lateral view.

Also beginning at the lower masseteric tubercle is a well developed masseteric crest. This passes postero-ventrally, more steeply than in Pedetes, across the lateral wall of the ramus. Ventrally it curves sharply round the incisive alveolus and into the angle which does not possess an anterior process. In its ventral portion the masseteric crest overhangs slightly anteriorly forming a shallow groove between itself and the incisive alveolus.

The angle arises from the postero-lateral edge of the incisive alveolus and is aligned postero-medially so that its posterior edge would lie behind the alveolus if it were preserved — the whole angle is not preserved in any specimen.

There does not appear to have been a pronounced medial shelf on the lower edge of the angle, as there is in Pedetes, for the insertion of m. pterygoideus internus: the lateral face and ventro-lateral edge of the angle form part of the insertion of m. masseter lateralis. The postero-ventral corner of the angle is rounded and the lower edge of the angle is curved rather than running horizontally as in the living animal.

The incisor rises well up into the condylar process but does not become fully vertical: posteriorly the alveolus is composed of solid bone and is not partially open as in the Recent animal. The end of the incisor does not produce a tubercle in the lateral wall of the process as it does in Pedetes. On the medial face the inferior dental foramen is immediately above the end of the incisor. The condyle is not clearly demarcated from the condylar process and has a very indistinct anterior edge. There is a pronounced insertion for m. pterygoideus externus below the overhanging medial edge of the condyle: the lateral edge of the condyle does not overhang. The upper edge of the coronoid process appears to have joined the condylar process at a more gentle slope than in Pedetes.

The symphysis is straight and slopes postero-ventrally; it forms a well developed bony projection ventrally. There are two openings of the foramen mentale, basically as in Pedetes, but the lower opening is just above the incisive alveolus and the dorsal opening may be missing. The lateral wall of the ramus is smooth as the ends of the cheekteeth do

not form tubercles. Postero-medial to m_3 there is a small tubercle.

Lower dentition:- The incisors are very similar to the upper incisors being strongly compressed transversely (Table 3.II), with the enamel covering about half of the side walls and the anterior face without any grooves.

The cheekteeth are rooted and brachyodont and show an occlusal pattern like that of the uppers except that the transverse infold is narrowest and shallowest, and the curvature of the lobes is greatest, on the buccal side. As in the uppers the infold does not extend through the full height of the teeth. In pm_4 and m_1 the anterior lobe is the smaller while in m_2 and m_3 the reverse is true: m_3 is the smallest tooth.

In the original description (MacInnes, 1957) two additional mandibles are mentioned and their measurements are given (ibid. p. 12). The specimen described as Sgr.70'48 is, in fact, two specimens combined: the true Sgr.70'48 (the left ramus only) is now KNM-So 1499 and the right ramus (with the field number Sgr.302'49) is now KNM-So 1500. The other mandible (366'48) is from Rusinga and is now catalogued as KNM-Ru 4023 (right ramus) and KNM-Ru 4024 (left ramus).

The m_3 in KNM-So 1500 has worn so that the lobes have joined on the lingual side and are separated by a postero-buccal infold - this is the reverse of the normal position. In KNM-Ru 4023 the pm_4 shows an anteriorly directed infold in the posterior enamel ridge of the anterior lobe as is found in Pedetes capensis.

Amongst the material collected since 1957 is part of a juvenile left mandible (KNM-So 3909B) from Songhor (Table 3.IV). The teeth in this mandible are erupting but are already slightly worn: they have been described in Lavocat & Michaux (1966). Even at this stage of wear these teeth are larger than the teeth from Maboko (see Chap. 6), which are much more worn.

Vertebral column:

Cervical vertebrae:- (Fig. 3.3A , B , C). There have not been any further finds of material of the cervical vertebrae since MacInnes (1957).

In the atlas the laminae of the neural arch are wider than in Pedetes and are almost horizontal rather than aligned dorso-medially. The neural spine is in the anterior half of the arch and is reduced to a tubercle. There is a relatively complex suboccipital foramen in the lamina of the neural arch just above the articular surface for the occipital condyle: a lateral branch passes out onto the anterior face of the transverse process. The ventral arch is quadrate, robust with a well developed facet for the dens of the axis. The transverse process is better developed than in the Recent genus: it is more vertical in the main paratype but slopes ventro-medially in the holotype in which it does not project out so far. The vertebrarterial canal is smaller than in Pedetes with its posterior opening just above the posterior articular surface.

The axis is not fused to Ce3. The neural spine is very

broad antero-posteriorly and is more massive than in Pedetes with the posterior edge bifid towards the top. There is a large dens that projects well forward: there is not a pronounced groove on the dorsal surface separating it from the centrum as there is in the Recent genus. Amongst the fragments associated with the main paratype there is a neural arch and spine of the axis: it is larger than in the holotype and broader relative to its height.

There is no evidence of fusion between any of the remaining cervical vertebrae as is sometimes found between the transverse processes in P. surdaster. The transverse processes themselves are more massive than in Pedetes. The centra are relatively thin with the ventral surface very slightly convex and the dorsal surface flat. Their anterior edges are slightly concave, the posterior, convex.

Thoracic vertebrae:- The first thoracic vertebra is present in the main paratype associated with the cervicals (BM(NH) M21610). Other parts of this region are represented in the holotype and LG.29/5.

In the more anterior members of the series the anterior vertebral notch is very small. At the posterior end of the series the vertebrae are very similar to those in Pedetes. Throughout the thoracic vertebrae the neural spines and transverse processes are more robust than in the Recent genus.

In LG.29/5 there is an almost complete thoracic vertebra present that has only suffered slight damage to the processes. On the basis of the length of the anapophyses and the

anterior tubercle on the transverse processes it is believed to be Th9 or Th10. The centrum is deeper than in Pedetes.

Lumbar vertebrae:- (Table 3.V). The centra have slightly concave dorsal surfaces, each with two foramina as in Pedetes. They are broader than they are long or deep. The ventral surface is concave longitudinally with a pronounced median ridge extending the whole length in the more anterior vertebrae but becoming restricted to the anterior half towards the posterior end of the series. A small foramen may be present in the ventral surface on either side of the median ridge. The neural arch is slightly broader than it is high and has the same proportions in Lu1 to Lu5: it is not preserved in Lu6 or Lu7. Significant remains of the transverse processes are only found in Lu6 but the bases remain in the other vertebrae. They appear to have been relatively broad and flat and are inclined anteriorly, although only slightly so in Lu1 and Lu2. Their greatest development seems to have been in Lu6; anteriorly, in Lu1 to Lu3, they are relatively small and more cylindrical. They arise at the junction of the neural arch pedicle and the centrum. Compared to Pedetes they are relatively thinner and in the more posterior members of the series they are slightly bowed in anterior aspect.

The anapophyses are best developed in Lu2 or Lu3 and appear to be reduced to a tubercle in Lu6 although as they are damaged their exact development is not known. Metapophyses are present by the prezygapophyses and are best developed in

Lu3 or Lu4 and become smaller further posteriorly. The zygapophyses are vertical and resemble those of Pedetes. The neural spines are inclined anteriorly and there is no evidence of a groove in the posterior faces. The posterior vertebral notch is larger than the anterior.

Sacrum:- (Table 3.VI). This is composed of two fused vertebrae in contrast to three in the Recent genus. In the first vertebra the base of the broken neural spine suggests that it was slender while that of the second vertebra was stronger and stouter. The centra are curved ventrally rather than being flattened as in Pedetes and both have a ventral median ridge in the anterior half. The auricular surface is J-shaped with the vertical section relatively larger than in Pedetes; the triangular horizontal section ends before the anterior tip of the expansion in contrast to the Recent genus. The articulation slopes ventro-laterally but it is more vertical than in Pedetes. The anterior tip of the sacro-iliac area shows signs of an expansion not found in Pedetes but the end is broken off, the upper edge overhangs slightly. There is a distinct foramen between Sa1 and Sa2 which opens laterally rather than more dorsally and ventrally as in the living animal. The prezygapophysis of Sa1 is less well developed than it is in Pedetes and in BM(NH) M21585 the zygapophyses between Sa1 and Sa2 are still visible although they are fused.

Caudal vertebrae:- (Table 3.VII). In the holotype Ca1 - Ca4 and three damaged centra from further distally are

preserved: in LG.29/5 there is a section of eight vertebrae, probably Ca7 - Ca15, and two other vertebrae, about Ca21 and Ca30. As there are only two sacral vertebrae in Megapedetes and the third sacral in Pedetes is presumably formed by fusion of the first caudal to the sacrum the first caudal in the Recent genus must be homologous with the second caudal (Ca2) in Megapedetes.

In the anterior caudals the zygapophyses are well developed and vertical. The neural spine is present in Ca1, except for the tip which is missing, and slopes slightly posteriorly. The size of the neural canal declines rapidly down the tail. The transverse processes are well developed and, as in the Recent genus, they are thicker along the posterior edge than along the anterior. In Ca1 they pass out laterally but further posteriorly they become inclined posteriorly: they are longer and less truncated than in Pedetes and arise at the junction of the centrum and the pedicle of the neural arch. There are no anapophyses. There is a very small anterior vertebral notch, the posterior notch is better developed. The centra are similar to those in Pedetes and are nearly as deep as they are broad. Ventrally there is a slight concavity between the two ventro-lateral ridges, which are pronounced at the anterior and posterior ends, especially the latter. At the posterior ends the ridges expand to form the base for the chevron bones, none of which have been found.

In LG.29/5 vertebrae from the middle of the tail are present and probably correspond to Ca7 - Ca15. They were

all closely associated in the original block but only the first two were articulated. Their order has been based on the relative development of the neural arch and spine in comparison with Pedetes in which they decline in size posteriorly. They are assumed to behave similarly in Megapedetes. Ca7 and Ca15 comprise only posterior and anterior halves respectively. All these vertebrae are very similar to vertebrae from the same region of the tail in Pedetes and suggest that Megapedetes similarly had a long tail. The neural arch and spine remain better developed further down the tail than in Pedetes. The lateral processes are better developed than in the Recent genus and, as in the latter, are divided into anterior and posterior halves by a median indentation and are joined by a ridge along the side of the centrum: the anterior portion is more rod-like, in the posterior half the dorso-ventral expansion of the posterior tip is less well developed. On the ventral surface the ridges remain distinct and do not converge and meet in the middle of the surface, as they do in Pedetes, until much further down the tail, around Ca13 compared to Ca7 in the living animal. The paired anterior ventral tubercles are larger at the anterior end of this series than in Pedetes.

Ca21 and Ca30 are similar to Pedetes vertebrae and are reduced to little more than a cylindrical centrum. This specimen provides the best evidence yet for the form of the tail in Megapedetes.

Sternum and ribs:

MacInnes (1957) does not mention the sternum and no

pieces of either the holotype or the main paratype have been identified as such. Subsequent excavations have also not produced any remains. However in the box of fragments associated with the holotype there is a piece of the manubrium sterni. The bone consists of a broad, flattened plate and a rounded posterior process. Running anteriorly across the plate from the process there is a straight ridge with the bone broken very close to it on one side. In anterior aspect the bone forms a flattened V with the ridge ventrally as in Pedetes. There is a large articulation on the dorsal surface for rib 1 but that for the clavicle is not pronounced. The posterior process presumably joined with the remainder of the sternum, which is not preserved.

In the main paratype left rib 1 and part of right rib 1 are preserved (BM(NH) M21611). These are similar to Pedetes but are stouter, although not in relative terms.

Clavicle (Table 3.VIII ; Fig. 3.3D , E):

No further remains of the clavicle have been found since MacInnes (1957) and the specimen preserved in the main paratype (BM(NH) M21601) is a right clavicle although labelled as a left one. The bone is larger than in Pedetes with a more flattened scapular end that bears a well developed facet for the acromion process. There are two pronounced tubercles: one on the ventral surface just by the sternal end and one on the dorsal surface just proximal to the scapular end. The upward curvature of the bone at the scapular end is not pronounced.

Scapula (Table 3.IX ; Fig. 3.4A):

There is no material, additional to that described in MacInnes (1957), available. The supraspinous fossa is better developed than in Pedetes but is relatively small; the infraspinous fossa is more expanded posteriorly. A teres major process is present but is not well developed. The anterior edge of the scapular plate curves out slightly laterally. There is a well developed and robust spine that extends to the dorsal edge of the plate; ventrally there is a well developed acromion process and a flattened metacromion is present but this is not especially pronounced. The glenoid fossa is like that of Pedetes: the coracoid process is broken but was probably larger and more robust than in the Recent genus. On the posterior edge of the scapular plate, just dorsal to the glenoid fossa, there is a slight tubercle.

Humerus (Table 3.X ; Fig. 3.4B , C):

The head is more elongated antero-posteriorly than in Pedetes and the well-developed greater tuberosity occupies a slightly larger part of the anterior surface. The lesser tuberosity is also large as is the delto-pectoral crest which is relatively thinner than in Pedetes. The supinator crest is not so well developed as in the Recent genus and merges gradually with the shaft at a relatively higher level. The medial epicondyle is less developed than in the living animal and lacks the dorsal hook-like process. In some specimens an entepicondylar foramen is present while in others it is not. There is no supratrochlear foramen; the

olecranon fossa is well developed. The trochlea, especially the medial ridge, is positioned a little more distally than the capitulum. It is broad and shallow; the capitulum is relatively small and there is a deep fossa above it on the anterior surface.

Ulna (Table 3.XI ; Fig. 3.3F ; Fig. 3.5A , B):

This bone is of even thickness throughout its length and is relatively robust with a flattened lateral face having ridges at its anterior and posterior edges. There is also a well developed antero-medial ridge. A facet for the head of the radius is present on the lateral side of the coronoid flange of the trochlear notch while the olecranon flange of this notch produces a pronounced lateral projection. The olecranon process is more elongated than in the Recent genus. There is virtually no sign of a postero-medial process at the free end of the olecranon process but there is a slight thickening of the postero-medial corner and a slight lateral process.

Radius (Table 3.XI ; Fig. 3.5C , D ; Fig. 3.3F):

The proximal facet is oval. The proximal end of the shaft is more robust than in Pedetes and the bicipital tuberosity is more prominent. In the distal half the shaft is flattened and there is a distal anterior tubercle. The styloid process is not well developed: the facet for the scapho-lunar is relatively larger and less deeply concave than in the Recent genus. The distal notch for the ulna is

poorly developed.

Manus (Table 3.XII ; Fig. 3.5E ; Fig. 3.6A):

This would appear to have been large and fairly robust. Of the carpus only the right unciform has been found: its articulation with the cuneiform is larger and more convex than in Pedetes, the facet for the magnum is smaller and crescentic. The distal facets for Mc.IV and Mc.V merge into one and a small facet articulates with the proximo-lateral process of Mc.III.

Metacarpal II is similar to Pedetes and articulates mainly with the trapezoid although it also makes contact with the trapezium. The facets for Mc.I are as in the Recent animal while the area articulating with the overlapping portion of Mc.III is relatively larger. Metacarpal III is also similar to the living animal and has a large process contacting Mc.II. The facet for the magnum is slightly concave and the proximo-lateral edge overlaps the proximo-medial edge of Mc.IV to articulate with the unciform.

Metacarpal IV is less expanded laterally than in Pedetes but is otherwise similar. The lateral wall is excavated to accommodate Mc.V which is not well preserved. In each case the distal articulation has a pronounced median keel that does not project distally but is almost confined to the ventral surface.

In the first phalanges the proximal articulation is divided almost completely into two by a shallow median groove to produce an articular surface with an inverted

U-shape. This division is not apparent in right digit 3 which is as described in MacInnes (1957). The distal end of Ph.I is hemicylindrical and does not have a deep median groove: this is also the case in the distal end of Ph.II. The ungual phalanges (Ph.III) are relatively broad and short. The manus would appear to have been a more efficient digging implement than in the Recent genus.

There is also a single, isolated phalanx that is probably Ph.I, left digit 3. This has a proximal articulation that is almost completely divided ventrally by a shallow median groove.

Innominate bone (Fig. 3.6B):

The ilium is stout with a triangular cross-section caused partly by the great development of the origin of m. rectus femoris. Running antero-ventrally across the ventral half of the ilium there is a distinct ridge. The auricular surface is oval.

The ilium and ischium form a horizontal bar with the acetabulum, which has a low ventral edge, at their meeting point. There is a small ischial spine on the medial surface of the ischium just posterior to the acetabulum. When MacInnes (1957) refers to the ischial spine it is actually referring to the ischial tuberosity. The shaft of the ischium is slender and of even thickness. The bone is similar to Pedetes. The pubis and ventral part of the ischium slant toward the midline at an angle of about 30° to the horizontal but this part of the bone is largely missing.

Femur (Table 3.XIII ; Fig. 3.6C , D):

The trochanter major continues the line of the shaft and is not displaced slightly laterally as it is in Pedetes. On the anterior face of the trochanter major there are two tubercles: the more lateral one is about as well developed as in the Recent genus and is slightly lower down the bone than the medial tubercle which is very large and level with the middle of the head. These tubercles make the trochanter major much wider at the level of the head than it is in the living species. There is a large fovea in the hemispherical head for the insertion of the ligamentum teres. The trochanter minor is large; there is no trochanter tertius. A distinct ridge runs from the trochanter minor along the posterior surface of the neck; this is not found in Pedetes. There is a well developed intertrochanteric crest and there is a distinct trochanteric fossa.

The shaft is straight and is not bowed forward significantly. It is compressed antero-posteriorly in the lower third. When standing on both condyles the shaft is either upright or leans slightly inward. There are ridges running down the posterior surface and the postero-lateral edge of the shaft.

The patellar groove is broad and is about the same width as in Pedetes but it is not deep; it is oblique to the longitudinal axis of the shaft. In LG.29/5 there is a tubercle on the lateral edge of the shaft about 7.5mm above the lateral condyle; this is slightly more distal than in the Recent genus. The facets above the lateral and medial condyles show that there were sesamoid bones, one in each, in the tendons of origin of m. gastrocnemius, with the tendon

of the caput laterale having the larger sesamoid. The sesamoid in the tendon of m. gastrocnemius caput mediale was probably relatively a little better developed than it is in Pedetes to judge from the facet. The fossae in the sides of the condyles are as in the living genus.

Patella (Table 3.XIV):

This is more symmetrical about the midline than it is in Pedetes. It has a rounded dorso-lateral corner.

Tibia (Table 3.XV):

In LG.29/5, the only complete example known, it is relatively short but stouter than in Pedetes. The cnemial crest is not so prominent as in the living animal because the antero-medial edge of the bone is straight rather than slightly concave. The proximal articular facets are separate and not joined by a broad articular surface: they are separated by the shallow transverse groove posterior to the proximal tuberosity as in Pedetes. The groove between the two facets is less deep than in the Recent genus: the proximal facet for the head of the fibula is on the postero-lateral corner.

The shaft is similar to the Recent genus and has a slight S-curvature; distally it curves anteriorly and medially. The three corner crests are well developed and visible as ridges down to the distal end. On the medial surface of the postero-lateral crest there is a groove with a nutritive foramen at its distal end as in Pedetes.

The distal end is generally quite similar to that in the Recent genus. However in the distal articulation the medial facet is deeper and the lateral facet is broader and shallower than in Pedetes while the ridge between them is relatively narrower. This is probably due to the different shape of the condyles of the body of the astragalus. The groove on the anterior surface between the two facets is less well developed. The antero-lateral process is not well developed and although the medial posterior process is well developed the two ridges on it are not as well developed as in the Recent genus. The medial edge of the anterior lateral process, that continues upwards as a ridge on the anterior face of the shaft in Pedetes, does not do so in LG.29/5.

Fibula:

The head is broader and shorter than in Pedetes and overall the bone is much more robust although still quite slender. In LG.29/5 the distal third of both left and right fibulae are preserved. There is no evidence for fusion with the tibia. Distally the end is set obliquely disto-anteriorly to the shaft but is more in line with the shaft than in the Recent animal in which the end is almost at right-angles to the shaft. There is a well developed antero-medial facet for articulation with the lateral face of the astragalus. Posterior to this facet there is a fossa and on the upper surface of the distal end there is a facet facing proximally and articulating with the lower end of the tibia.

Tarsus (Plate 4):

Astragalus:- (Table 3.XVI ; Fig. 3.8B - D ; Fig. 3.9A - D).

This is relatively short, broad and stout with a flat articulation for the distal end of the fibula. In the articulation for the distal end of the tibia the median groove is shallower than in Pedetes, the lateral condyle is flatter and more rounded and it does not project so far distally: the fossa in the lateral face is of a different form to that in the living genus. The medial condyle is smaller than the lateral and its ventral edge projects medially more than in Pedetes. On the ventral surface of the body the facet for articulation with the central eminence of the calcaneum is large: immediately distal to this primary articulation, on the lateral edge, there is a small facet that articulates with the dorsal surface of the calcaneum. The sulcus tali is much better developed than in Pedetes and is continuous with the groove of the trochlear surface.

The neck is less attenuated than in the Recent genus and bears distinct dorso-lateral and medial fossae. The second calcaneal facet is relatively larger than in the living animal but as the medial plantar ridge is apparently less well developed the second calcaneal facet extends to the medial edge of the bone and is not restricted to the lateral side of the ridge. This ridge extends further distally than in Pedetes as the facet for the navicular does not extend so far onto the ventral surface. The disto-lateral face is hollowed out and the dorso-lateral corner of the distal end bears a small tubercle; this corner is separated from the

calcaneum by the cuboid, the facet for this bone truncates the ventro-lateral corner of the distal facet rather than the dorso-lateral. There is a facet on the medial surface distally for the proximal end of the first cuneiform but this facet is not always clear.

Calcaneum:- (Table 3.XVII ; Fig. 3.7C ; Fig. 3.9A - D).

The tuber calcis is just as in Pedetes except that the lateral surface is only slightly hollowed instead of being pronouncedly so: it is about the same length as in the living animal. The principal astragalar facet has a distinct side portion on the medial face of the central eminence; this is larger than in the living genus. The sustentaculum is well developed and, together with the secondary astragalar facet on its dorsal surface, projects medially more than in Pedetes.

Distal to the central eminence the bone is slightly shorter but is much broader than in the Recent genus. The facet for the cuboid does not project so far beyond the distal edge of the plantar surface as it does in Pedetes but it is much broader transversely and does not curve round onto the medial face so much. The dorsal surface is very similar to that in the Recent animal except that the disto-lateral groove in which the peroneal tendons lie and the tubercle medial to it are less well developed. The distal end of the calcaneum is separated from the astragalus by the cuboid.

Navicular:- (Table 3.XVIII ; Fig. 3.10F , G ; Fig. 3.11A ,

B). This bone is relatively short and, on the medial surface, it bears a pronounced trough for the first cuneiform. The facet for the proximal process of the cuboid is relatively larger than in Pedetes but the dorsal portion is reduced as the cuboid is aligned more laterally in association with the greater width of the foot.

Just below the distal facet for the third cuneiform there is a facet for the cuboid. This is also found in Pedetes but in the latter genus it is clearly separated from the third cuneiform facet by a wide groove whereas in this genus it is only separated by a slight ridge. The medial portion of the facet forms a second facet for the third cuneiform which is confluent with, and hence almost indistinguishable from, the cuboid facet. There does not appear to be a flattened area just distal to the second cuboid facet, on the plantar process, as is referred to in MacInnes (1957) and such as is found in Pedetes.

The facet for the second cuneiform is very much as in Pedetes but with a less clear distinction between the main facet and the dorsally facing distal portion: in Megapedetes they are confluent. This lower portion of the second cuneiform facet and the second facet for the third cuneiform are much closer together than in Pedetes. The plantar process, extending distally, is shorter and more robust than in the Recent genus.

Cuboid:- (Table 3.XIX ; Fig. 3.10A - E). There is no trace of an articulation with Mt.III such as is found in Pedetes; there is also no secondary articular facet for the calcaneum

as described in MacInnes (1957) unless this paper refers to the portion of the proximal facet that curves under so as to face proximo-ventrally. This is, however, continuous with the rest of the facet and cannot really be described as a secondary facet. As in Pedetes the facet for the calcaneum extends onto the lateral face of the proximal process which is larger than in the Recent genus.

On the proximal end of the proximal process there is a facet for the astragalus; on the ventral and medial faces of the process there are facets for the navicular. In the ventral half of the medial face of the main body of the bone there is a facet for the navicular, about halfway along the bone and facing a little proximally; this facet is larger and more dorsally placed than in the living genus. Separated from this facet by a ridge and facing rather distally there is a facet for the third cuneiform: compared with the Recent genus this is broader relative to its height. Also about halfway along the bone, in the dorsal half, there is a second facet for the third cuneiform. These two facets may be confluent. All the facets on the proximal process are separated from one another by ridges; except where otherwise stated the facets on the main body of the bone are separated by grooves. On the dorsal surface there is not a groove medial to the dorsal tubercle, as there is in Pedetes. The distal end of the bone forms a large facet for Mt.IV and along the lateral edge there is a narrow facet for Mt.V.

First cuneiform (C1):- (Table 3.XX ; Fig. 3.8A). This bone is quite robust and articulates distally with Mt.I. It is a

somewhat rectangular plate with a proximal process arising from the ventral half of the proximal edge of the plate. On the proximal end of the process there is a facet that articulates with the astragalus. There is a prominent tubercle on the medial wall for the ligament of m. tibialis anterior. The distal facet for Mt.I is convex; beginning just below it and running proximally there is a distinct plantar ridge. The plantar process of Mt.I presses against the end of this which suggests that there was very little flexion at this joint although the joint surfaces are of the right shape to allow this. When articulated with the second cuneiform, by a large concave facet on the dorso-proximal corner of the main plate of the bone, the first cuneiform probably stood away from Mt.II which would explain the absence of a facet on the latter bone.

Second cuneiform (C2):- (Table 3.XXI ; Fig. 3.9E , F). This is similar to the second cuneiform in Pedetes. The proximal facet for the navicular curves onto the lateral surface at the ventral end; in the Recent genus this portion is separated off as a second facet. There is a facet on the dorso-lateral edge articulating with the third cuneiform while the facet on the medial face for the first cuneiform is similar to but larger than in Pedetes. The distal facet for Mt.II is concave dorso-ventrally and convex transversely and compared with the Recent genus the disto-ventral corner of the bone is somewhat elongated.

Third cuneiform (C3):- (Table 3.XXI ; Fig. 3.9G - I).

Although very similar to Pedetes it is slightly shorter. The proximal face has a convex facet for the navicular. On the lateral face there may be two separate facets for the cuboid, as in the living genus, or a single L-shaped one. Next to the lower part of this articulation for the cuboid and separated from it by a slight ridge there is a small proximo-ventral facet that articulates with the navicular. This facet flattens the proximal edge of the cuboid facet and is absent in Pedetes in which the third cuneiform does not quite reach the navicular at this point due to the slight differences in the relative positions of the tarsals.

The facets on the medial face are similar to those in Pedetes except that the proximo-dorsal facet is relatively larger and the disto-dorsal facet is less elongated proximo-distally.

In distal view the lateral edge is more concave than in the living genus. The facet for Mt.III is relatively more elongated dorso-ventrally so that the disto-ventral corner is the most ventral point of the bone whereas in Pedetes this corner is at the same level as the ventral edge of the lateral cuboid facet.

Metatarsus (Plate 4):

Metatarsal I (Mt.I):- (Table 3.XXII ; Fig. 3.11C - F). The proximal end is expanded ventrally to produce a well developed proximal plantar process, there is also a proximal process arising from the medial wall of the shaft. The facet for C1

is found between these two processes. On the dorsal surface of the medial tubercle there is a slight groove. The lateral surface of the shaft is roughened toward the proximal end for the ligamentous attachment to Mt.II. A small indistinct facet may be present. The shaft curves out medially at the distal end and has a flattened lateral and a rounded medial face. The distal end is asymmetrical, oblique to the shaft and slightly narrower than in Mt.V; the ventral median keel is displaced laterally. There is a fossa in each side wall for the joint ligaments.

Metatarsal II (Mt.II):- (Table 3.XXIII ; Fig. 3.11C). This extends well proximally of Mt.III. The proximal facet is triangular, concave transversely and slightly more convex dorso-ventrally than in Pedetes. On the lateral face, proximally, there is a dorsal and a ventral facet for the third cuneiform as in the Recent genus. Just distally to the ventral facet there is a second facet that articulates with the proximal plantar process of Mt.III. This facet is very small and forms the only articulation between these two bones which are mainly joined by a ligamentous connection as is shown by the roughened lateral face of Mt.II proximally. The lateral face is also a little more hollowed out than in Pedetes. The proximal plantar process is completely preserved in LG.29/5 and is compressed transversely. On its ventro-medial edge a facet articulating with Mt.I is present while the medial surface of the shaft is roughened proximally for the ligaments to Mt.I.

The shaft curves out, medially, and, at the distal end,

more strongly than in Pedetes. The axial twist of the shaft and the distal articulation, which is strongly oblique to the shaft, are as in the Recent animal.

Metatarsal III (Mt.III):- (Table 3.XXIV). The proximal end is at the same level as that of Mt.IV and so the dorso-lateral corner does not form a pronounced process and does not articulate with the cuboid. The fossa in the lateral wall for the tubercle on Mt.IV is better developed than in Pedetes. The proximal facet is triangular and extends to the ventral edge of the proximal plantar process rather than stopping short as in the living animal. It is set obliquely, disto-medially, as in the Recent genus. The proximal plantar process is positioned right at the proximal end of the bone and not a little way distally as in Pedetes. On its lateral wall there is a facet for Mt.IV and on the proximal ventro-medial corner there is a small facet for Mt.II.

The medial wall of the shaft is roughened at the proximal end for the ligamentous connection to Mt.II and bears a slight tubercle. The shaft is straight and the distal end is as in the Recent animal.

Metatarsal IV (Mt.IV):- (Table 3.XXV ; Fig. 3.11C). The proximal end is at the same level as or slightly proximal to the proximal end of Mt.III. The facet is triangular and similar to that in Pedetes. On the medial side the articulation with Mt.III is not significantly more separated from the proximal facet than in Pedetes but does form a relatively less protruding tubercle with more of the facet

on the dorsal surface. There is a distinct medial facet on the plantar process for the articulation with Mt.III as in the Recent animal. The lateral edge of the proximal face bears a small facet that would have articulated with Mt.V when this bone was swung out from the foot. Proximally the lateral surface of Mt.IV bears a very well developed fossa into which the proximal end of Mt.V fitted. The proximal plantar process is better developed than in Pedetes and makes contact with Mt.V in KNM-Ru 4057A.

The shaft has a flattened medial side, it and the distal end are basically as in Pedetes. The distal articulation is slightly oblique to the shaft but this is less pronounced than in the Recent genus.

Metatarsal V (Mt.V):- (Table 3.XXVI ; Fig. 3.12A , B , C).

The proximal facet is much larger than in Pedetes and articulates with the cuboid. On the medial surface there is a tubercle articulating with Mt.IV toward the proximal end and just proximal to this tubercle there is a small facet for Mt.IV. On the proximal dorso-lateral corner there is a tubercle which is connected to the plantar process to form a proximo-lateral ridge. The bone is generally similar to Pedetes but the shaft is more rounded and robust; it curves out laterally. The distal articulation has a flattened medial side which is much deeper than the lateral side. The median keel is restricted to the ventral surface and does not extend onto the distal end to any extent. There is a transverse fossa on the dorsal surface marking the edge of the distal articular surface.

Phalanges:

Phalanx I (Ph.I):- (Table 3.XXVII). This is basically similar to Pedetes. The proximal articulation is saucer-shaped with a median groove in the ventral half to fit the keel on the metatarsal. On either side of this groove there is a ventral tubercle which has a facet on the proximal face for the sesamoid in the flexor tendon. The proximal articulation is set slightly obliquely to the shaft in digits 2 and 4, more so in digits 1 and 5. In digit 4 the lateral side of the proximal end is a little inflated. The proximal articulation of digit 1 is better developed on the medial side than on the lateral with the ventral edge projecting further proximally on the former: at the proximal end the ventral surface bears a well developed lateral tubercle and a small medial tubercle which articulates with a sesamoid. In digit 1 the proximal articulation is deeper dorso-ventrally, relative to its transverse width, shallower and with a less developed groove for the metatarsal than is Ph.I of digit 5 in Pedetes. The proximo-dorsal tubercle is better developed in digit 3 than it is in Pedetes but in digits 4 and 5 it is less well developed.

The shaft is straight in digit 3 and curves toward the midline of the foot in the other digits. Digits 4 and 5 are, however, slightly straighter than in the Recent genus with the latter mainly curving in at the distal end only. Similarly in digit 1 the curve of Ph.I is largely restricted to the distal end. The shaft is slightly compressed dorso-ventrally in digits 2 and 3, transversely in digits 1, 4 and 5. Just

proximal to the distal articulation the two tubercles on the plantar surface are better developed than in the living genus.

The distal articulation is convex dorso-ventrally, flat transversely in digit 1 but slightly concave transversely in the other digits. It only just extends onto the dorsal surface. In all digits, except digit 3, the distal facet of Ph.I is set obliquely to the shaft.

The phalanx I of digit 1 is very similar to that of digit 5 which is larger and more robust than in Pedetes.

Phalanx II (Ph.II):- (Table 3.XXVIII ; Fig. 3.12D , E , F).

The proximal end is expanded compared to the shaft and the proximal articulation is as in Pedetes although in digits 2 and 4 there is a slight median ridge that fits the slightly concave distal facet in the phalanx I. The proximo-plantar edge forms two small tubercles with a single transverse facet for the flexor sesamoid.

The shaft is basically cylindrical with a flattened plantar surface. In digit 3 this phalanx is shorter and stouter than in the living animal.

The distal articulation is convex dorso-ventrally; flat or slightly concave transversely. It just extends onto the dorsal surface. It is slightly asymmetrical in digits 2 and 4 with the side nearer the midline of the foot more vertically orientated, the other side more sloping.

Phalanx III (Ph.III):- (Table 3.XXIX). From the holotype this bone appears to be very similar to Ph.III (the ungual

phalanx) in Pedetes: the extra two Ph.III mentioned in MacInnes (1957) have not been found and so have not been examined. In LG.29/5 this bone is only preserved in digit 1. It is highly asymmetrical with a proximal articulation that is concave dorso-ventrally and flat transversely; the proximo-dorsal edge does not project back much. There is a well developed proximal plantar tubercle which is displaced a little to the lateral side. Beyond the proximal tubercle the plantar surface is twisted so as to face ventro-laterally. On the plantar surface a groove runs proximally from the apex and passes to the lateral side of the plantar tubercle.

In the distal half there is a slight flange around the ventral edge of the bone. Just before this flange begins the bone is slightly constricted. The dorsal surface of the bone forms a longitudinal ridge.

Flexor sesamoids:

These were not found in situ in LG.29/5 but similar bones are present in situ, below the distal ends of the metatarsals, in the left pes of the holotype. They are kidney-shaped with two facets separated by a ridge. The dorsal facet articulates with the main body of the metatarsal; the second facet, facing dorso-medially, articulates with the median keel of the distal articulation of the metatarsal. The ventral surface forms a distinct crest.

CHAPTER 4

Parapedetes namaquensis Stromer, 1924.

Genus Parapedetes Stromer, 1924.

Diagnosis:- Stromer (1923) does not give a separate diagnosis of the genus; the genus and species are described as one on pp. 261 - 263 of that paper.

Type species:- Parapedetes namaquensis Stromer, 1924

Parapedetes namaquensis Stromer, 1924.

Diagnosis:- Stromer (1923) does not give a diagnosis of the species separate from the description. In Stromer (1926) the species is diagnosed as follows:-

"Pedetes ähnlich, von Eichhorngrösse, in vielem primitiver. Schädel auch mit grossem hohem For. infraorbit. und harter Gaumen nur bis Grenze von M1 und 2, aber gestreckter und niedriger, ohne Fossae pterygoideae und knöcherne Gehörgänge. Unterkiefer-Symphyse nich fest, Masseterleiste von P4 an zu dem weit rück-, aber wenig abwärts ragenden Angulus, der aussen am Unterrand entspringt. Gelenk nicht hoch über der Zahnreihe, Kronfortsatz wohl entwickelt, breit. Nagezahne viel dicker als breit, obere vorn mit mesialer Kante. Vier gleichartige, prismatische Backenzahne, obere nach innen, untere nach aussen konvex gekrummt, oben wie unten etwas breiter als lang und mit nur einer mittleren schmalen und sehr tiefen Querfalte, von aussen bis nahe zum Innenrande. Zahnwechsel spat, Md mit Wurzeln, sonst wie P4."

Introduction:

Parapedetes namaquensis was first described, briefly, by Stromer in 1924 and, subsequently, in 1926 in considerably more detail. In the former description it is described as a new genus and a new species. The paper in which the first description occurs (Stromer, 1923) was, in fact, issued in 1924 and the name takes its date from the date of issue. In the latter description (Stromer, 1926) Pa. namaquensis is only described as a new species and it is to this second, more complete, description that I mainly refer.

This species is known only from a single site in South West Africa – Elisabethfeld, which is 38km south of Luderitz Bay (Stromer, 1926). Known material comes from a single collection made by Erich Kaiser and is amongst the best preserved of the material from Elisabethfeld. A similar situation is found at Laetoli where, also, the springhares are relatively well preserved (see Chap. 5) whilst larger and more robust forms are fragmentary. Possible reasons for this will be discussed later (see Chap. 8). On the basis of the faunal evidence the site at Elisabethfeld is dated as Lower Miocene: absolute dating has not been attempted and, given the absence of volcanic deposits, is not possible in the way it has been in East Africa.

Stromer (1926) lists all the material that was available at the time. It formed a quite substantial sample of 35 pieces including, in total, eight skulls. Unfortunately much of this material was destroyed during the Second World War although a number of the best pieces survived and are

now housed in the Universitäts-Institut und Staatsammlung für Paläontologie und Historische Geologie in Munich where the Bavarian State Palaeontological Collections are kept. The destruction of most of the original material means that a number of features described by Stromer can no longer be seen while other features, apparently well preserved amongst the material then available, are now only found poorly preserved.

In neither of his papers (Stromer, 1923 & 1926) did Stromer describe Pa. namaquensis in very great detail, which, since he had so much more material available to him, is very unfortunate. Much additional information can, therefore, be obtained even from the small amount of material still remaining. Further preparation of blocks 1926X15 and 1926X510 was kindly carried out by the Museum authorities in early 1979 and although this left the material still half embedded in matrix with only one surface exposed a number of features were made clearer and several new pieces of bone were revealed. Further fragments of bone and more information might be obtainable if yet more of the matrix were removed but, except for some especial reason, the Museum authorities are understandably reluctant to remove individual bones from the blocks.

Stromer did not designate any of his specimens as the holotype and consequently all are syntypes. Block 1926X15, which is Stromer's specimen 1 (Stromer, 1926 : 128), has been labelled as a lectotype but there is no record of the publication of this designation in either Hopwood & Holly-

field (1954) for the period up to 1950 or in the Zoological Record since 1950. The block is figured (Stromer, 1926 : Plate 42, Fig. 1) but cannot act as a lectotype in its entirity since the implication in the International Code of Zoological Nomenclature (1961 : Article 72a) is that the type of a species should be a single individual. In consequence it seems best to consider as the lectotype the individual in block 1926X15 consisting of a badly damaged skull, most of the vertebral column and part of the fore-limb (Stromer's specimen 1a). The other individuals in block 1926X15 together with the remaining pieces: 1926X510 (Stromer's specimen 8), 1926X511 (Stromer's specimen 24) and 1926X501 plus 1926X502 (Stromer's specimen 2) are all paralectotypes.

Details of the remaining material in Munich are given in Appendix IV: specimens 1926X15 and 1926X510 are shown in Plates 5 & 6. A full description of the species based on this material follows: where features are no longer present Stromer's description will be given in translation (Johnson, 1947).

DESCRIPTION.

Cranium (Table 4.I):

There are remains of three crania in Munich compared with the remains of eight that Stromer lists (Stromer, 1926). There are two crania in block 1926X15: the lectotype, which is very badly damaged, and Stromer's specimen 1b, which, although damaged, provides the clearest view of the basi-cranium. The most complete cranium is 1926X501 and the

description is based primarily on this specimen.

Dorsal aspect:- (Fig. 4.1A). The anterior tip of the nasals is missing but the form of the bone at the break suggests that there was a slight upward expansion. In 1926X501 the nasals probably form about 30% of the total cranial length and are 115% of the frontal length. They are parallel-sided and at their posterior end form a slightly flattened U-shaped curve with the flat bottom formed by the naso-frontal suture which lies at the level of the preorbital bar. The premaxilla on each side edges the nasal rather as in Pedetes and a short distance before the preorbital bar its dorsal aspect widens. It then continues back to the level of the posterior edge of the preorbital bar forming a process into the frontal. This process curves slightly medially.

The frontals extend back to the level of the posterior edge of the orbit and there is no depression in the anterior half. They comprise 27% of the total cranial length in 1926X501. The upper rims of the orbits are sharply concave so there is a pronounced interorbital constriction with the least interorbital distance just anterior to the middle of the orbit. There is no post-orbital process. The fronto-parietal suture has a pronounced posterior embayment on either side of the midline: behind it the cranium is damaged making some of the features difficult to determine.

It appears that there was a distinct interparietal but the exact extent of this bone cannot be determined. The mastoid bullae are inflated, but not apparently to the same extent as in Pedetes, and were probably visible in dorsal

view at the postero-lateral corners of the cranium. From what can be seen it is unlikely that they projected beyond the supraoccipital. Apart from a possible slight inflation of the parietals the dorsal surface is flat

The preorbital bar is relatively wide and forms an anterior angle of about 90° with the rostrum. Anteriorly it is formed by the maxilla which probably overlapped the posterior part of the premaxilla before turning out onto the preorbital bar. The squamosal root of the zygoma is just posterior to the fronto-parietal suture and is directed antero-laterally.

Profile:- (Fig. 4.1B). Overall the cranium is less deep than in Pedetes. The incisors are slightly opisthodont and the incisive alveolus forms a broad ridge across the rostrum reaching to the dorsal edge at its highest point and terminating at the level of the infraorbital foramen. There are no lateral nasal wings, as are found in the Recent genus, but anterior to the incisive alveolus a plate of the premaxilla performs the same function. The premaxilla-maxilla suture forms a curve, convex anteriorly, across the rostrum.

The preorbital bar is formed by the maxilla anteriorly and the jugal and lachrymal posteriorly. The latter two make contact and the lachrymal forms a preorbital process. In the zygoma the maxilla sends a stout process back under the jugal: this process ends at the level of m^{3}. The jugal appears to be fairly strong but is not especially deep. The origin of m. masseter lateralis is restricted to the lower

edge of the zygoma and only extends slightly onto the lateral surface toward the posterior end. There is a horizontal jugal-squamosal suture: posteriorly the jugal projects a little beyond the squamosal root. This is unlike Pedetes in which the jugal thins and gradually merges with the squamosal. The lower edge of the zygoma is straight.

Along the upper edge of the orbit there is a slight ridge which curves round onto the posterior edge of the preorbital bar. The internal structure of the orbit is not well preserved in any specimen but in 1926X15b the sphenoidal fissure appears to be at the level of the posterior maxillary notch. The ends of the cheekteeth rise up high in the floor of the orbit.

The absence of a well developed groove implies that m. temporalis was very reduced. There may have been a squamosal process passing back onto the mastoid bulla but damage to the bulla makes it impossible to be certain that a groove for such a process is present. In the lateral aspect the bulla occupies most of the cranium behind the orbit.

Ventral aspect:- (Fig. 4.1C). The incisive foramina are set almost halfway between the incisors and the cheekteeth but are slightly nearer the latter. They are confluent and are in a very shallow palatal groove. The premaxilla-maxilla suture joins the foramina just anterior to the postero-lateral corner and passes postero-laterally for a short distance before turning sharply and running antero-laterally. The ventral root of the zygoma arises well back, immediately anterior to pm^4, which gives the cranium an appearance quite

unlike that of any other pedetid. On the ventral surface of the lower zygomatic root the origin of m. masseter superficialis is quite distinct. It forms a ridge that ends medially level with the lateral edge of the toothrow.

The toothrows are slightly curved, convex laterally, and are parallel. Although the posterior end of the palate is damaged, being broken at the level of m^1 in 1926X501, it appears to have terminated at the level of the anterior lobe of m^2. The maxilla-palatine suture is apparently at the level of the posterior lobe of m^1 and the posterior palatal foramina are positioned on it. There is a ventral median ridge along the palate. Posterior to the toothrow there is a well developed posterior maxillary notch and beyond this the medial lamina of the pterygoid continues posteriorly for about 7mm. As the lamina is broken its exact development is unknown but, particularly from 1926X15b, it appears to have been low and little more than a ridge. Near the posterior end of this ridge in 1926X15b there is a small tubercle that may represent the origin of mm. pterygoidei.

The basicranial region is best preserved in 1926X15b. In this specimen there is a distinct suture between the presphenoid and the basisphenoid. At the level of this suture there are large oval fenestrae, one on either side, opening laterally from the mesopterygoid fossa; these are similar to the fenestrae in Pedetes between the orbit and the nasal passage. In this specimen, however, they are relatively further posterior and may have opened into the cranial cavity with the anterior part opening into the orbit

and possibly forming part of the sphenoidal fissure: this region cannot be seen clearly in any of the specimens. There is a shallow groove running postero-laterally from either fenestra medial to the pterygoid lamina of that side and back to the bulla where it connects with the foramen ovale.

There is no trace of a median foramen, such as is found in Pedetes, in either the basisphenoid or the basioccipital but in 1926X501 there is a small tubercle in the midline about 2mm anterior to the condyles. The basioccipital has well developed lateral wings into which lock the ventral antero-medial processes of the bullae. Between the posterior end of the lateral wing and the condyle there is a shallow groove in the basioccipital into which the hypoglossal foramen probably opened, although this cannot be seen. The jugular foramen is antero-lateral to the condyle between the basioccipital and the bulla, it opens into a groove that runs anteriorly to end at the antero-medial flange of the bulla. There is no foramen visible through this flange.

Bony pterygoid fossae are not present and lateral to the reduced pterygoid lamina the ventral surface of the cranium is bony, extending to the glenoid fossa and curving smoothly anteriorly into the posterior wall of the orbit. The very large foramen ovale, found in Pedetes, is not present. There is a small foramen ovale, just anterior to the bulla, into which runs the shallow groove medial to the pterygoid lamina. Antero-lateral to the foramen ovale there is another foramen, or possibly two foramina set closely

together, in a shallow fossa. This probably represents the combined opening of the buccinator and masticatory nerve canals. (If there are, in fact, two foramina then it would suggest that the two nerve canals are separate in this species, in contrast to Pedetes.) A foramen is present just anterior to the bulla and behind the glenoid fossa, this may be either a post-glenoid foramen or a temporal foramen as is found in the Recent genus. The glenoid fossa is very shallow and is composed entirely from the squamosal without any contribution from the jugal.

The zygomata diverge rather strongly from the toothrows.

Anterior aspect:- The rostrum has the shape of an inverted triangle. The nasal aperture is similar to Pedetes although the presence of premaxillary wings makes it appear more enclosed. The infraorbital foramen is enlarged and rounded.

Posterior aspect:- The foramen magnum is hexagonal. There is a well developed external occipital crest that bifurcates at the dorsal end and joins the nuchal lines as in Pedetes. The styloid processes are missing but their bases suggest that they were probably quite thin: they are in line with the midline of the bullae, which are easily visible in this aspect.

Auditory bulla:- Both the tympanic and the mastoid portions of the bulla are inflated, with the former relatively more inflated than the latter in comparison with Pedetes. The mastoid flange is well developed and forms a pronounced posterior edge to the external acoustic meatus which is

completely unossified. There is a pronounced ridge along the anterior edge of the external acoustic meatus. The opening of the Eustachian tube is in the normal position and it is not ossified beyond the bulla. An antero-medial process locks the bulla into the basioccipital. In the intact cranium the bulla probably laid somewhat obliquely as in Pedetes.

Upper dentition:- Stromer (1926) describes this in some detail and generally accurately. The upper incisors are as described by Stromer: "The incisors ... has a sharp edge at the medial margin in front, and is flat in front, strongly arched behind, and about twice as thick as it is broad." (Johnson, 1947 : 43). Although not mentioned in the text there is a ridge along the medial edge of the anterior surface; this is quite clear in the diagram as is the rounded antero-lateral corner (Stromer, 1926 : Plate 42 , Fig. 4c).

The basic pattern of the cheekteeth is two sub-equal lobes joined on the lingual side and separated by a narrow buccal infold that is aligned slightly posteriorly (Fig. 4.2A). In pm^4 - m^2 the posterior lobe is larger than the anterior but in m^3 the anterior lobe is the larger. In contrast to Pedetes the pulp cavities do not remain open throughout the animal's life and the buccal infold does not extend through the whole height of the tooth. Initially, as in the Recent genus, the occlusal pattern consists of two lobes, that are completely separate, with the groove between them shallower on the lingual side than on the buccal. This stage is shown only in the right m^3 of 1926X501. The remaining cheekteeth

of 1926X501 show a slightly later stage in wear and have the typical pattern on the occlusal surface. The pulp cavities are open and the ends of the teeth pass up high into the floor of the orbit as in Pedetes. Pm^4 curves sharply anteriorly and the molars curve slightly posteriorly. In older animals, as shown in 1926X15b, the pulp cavities begin to close so that each tooth has a single root, which still passes up high into the floor of the orbit. Finally in even older animals (1926X15a) the teeth, now with closed roots, are low and the bilobed occlusal pattern is obliterated. The pattern visible in 1926X15a is an enamel ring with a small central enamel island, which is all that remains of the buccal infold, except in m^2 where there is, in addition, a slight infold still present in the buccal enamel.

Stromer (1926) describes the presence of deciduous premolars and includes amongst his examples 1926X501. I find that there is insufficient evidence to say that the pm^4 in this animal is deciduous because the root is not exposed. The other examples of deciduous upper premolars given in Stromer (1926) are no longer extant.

Mandible (Table 4.II ; Fig. 4.2B , C):

There are no examples of a complete mandible amongst the material in Munich. Four partial mandibles are present and, contrary to the statement in Stromer (1926), the angular region is amongst the best preserved parts, which is unusual. Parts of all the mandibles are obscured by matrix and/or other bones and it is not possible to give a complete

description of the lower jaw.

The symphysis menti is not fused but the strength of the ligaments holding the two rami together is not known so that the degree to which independent movement of the rami might have been possible is uncertain. There is no external ridge on the symphysis nor is there a descending process at the posterior end below the incisor. The lateral opening of the foramen mentale is at the level of the dorsal edge of the incisor: the dorsal opening is not preserved but, according to Stromer, it was not present (Johnson, 1947 : 43 :- "The foramen mentale, finally, is simple, not double, and lies about in the middle of the diastema, below the middle of its height.").

The medial surface of the ramus contains a few foramina but the lateral surface contains a large number of small foramina. The masseteric crest is better developed than in Pedetes and projects laterally of the incisive alveolus; it does not curve under the alveolus posteriorly but remains lateral to it and curves smoothly into the lower edge of the angle. This eliminates any trace of the anterior process of the angle. The jaw, however, is still sciurognath although the angle arises a little more laterally than in the living genus and this makes the jaw look a little more hystricognath.

The angle does not project below the incisive alveolus and it is more massive than in Pedetes. The ventral edge is thickened producing both lateral and medial ridges: the medial ridge presumably provided the insertion for m. pterygoideus internus; the lateral ridge forms a pronounced

lateral projection at the postero-ventral corner. In the right ramus of 1926X15a the plate of the angle appears to be pierced by a triangular fenestra but since the edges are damaged it is impossible to be certain that the fenestra itself is not the result of damage.

The coronoid process arises at the level of m_2 and rises steeply; its dorsal edge is just below the level of the condyle. It is thick and quite strong. The condyle is distinct from the ascending ramus and overhangs laterally and medially. It is large and oval; laterally the facet extends ventrally for a short distance. Below the medial edge of the condyle there is a small insertion for m. pterygoideus externus. Stromer was correct in saying that the condyle is less high above the toothrow than in Pedetes.

As in the Recent genus the incisive alveolus rises high in the ascending ramus, almost to the level of the condyle, and the inferior dental foramen is at its tip. In contrast to Pedetes capensis the alveolus is aligned postero-dorsally and does not become vertical in the ascending ramus; also it does not project medially but forms a flat surface with the medial face of the coronoid plate. The posterior edge of the mandible is well behind the condyle and forms a smooth concave curve from the ventral edge of the angle to the upper edge of the condyle.

Lower dentition:- (Table 4.III). The lower dentition is described fairly well in Stromer (1926). The only remaining relatively complete lower incisor is in 1926X502 and it has a sharp antero-medial corner and a smoothly rounded antero-

lateral one. There is no ridge on the anterior surface.

Examples of the lower cheekteeth are only preserved in 1926X502 (Fig. 4.2D) and 1926X510U. As in the upper cheek-teeth the basic occlusal pattern consists of two sub-equal lobes joined on the lingual side and separated by a narrow buccal infold. There is also a slight vertical groove in the lingual face of each tooth except in the pm_4 of 1926X510U. The postero-lingual corner forms a projection and in pm_4 the tooth tends towards a triangular shape.

In 1926X510U the normal pattern is already established in pm_4 although in addition the anterior lobe of the tooth contains a small enamel island. In the three molars the two lobes of each tooth have not yet been joined by wear on the lingual side but are still separate. The posterior lobe in m_1 and m_2 also contains a small enamel island, possibly representing the remains of a valley between two large cusps. In 1926X502 the normal occlusal pattern is found and the buccal infold does not extend through the full height of the crown but only for about 3mm below the occlusal surface. Thus wear would eventually remove it and leave a plain enamel ring. The toothrow is slightly convex buccally and the ends of the teeth curve slightly anteriorly; they pass laterally to the incisor. In 1926X502 the pulp cavities are open but it is not possible to see the ends of the teeth in 1926X510U.

Four isolated cheekteeth are also preserved although it is not possible to say whether they are upper or lower teeth. They are associated with 1926X15, possibly with the lectotype. All these teeth are very well worn. In three

cases the crown pattern consists of an enamel ring with a smaller central enamel ring; in the fourth tooth the central ring is not present. There is a single root in each tooth although this may be formed by several fused rootlets. The teeth are somewhat triangular with the side opposite the apex having had the infold – based on the slight extension of the central enamel ring towards this side in one of the teeth and the situation in less worn teeth in other specimens.

Vertebral column:

The vertebral column has been relatively well preserved especially in 1926X15. The most complete remains are those of the lectotype.

Cervical vertebrae:- (Table 4.IV). The atlas is only preserved in the lectotype and even in this individual it is partially obscured. There is a pronounced median tubercle on the ventral surface and the transverse process resembles Pedetes. The anterior opening of the vertebrarterial canal cannot be properly seen but posteriorly the canal opens into a groove between the facet for the axis and the transverse process. As in Pedetes the anterior groove for the vertebral artery is enclosed producing a large foramen in the dorsal arch of the vertebra.

The axis is preserved in two individuals in 1926X15 and also in 1926X510H. There is a pronounced dens. The neural spine is expanded antero-posteriorly into a broad plate but neither it nor the rest of the axis is fused to Ce3. The vertebrarterial canal and the transverse process are similar

to Pedetes although the transverse process is rather more robust.

Cervicals 3 - 7 (Ce3 - 7) are basically as in Pedetes. The transverse processes are well developed and that of Ce5 bears a pronounced anterior process while that of Ce7 appears to have been pierced by a vertebrarterial canal, although it is difficult to be certain of this. Anteriorly in the series the transverse processes are inclined slightly posteriorly but this becomes less pronounced further back and in Ce7 the process projects at 90° to the centrum. The centra have median ventral ridges that are well developed in the axis - Ce4: the centrum of Ce6 has pronounced lateral ventral processes. All the vertebrae have damaged neural spines except Ce7 of 1926X15c in which the spine is reduced to a tubercle. There is no evidence of fusion between any of the cervical vertebrae or their transverse processes. The laminae of the neural arches are straight, not curved; the zygapophyses are as in the Recent genus. Ce7 bears part of the facet for rib 1.

Thoracic vertebrae:- (Table 4.IV). The thoracic series is very well preserved although none of the specimens includes a complete, articulated series. In the lectotype there are only 11 thoracic vertebrae, the vertebral column is broken in the region of Th5 and this vertebra appears to be missing. A small piece of bone protruding from the matrix between Th4 and the next complete vertebra may represent the end of the transverse process of Th5 and if this is so then the thoracic series contains 12 vertebrae as in Pedetes.

Further evidence as to the length of the thoracic series comes from the vertebrae adjacent to skull 1926X15b: this is an articulated series of 11 thoracic vertebrae, probably from a juvenile, since the ends of the centra are not fused to the bodies. The 11th, and last, vertebra in this specimen has lost the posterior end of the centrum and, lying close to it, there is another specimen, consisting of the posterior end of a thoracic vertebral centrum, a complete thoracic vertebra and two lumbar vertebrae, in which the ends of the centra are not fused to the bodies. Although not actually attached to the first specimen the close proximity and similar developmental stage of this second specimen strongly suggest that it comes from the same individual. If this is so then the thoracic series contains a total of 12 vertebrae as in Pedetes. In the absence of better evidence to the contrary it is assumed that this is the case.

The neural spines are well developed throughout the series. In the anterior members they are relatively slender and slope distinctly posteriorly although in Th1 and Th2 they may be nearly vertical. They have a thicker lower half that is quite sharply demarcated from the thinner upper half. The anticlinal vertebra is usually Th11 although, as in the Recent genus, it may be Th10. In the vertebra immediately posterior to the anticlinal vertebra the neural spine is transversely compressed, very robust, quite short and is inclined very slightly anteriorly.

The transverse processes are very similar to Pedetes. Anapophyses and metapophyses first become present in Th7 as

small tubercles on the process. In Th8 these tubercles are larger and both the anapophyses and the metapophyses become increasingly well developed posteriorly and lose their contact with the transverse process which is gradually reduced in size as the facets for the rib come closer together. In Th11 and Th12 there is a deep oval fossa at the base of the anapophysis.

All the centra have a ventral median ridge. In the anterior centra the ventral surface is flat; more posteriorly it becomes concave antero-posteriorly. The transition between the cervical and thoracic series is damaged but it appears that Th1 bore most of the facet for rib 1 and that, in the lectotype, the disc between Ce7 and Th1 was calcified — it appears to be still present and resembles the vertebrae in colour and state of preservation.

Lumbar vertebrae:- (Table 4.V). The lumbar series is complete in the lectotype and contains seven vertebrae. Parts of the series are also found in several other specimens. The neural spines are well developed: they slope anteriorly in the more anterior members of the series and have a groove in the posterior surfaces; in the more posterior members they are more vertical and lack the posterior groove. The transverse process in Lu1 is a small tubercle that is much less well developed than in Pedetes: a horizontal ridge runs back from it in 1926X15f. Posteriorly the transverse processes become better developed and reach their greatest development in Lu6. In Lu7 the process is less well developed than in Lu6 but it is much wider than the transverse

process in Lu7 of Pedetes.

Anapophyses and metapophyses have been damaged in most of the vertebrae so that their exact degree of development is uncertain. Metapophyses are present throughout the series and appear to reach their greatest development in Lu3 or Lu4. Anapophyses are present at least as far back as Lu6 and may have been present in Lu7. They also reach their greatest development in Lu3 or Lu4: in more posterior members of the series they are very thick. At the base of the pedicle of the neural arch there is, on the lateral surface, a large shallow fossa, with a pronounced ridge along the ventral edge in Lu4 - 6. This fossa is developed from the fossae found in Th11 and Th12 at the base of the anapophyses.

Each centrum has a median ventral ridge that is a little better developed at the anterior than the posterior end and is slightly concave antero-posteriorly although this is not so pronounced as in Pedetes. The dorsal surfaces of the centra are concave transversely. On either side of the median ridge the ventral surface may have a foramen.

Sacrum:- (Table 4.V). This is only preserved in the lectotype and even in this specimen it is very badly damaged. It consists of three vertebrae that decrease greatly in size posteriorly. The transverse processes are similar to Pedetes with the sacro-iliac joint formed mainly from Sa1 with Sa2 providing a little support along the posterior edge. The neural spines are broken near their bases but that of Sa1 was apparently vertical and the other two slope progressively more posteriorly so that it is unlikely that

there was any fusion between them.

Caudal vertebrae:- (Table 4.V). This series is best preserved in the lectotype in which there are remains of the first 12 caudal vertebrae. A second relatively long section is found in 1926X510K in which remains of Ca3 - 10 are present; a few isolated vertebrae are also found. All the remains come from the anterior part of the tail.

In the lectotype Ca1 - 2 are represented only by the neural spines. They are quite long and point slightly posteriorly. These two vertebrae are found, more complete, in 1926X510J. The dorsal surface of the centrum is slightly convex transversely; the ventral surface is concave antero-posteriorly and bears two parallel longitudinal ridges, between which the surface is slightly concave transversely, and which form slight tubercles in the anterior third. There are small metapophyses present but no anapophyses. The transverse processes are broken but the bases suggest that they were quite large, flat and directed postero-laterally.

In Ca3 - 12 of the lectotype the centra have a ventral median ridge that splits into two at the posterior end to produce a small flat triangular area. However in Ca3 - 10 of 1926X510K the ventral surfaces of the centra have two parallel ridges. The anterior ventral tubercles that support the haemal arches are very well developed from Ca7 back. The haemal arches do not seem to have been fused to the vertebrae but, except in Ca9 of the lectotype, they are not preserved. In this vertebra a fragment of bone may be the remains of the haemal arch: it is very small but it is not fused to the

centrum. Distally in the series the centra become more elongated.

The transverse processes are well developed as far back as Ca8 and resemble those of Pedetes. They are horizontal plates with the postero-lateral corner projecting back and thickened. From Ca6 back the middle of the lateral edge becomes emarginated thus tending to divide the processes into two. The neural arch is complete as far back as Ca12 but becomes restricted to the posterior part of the vertebra. Metapophyses are quite well developed in Ca3 of the lectotype, in the other caudals they are damaged so that their degree of development is unknown. Articulation of the zygapophyses between the vertebrae appears to continue back at least as far as the anterior end of Ca12 as there are what appear to be facets on the postzygapophyses of Ca11. The position of the vertebrae is such, however, that it is difficult to see the postzygapophyses clearly and the vertebrae are not now properly articulated.

Although only the anterior part of the tail is preserved it seems likely, given the close morphological similarity of the vertebrae to Pedetes, that the tail was elongated as in the living genus to serve as a balancing organ during bipedal locomotion.

Ribs and sternum:

There are fragments of the ribs associated with a number of individuals in both 1926X15 and 1926X510. They are just like the ribs in Pedetes.

Remains of the manubrium sterni (Fig. 4.3A , B) are found in the lectotype and in 1926X510M (Table 4.VI). The fragment from the lectotype (Fig. 4.3A) was, it seems, identified by Stromer as a fragment of scapula (Stromer, 1926 : 131) while the only fragment that he described is no longer extant. The identification of the lectotype fragment is based on its resemblance to the manubrium fragment in 1926X510M and to Stromer's description; in addition its position is consistent with its being the manubrium sterni. It lies medially to the left forelimb under and parallel to the last cervical and first thoracic vertebrae and, given the absence of dispersion of the material, this is likely to be close to its natural position.

From 1926X510M, which is badly damaged, it can be seen that the manubrium sterni consists of an anterior quadrilateral plate and a posterior process. Only the dorsal surface is preserved: the antero-lateral corners form rounded projections and in the middle the anterior edge is concave. On each antero-lateral projection there is a large shallow fossa for the attachment of the clavicle; between these fossae there is a central tubercle. Postero-laterally there is a small fossa for rib 1. The plate then narrows to form the posterior process.

In 1926X15a most of the anterior plate has been destroyed. However, sufficient remains to show that the ventral surface had a median ridge about which the bone was symmetrical. The posterior process is here about 8mm long and its posterior end, which has a hexagonal cross-section, is roughened for

contact with the first sternebra. There are no identifiable remains of the sternebrae or the xiphoid process.

Clavicle:

There is a complete left clavicle in 1926X510N with the scapular end still obscured. The sternal end is expanded for the connection to the manubrium sterni and the antero-ventral surface bears a slight ridge from which probably originated the superficial part of m. pectoralis major. Towards the scapular end the bone curves dorsally and becomes flattened antero-posteriorly. Overall it is very similar to Pedetes.

Scapula:

Stromer (1926) states that there are remains of the scapula in specimens 1a and 18. The latter specimen has been destroyed but there is a fragment of the right scapula in the lectotype (1926X15a). This fragment cannot be the piece referred to by Stromer since it was only revealed by the additional preparation carried out in 1979. An examination of the text-figure (Text-figure 20) in Stromer (1926) together with the short description given suggests that Stromer misidentified the fragment of the manubrium sterni found in the lectotype as a fragment of the glenoid region of the scapula.

The fragment of the scapula in the lectotype only consists of a small piece from around the glenoid fossa. The spine and acromion process are well developed, about as

in Pedetes, but the acromion does not become wider in the middle, as it does in the living genus, being of equal width throughout. The glenoid fossa itself cannot be seen properly but the coracoid process is well developed. The posterior edge of the scapular blade is thickened, as in Pedetes.

Humerus (Table 4.VII ; Fig. 4.3A , C):

There is a complete left humerus in 1926X15a and a distal right humerus that may belong to 1926X15a: they are both partly obscured. Some features of the humerus described in Stromer (1926) come from specimens now destroyed.

The lesser tuberosity is very pronounced with a distinct ridge running ventrally from it; this ridge suggests that there was a well developed m. teres major. The bicipital groove, greater tuberosity and delto-pectoral crest are all well developed and the delto-pectoral crest overhangs ventrally and medially implying that m. pectoralis was well developed. The development of the delto-pectoral crest makes the upper half of the humerus very much thicker than the lower half in medial view.

The shaft is slightly bowed, convex postero-laterally. There is an entepicondylar foramen and there may have been a supratrochlear foramen but this region has been damaged, Stromer (1926) states that a supratrochlear foramen is present. The supinator ridge is not well developed and falls back into the side of the humerus at a lower level than in Pedetes. There is a distinct medial ridge to the trochlea.

Ulna (Table 4.VII ; Fig. 4.3A , D):

The olecranon process is not so well developed as in Pedetes but there is a pronounced postero-medial process. The trochlear notch has well developed olecranon and coronoid processes: the former projects laterally but the latter does not project medially as it does in the Recent genus. The facet for the head of the radius is not distinct.

The shaft is relatively straight with a rounded posterior surface and a flat anterior one. There is a well developed antero-lateral ridge and an antero-medial ridge that is well developed especially at the distal end. The styloid process is about as well developed as in Pedetes and is hook-like.

Radius (Table 4.VII ; Fig. 4.3A , D):

The left radius is preserved in the lectotype and part of the right radius in 1926X510P. The proximal end is not visible in either of the specimens. The shaft is of more even thickness than in Pedetes and expands less distally. There is an oval distal facet with a styloid process that is less well developed than in the living genus. On the ulnar side of the distal end there is a groove as in Pedetes. At the distal end the ulna and radius were held together as in Pedetes and the normal aspect of the manus was probably the same as in the living animal with the palmar aspect turned medially and the pollex antero-dorsally. Rotation of the forearm may have been possible.

Manus:

The only remains of the manus is a first phalanx (Ph.I)

in 1926X510Q. It is not known from what digit this bone came. The proximal end is expanded, especially transversely, for the facet, which is deep and cup-shaped with a ventral groove for the ridge on the metacarpal (Mc.). Above the groove the facet may be divided into two but this cannot be clearly seen. The distal facet is simple, convex dorso-ventrally. The shaft is straight with the distal end set obliquely.

Innominate bone:

There are only two fragments of this bone remaining, both from 1926X15: one fragment belongs to the lectotype, the other may belong to the lectotype but cannot be directly associated with it. The two relatively complete innominate bones mentioned by Stromer are no longer extant.

Immediately anterior to the acetabulum the medial surface is convex. The distinct acetabular notch is as in Pedetes. Behind the acetabulum the ischium passes straight back and expands posteriorly into the ischial tuberosity which is much less well developed than in the living genus. The posterior edge of the ischium is convexly curved in contrast to Pedetes: this is as stated by Stromer, "... the ischium ends behind simply convex without a very strong tuber ...." (Johnson, 1947 : 46). Although very badly damaged it appears that the pubis turns back just below the acetabulum to run below the ischium, diverging slightly from it. This agrees with Stromer's description: "... the os pubis seems to project less ventrally, ... and the foramen obturatum is

strongly longotudinally (sic.) oval and less broad." (Johnson, 1947 : 46). On the lateral surface of the pubis there is a ridge, as there is in Pedetes, but it is angled across the bone more, towards the anterior edge.

Femur (Table 4.VII ; Fig. 4.4A):

A complete right femur is found in 1926X510R but the posterior and medial surfaces are embedded in matrix except at the distal end. The head is hemispherical and set on a short neck; the articular surface does not extend over the postero-dorsal surface of the neck as it does in Pedetes. There is a well developed trochanter major that rises high above the head although relatively less than in the living genus. At the level of the head the anterior surface of the trochanter major is relatively wider than in Pedetes due to the greater development of the anterior tubercles. There are two of these: the medial one is at the level of the dorsal surface of the neck, points antero-medially, and is connected by a ridge to the larger lateral tubercle that is lower down, level with the ventral surface of the neck, and directed antero-laterally. The trochanter major is set laterally to the line of the shaft so that the trochanteric fossa is more open dorsally than in the living animal. A triangular area, bounded by the antero-dorsal tip of the trochanter major and the two anterior tubercles, forms a distinct fossa.

The shaft is slightly bowed forward and has a lateral ridge as in Pedetes. The patellar groove is bounded by

pronounced lateral and medial ridges. Both femoral condyles are at the same level and the facets are completely separated anteriorly by the deep indentation of the patellar groove. The medial facet is not continuous with the patellar groove but is separated from it by a low ridge. There is a deep intercondylar notch and the medial condyle is slightly expanded posteriorly. Sesamoid bones were present in both heads of m. gastrocnemius as facets for them are present. The three fossae on the lateral face of the lateral condyle are small while on the medial face of the medial condyle there is a single large fossa with a distinct anterior ridge.

Patella:

A right patella with the distal end missing is found in 1926X510S. It is triangular with both upper corners rounded and the whole anterior surface is slightly convex. The posterior surface is still embedded in matrix.

Tibia (Table 4.VII ; Fig. 4.4B):

Two distal tibiae are preserved in 1926X510C & D and a complete right tibia in 1926X511. The basic form is very similar to Pedetes. There is a well developed cnemial crest with a distinct insertion for the patellar tendon. There is a transverse groove separating the cnemial crest from the tibial condyles posteriorly: the two facets are separate and do not meet anteriorly. The lateral facet projects further anteriorly than the medial: the two are separated by a deep groove posteriorly but by a flat non-articular area

anteriorly. The lateral edge of the bone is damaged so the facet for the head of the fibula is not preserved.

The cnemial crest extends just over halfway down the shaft. There are well developed crests on the postero-lateral and postero-medial edges with the former crest extending to the distal end of the bone where it broadens out. The fibula crosses the postero-lateral ridge about halfway down the bone, it appears to merge with the ridge but becomes free again beyond it. The shaft of the tibia is slightly convex anteriorly just below the top of the cnemial crest and slightly concave anteriorly for the remainder of its length.

At the distal end the medial posterior surface is prolonged downwards as a distinct process, which forms the edge to the postero-lateral side of the medial facet. There is no lateral anterior process such as is found in Pedetes. The facets for the astragalus are aligned slightly antero-medially and are separated by a broad ridge: their alignment is less oblique than in the living animal thus giving the distal end of the tibia a more rectangular appearance. The lateral facet is shallower than the medial and has a facet for the distal end of the fibula along its lateral edge as in Pedetes. There is an indentation of the anterior surface between the two facets.

Fibula:

There are remains of the right fibula in both 1926X510C and 1926X511. It appears to fuse with the tibia about half-

way down but it may be only closely apposed without true fusion. The proximal half is missing but, from the evidence of the proximal break, it was relatively stout, broader antero-posteriorly than transversely with a slightly concave medial surface and a slightly convex lateral one. The extreme distal end of the bone is missing but this end was not fused to the tibia.

Tarsus (Table 4.VIII ; Fig. 4.4C , 4.5A):

Astragalus:- This is not well preserved in any specimen and all aspects cannot be seen. It is similar to Pedetes but with a less elongated neck. The trochlear surface for the tibia consists of two ridges separated by a groove: the lateral ridge is larger than the medial and the groove separating them is set toward the medial side of the bone. On the lateral surface of the lateral condyle there is a facet for the distal end of the fibula. The body occupies over half the total length of the bone.

Calcaneum:- (Fig. 4.5A , B). Two calcanea are preserved in 1926X510C & E although neither allows a complete view of the bone. The tuber calcis is relatively long and comprises 60% of the length of the bone. At its posterior end the tuber calcis expands transversely more than in the living genus. The postero-medial edge is prolonged as a transversely flattened process which is aligned more medially than in Pedetes.

The primary articular facets for the astragalus on the central eminence face medially and distally: the lateral

face of the central eminence bears a slight fossa. There is a well developed sustentaculum that is larger than in Pedetes and thus projects more medially. The sulcus calcanei is also well developed. On the plantar surface of the sustentaculum there is a facet for the tendon of m. flexor hallucis longus but no groove.

Distal to the central eminence the bone is broader than in the living genus. A small portion of the primary facet for the astragalus just continues onto the dorsal surface of the bone beyond the central eminence. The distal facet for the cuboid is very slightly concave dorso-ventrally and is set obliquely, disto-laterally. It is not sharply curved transversely as it is in Pedetes. Just proximal to this facet on the medial surface there is a pronounced tubercle that is difficult to see clearly but that appears to carry a small facet that may have articulated with the head of the astragalus. At the distal end of the dorsal surface there is a distinct groove bounded by a lateral and a medial ridge. On the ventro-lateral surface there is a shallow groove.

Navicular:- The right navicular is still present in 1926X510C but most of it cannot be seen. The distal plantar process is short and rounded. Part of the facet for C3 is visible and there may have been a facet for the cuboid below it as in Pedetes but damage to the bone makes it impossible to be certain.

Cuboid:- The right cuboid is also preserved in 1926X510C. It is relatively much shorter than in Pedetes and although

the proximo-medial corner is still partly buried in matrix there does not appear to have been a proximal process from it. The proximal facet for the calcaneum is nearly flat to match the distal facet of the latter bone. There is a large lateral tubercle in the proximal half of the bone that corresponds to the hook-like process found in Pedetes. The distal surface is flat and lacks a projecting dorso-lateral corner. As in the Recent genus the proximal half projects ventrally a little more than the distal half.

First cuneiform (C1):- There is only one example of this bone, partly buried, in 1926X510B. It was revealed by the additional preparation done in 1979. The bone is thin with the proximal end articulating either with the medial wall of the navicular or with the medial wall of the distal end of the astragalus. Unfortunately, as preserved, it does not have either of these two bones in contact with it. Just before the proximal end of Mt.II there is a slight dorsal process that is poorly developed. The distal end of the bone overlaps Mt.II but does not cover the whole of the flat roughened area on the medial surface of the metatarsal. I can see no evidence to suggest that C1 is not in its natural position in relation to the metatarsal. The gap between the two bones is very narrow and is not filled with sand grains but only with the cementing substance of the matrix; this suggests that there has been little movement between the two bones. The distal end of the bone expands slightly and is aligned disto-laterally, it is convex dorso-ventrally: it may have had a distal facet but it is not sufficiently clear

for this to be certain.

Second cuneiform (C2):- There are no remains of the second cuneiform in any of the specimens.

Third cuneiform (C3):- There are two third cuneiforms in 1926X510B & C but they do not allow all aspects of the bone to be seen. The dorsal surface is rectangular and the proximal facet for the navicular is convex dorso-ventrally, both as in Pedetes. The disto-medial corner projects slightly medially as in the living animal and bears an oval facet along the dorsal edge for Mt.II. This facet is smaller than in Pedetes and corresponds only to the proximal part of the facet in this latter genus. This suggests that only the proximo-lateral tip and not the whole edge of Mt.II contacted C3.

The distal face projects well ventrally and produces the most ventral point of the bone: the plantar edge is then concave back to the proximo-ventral corner. This region is still a little obscured but there may have been a facet for the cuboid on the lateral proximo-ventral corner – if this is so then it is not set on a slight tubercle as it is in Pedetes.

Metatarsus (Table 4.IX , 4.X , 4.XI , 4.XII ; Fig. 4.4C):

Stromer (1926) states that the hallux is missing in Pa. namaquensis and that the foot is more paraxonic than in Pedetes with Mt.III and Mt.IV equally developed; digit 2 is described as slightly reduced and digit 5 as very reduced. Whilst the paraxonic form of the pes is quite accurately

described there is now some, very equivocal, evidence for the presence of a hallux. During the further preparation of 1926X510 carried out in 1979 extra material of one of the preserved feet (1926X510B) was exposed. This material included the first cuneiform (see above). Lying at the distal end of the first cuneiform and angled under Mt.II there is a bone of which only the end can be seen. Just proximal to this bone there is a small bone that appears to be a sesamoid. At the proximal end of the bone there is a plantar process, projecting proximally, and a proximo-medial process. It thus shows some resemblance to Mt.I in Megapedetes but too little of it is visible to be certain what it is. This region is not well preserved in any of the other specimens and there is no further information about it. The remaining four metatarsals are all better preserved.

Metatarsal II (Mt.II):- (Table 4.IX ; Fig. 4.4C , 4.5A). There are the remains of two complete, one distal end and one fragment of the Mt.II in 1926X510. At the proximal end the shaft thins and curves a little laterally, it overlaps the end of Mt.III and the lateral surface articulates with the medial surface of C3: the lateral surface is, however, not exposed in any of the specimens so that the details of the facets are not known. The proximal facet for C2 has a concave lateral edge and a convex medial edge. On the medial surface of the bone the proximal end is roughened for a short distance and there may have been an oval facet at the distal end of this area, probably for the end of Mt.I: in the only specimen (1926X510B) in which this region can be seen at all

it is largely obscured by the overlying C1. The proximal plantar process is thin and ridge-like; it curves laterally, following the line of the upper surface.

The shaft is flattened on the lateral side and more rounded medially: it curves to the medial side throughout its length.

The distal articulation is barrel-shaped with a ventral median keel. It is set obliquely, disto-laterally, to the longitudinal axis of the foot. There is a large fossa on either side for the joint ligaments and on the dorsal surface there is an indistinct oval fossa just proximal to the facet.

Metatarsal III (Mt.III):- (Table 4.X ; Fig. 4.4C). In 1926X510 there are the remains of one complete Mt.III, two distal ends and one with the middle section missing. The proximal end is largely obscured in both of the specimens in which it is preserved but it appears that the facet was set transversely to the shaft and not slightly obliquely as in Pedetes. On the medial side there appears to have been a slight tubercle, as in the Recent genus, to assist in the contact with Mt.II: the lateral surface seems to be hollowed out for the tubercle on the medial surface of Mt.IV. There is no evidence to suggest that Mt.III articulated with the cuboid as the proximal dorso-lateral corner does not appear to form a process. The proximal plantar process is thin and there is no ventral tubercle as is found in Pedetes: it may articulate with Mt.II and/or Mt.IV.

The shaft curves slightly medially toward the distal end: it has a quadrilateral cross-section with rounded corners.

The distal articulation is barrel-shaped with a well developed ventral median keel. The slight transverse convexity is not symmetrical but is set slightly laterally of the midline although nearer to it than in Mt.IV. The fossa in either side wall for the joint ligaments is well developed as is the dorsal fossa just proximal to the facet.

Metatarsal IV (Mt.IV):- (Table 4.XI ; Fig. 4.4C). There are two complete Mt.IV, one distal end and one with the middle section missing in 1926X510. Proximally the facet for the cuboid is transversely convex and is aligned proximo-ventrally; it is not set obliquely to the shaft transversely as it is in Pedetes. It extends laterally to form a slight proximo-lateral process leaving a slight hollow in the lateral wall into which the proximal end of Mt.V fitted. The attachment for Mt.V was ligamentous and there is no facet in the hollow which is less well developed than in the living animal. On the medial surface there is a tubercle for articulation with Mt.III: it is in the dorsal half of the surface and is less developed and a little further distal than in Pedetes. A short distance from the proximal end there is a small tubercle on the lateral edge of the dorsal surface. The proximal plantar process is not well developed; its medial surface is covered but it may have contacted Mt.III.

The shaft curves laterally towards the distal end and has a flattened medial side and a more rounded lateral surface although this, too, is slightly flattened, especially proximally, for Mt.V. There is a very pronounced axial twist

of about 50°.

The distal articulation is barrel-shaped with a ventral median keel: the slight transverse convexity has its most distal point a little medially of the midline. The fossae in the two sides, for the joint ligaments, and the dorsal transverse fossa, proximal to the facet, are all well developed.

Metatarsal V (Mt.V):- (Table 4.XII ; Fig. 4.4C). There are two examples preserved in 1926X510 but in both the proximal end is missing. This bone is very reduced and is little more than a splint. The shaft has a flattened medial face and an approximately triangular cross-section. It curves out laterally. At the distal end the bone expands, especially to the lateral side, to form the distal articular surface which is convex both dorso-ventrally and transversely. There is a ventral median keel. On the dorsal surface, proximal to the facet, there is a ridge in the medial half and a fossa in the lateral half: on the lateral surface, at the distal end, there is a tubercle on which there is the lateral fossa for the joint ligaments. There is a corresponding fossa in the medial wall at the distal end.

Phalanges:

Phalanx I (Ph.I):- (Table 4.XIII ; Fig. 4.4C ; Fig. 4.5C , D). In 1926X510 there are 13 examples of this bone preserved: they are in various states of preservation and come from digits 2 - 5. In all cases the distal articular surface is

convex dorso-ventrally and curves up just above the level of the dorsal surface of the shaft. There is no ventral keel or dorsal transverse fossa but on the ventral surface just proximal to the facet there is a large tubercle on either side, at the edge of the shaft.

The shaft is slightly curved, concave ventrally, in its longitudinal axis. The proximal facet is saucer-shaped and has a median groove in the plantar half to fit the keel on the metatarsal. As in Pedetes there is a proximo-ventral tubercle on either side of this groove. There are slight differences between the bones from different digits. In digit 2 the medial part of the proximal end is better developed and projects further back than the lateral part; the shaft also curves somewhat laterally and the distal articulation is slightly oblique to the shaft so as to face distally. The proximal facet is almost symmetrical in digits 3 and 4 but in the former the medial side is slightly better developed and projects back while in the latter it is the lateral side that does this. In both these digits the shaft is straight and the distal articulations are symmetrical. The Ph.I is very reduced in digit 5 and curves medially; at the proximal end the lateral part is very much better developed than the medial. The distal articulation is symmetrical and there are no disto-ventral tubercles on the shaft.

Phalanx II (Ph.II):- (Table 4.XIII ; Fig. 4.4C ; Fig. 4.5E). There are 12 partial or complete examples of this bone preserved in 1926X510. The proximal facet is concave dorso-

ventrally and flat transversely. The proximo-ventral edge projects slightly, but less than in Pedetes, and bears a facet for the flexor tendon sesamoid. There is a shallow but quite wide groove in the ventral surface dividing it into small proximal tubercles. The proximo-dorsal edge projects back to a greater extent than in the living animal.

The ventral surface of the shaft is flat and the other surfaces are rounded. The distal articular surface is hemi-cylindrical with a deep fossa in either side wall for the attachment of the joint ligaments. In all the digits this phalanx is symmetrical and straight whereas in Pedetes this is only true in digit 3.

Phalanx III (Ph.III):- (Table 4.XIII ; Fig. 4.4C ; Fig. 4.5F , G). Nine partial or complete specimens are preserved in 1926X510. They are relatively long and claw-like, expanding at the proximal end, and with a well developed, proximal plantar process that projects proximo-ventrally and bears a proximal facet for the flexor sesamoid. In either side wall of the proximal plantar process there is a small fossa containing a foramen. The main proximal articular surface is concave dorso-ventrally and flat transversely. The upper edge does not project back over Ph.II. In all the digits the bone is symmetrical and not twisted as it is in digits 2, 4 and 5 of Pedetes. Distal to the proximal plantar process the ventral surface is flat. There is a flat dorsal surface at the proximal end of the bone: the dorsal surface forms a ridge, running distally from this, and expanding at the distal end to form a small, flat dorsal

area.

Flexor tendon sesamoids:

In 1926X510 some of these are still in position. There are examples of those at the distal ends of the metatarsals and Ph.II.

The sesamoids at the distal ends of the metatarsals are kidney-shaped with a dorsal facet for the metatarsal and a distal facet, slightly concave dorso-ventrally, for the proximal end of Ph.I. Proximally and ventrally the bone thins to a crest.

The sesamoid at the distal end of Ph.II is a simple, transverse bar that sits below Ph.II immediately proximal to the plantar process of Ph.III.

CHAPTER 5

Pedetes laetoliensis sp. n.

Pedetes laetoliensis sp. n.

Name :- After the Laetoli site from which the material comes.

Diagnosis :- Small Pedetes about 85% of the size of the living species of the genus Pedetes; cheekteeth with pulp cavities remaining open into adult life but closing in older animals with the loss of the bilobed pattern found on the occlusal surface, lower cheekteeth not normally producing pronounced tubercles in the lateral wall of the mandibular ramus; cranium less deep than in the Recent species of Pedetes; nasals 92% of frontal length; infraorbital foramen enlarged, extending further dorsally and having a relatively wider base than in living Pedetes; fossa in side of rostrum below incisive alveolus; palatal groove shallow; incisive foramina relatively long (about 35% of the diastemal length); basi-sphenoid with large median foramen; lateral wings of basi-occipital well developed; pm_4 with posterior enamel ridge of anterior lobe possessing an anterior fold. No trace of fusion in cervical vertebrae; large tubercle on anterior face of trochanter major of femur.

Holotype :- Laet.'79 5514. Adult skull and associated post-cranial remains (Fig. 5.1A, B ; Fig. 5.3C - F ; Fig. 5.4B, C ;

Fig. 5.5 ; Plate 7). Housed at Olduvai Gorge.

Referred material :- Additional material collected at Laetoli and largely fragmentary can also be referred to this species. Most of the material is housed at Olduvai Gorge but there is a small amount at TILLMIAP and one piece in the BM(NH) which comes from north-east of Lake Eyasi (MacInnes, 1953). A detailed list of all the material examined is given in Appendix V.

Provenance :- Laetolil Beds at Laetoli in northern Tanzania (approx. Long. 35°12'E : Lat. 03°10'S). K-Ar dating : 3.59 - 3.77 million years (Leakey et al., 1976). Beds at Laetoli Locality 14. The material in TILLMIAP and the BM(NH) is of uncertain provenance.

Introduction:

Pedetes laetoliensis is known only from material collected in the Laetoli area of northern Tanzania. The first collection from this site was made just before the Second World War by L. Kohl-Larsen and the material was described in Dietrich (1942). The small amount of springhare material in this collection was ascribed to Pedetes surdaster subsp. apparently on the basis of its shallow palatal groove. The exact provenance of this material is not known but the measurements given for it show that it is much smaller than is normal in the modern species. This suggests that it represents Pedetes laetoliensis.

Small amounts of material, including springhare material, were collected at Laetoli in 1959 and are now housed at TILLMIAP: there is a single piece, an articulated astragalus and calcaneum, in the BM(NH). This specimen comes from the north-eastern end of Lake Eyasi and hence, apparently, not actually from Laetoli. Pedetes laetoliensis was collected at Laetoli between 1974 and 1979 and these specimens are presently housed at Olduvai Gorge. All the material from the 1959 and later collections that could be found has been examined.

The springhare material at Laetoli is exceptionally well preserved, as also is the lagomorph material. Material belonging to other groups is very fragmentary and often scattered (Leakey et al., 1976). As was noted above a somewhat similar situation is found at Elisabethfeld with Parapedetes and this seems to provide interesting evidence on the way of life of these fossil pedetids as will be discussed below (see Chap. 8).

DESCRIPTION.

The description is based primarily on the holotype specimen. The other material has been used to supplement this information and to provide an initial idea of the individual variation within the species: material from at least 35 individuals is present in the collections housed at Olduvai Gorge. This minimum number of individuals is the sum of the minimum number for each locality and at each

locality the minimum number is based on the most common skeletal part at the locality. Throughout the description this species is compared with the two Recent species of the genus Pedetes, but principally with the East African form, Pedetes surdaster.

Cranium (Table 5.I):

The overall appearance of the cranium shows great similarity with Pedetes surdaster but with some differences in detail, in a number of which it resembles Pedetes capensis. The holotype cranium is a little over three-quarters of the size of an adult cranium of the modern species (see Tables 2.I and 5.I) and the only other complete cranium, Laet.'75 1673, is of like size.

Dorsal aspect:- (Fig. 5.1A). The nasals taper slightly anteriorly; in length they are about 35% of the cranial length and 92% of the frontal length; they are relatively longer and narrower than in P. surdaster and more nearly resemble P. capensis. The naso-frontal suture is straight and just anterior to the preorbital bar which forms an anterior angle of about 90° with the rostrum. For much of their length the nasals are edged by the premaxillae which project a short way back beyond the naso-frontal suture into the frontals. Lateral to each premaxilla, at its posterior end, there is a plate of the maxilla.

In the anterior half of the frontals there is a slight median depression, as in the Recent species, within which the midline suture forms a distinct ridge. This depression does

not extend to the lateral edges of the cranium. The upper edges of the orbits are slightly concave with the inter-orbital constriction between one-third and halfway back. In their posterior half the upper rims of the orbits form slight ridges continuous with the post-orbital tubercle. This tubercle is all that remains of the post-orbital bar and it is positioned directly above the squamosal root of the zygoma. Relative to it, the fronto-parietal suture, which has a smoothly curved, median, anterior salient, is more anteriorly placed than in the living species. There is a slight groove for m. temporalis extending postero-medially, from between the post-orbital tubercle and the squamosal root of the zygoma, along the posterior edge of the parietal almost to the inter-parietal. This groove is relatively better developed than in the Recent species and has a particularly distinct anterior edge.

The parieto-squamosal suture is positioned further laterally than is normal in Recent Pedetes so that the squamosal is almost excluded from the dorsal surface. Expanded auditory bullae occupy the postero-lateral corners of the cranium and project a little way beyond the supra-occipital, which just extends onto the dorsal surface along the posterior edge of the interparietal. This latter bone may be slightly sunken below the general dorsal surface of the braincase.

Profile:- (Fig. 5.1B ; Plate 7). The cranium is less deep than in Recent Pedetes. Its dorsal surface is flat over the orbits and the rostrum except that the anterior tip of the

nasals is slightly depressed. The median depression in the frontals is not visible in profile. Posterior to the orbits the dorsal surface curves down quite sharply so that the bullae are orientated a little less vertically than in living Pedetes.

Anterior to the premaxilla the nasal has a well developed lateral wing. The lower maxillary root of the zygoma arises immediately behind the incisive alveolus and much of its base is formed by the premaxilla. It is inclined postero-ventrally and is a little more robust than in the Recent species. A distinct ridge, marking the edge of the origin of m. masseter medialis, begins at the dorsal edge of the lower zygomatic root and runs along the anterior and dorsal edges of the rostrum back to the preorbital bar where it turns out and continues along the antero-dorsal and antero-lateral edges of the bar. The incisor arises at the level of the infra-orbital foramen and the incisive alveolus forms a curved ridge across the rostrum reaching to three-quarters of the muzzle height, at its highest point, as in the living species. The rostrum below the incisive alveolus forms a slight fossa with its ventral edge formed by the ridge resulting from the forward curving root of pm^4: this ridge is obscured in lateral view by the lower maxillary root of the zygoma. The fossa is absent in Recent Pedetes and the end of pm^4 does not produce a ridge.

In the zygomatic arch the maxilla sends back a short process below the jugal. As in the living species the jugal and lachrymal meet in the preorbital bar and form its main

components. The lachrymal does not form a significant pre-orbital process. On the lateral surface of the jugal and the posterior part of the maxilla the origin of m. masseter lateralis is clearly defined: it includes several well developed ridges, especially around the suture of the maxilla and jugal. These ridges presumably increased the strength of the muscle origin and it would seem that the muscle was relatively more powerful than in the living species in which there are only slight ridges edging two or three shallow conchoidal fossae. The posterior corner of the jugal is broken off but on the lateral surface two parallel ridges run postero-ventrally towards it. The squamosal root of the zygoma is like that in Recent Pedetes but is relatively more robust.

Very little detail of the orbit can be seen in any specimen. There appear to have been two ethmoid foramina in the same positions as in the living species. About half the anterior wall of the orbit is formed by the large lachrymal; most of the inner wall by the orbital plate of the frontal. As in Recent Pedetes the end of m^1 rose high in the floor of the orbit at its anterior edge.

Behind the orbit the cranium is occupied largely by the auditory bulla which is like that in the modern species except that the bony external acoustic meatus is not continued by a ridge down the lateral surface of the tympanic bulla. The squamosal sends back a thin, simple, process above the external acoustic meatus, lying in a groove in the mastoid. Where this process joins the main body of the

squamosal there is a ventrally directed temporal foramen as in Recent Pedetes.

Ventral aspect:- (Fig. 5.2A). In the holotype parts of this aspect are still obscured by matrix and the articulated lower jaw: even the other specimens do not enable a complete description of this aspect to be made. The incisive foramina are set immediately behind the incisors in a shallow palatal groove that extends back to the anterior edge of pm^4. They are relatively longer than in P. surdaster being 35% of the diastemal length in Laet.'75 1673 compared with 29% in the latter species. They are, thus, more like the incisive foramina in P. capensis which are 37% of the diastemal length (see Tables 2.I and 5.I). The interforaminal septum is bony and almost completely separates the two foramina, which just join posteriorly. The premaxilla-maxilla suture meets the sides of the incisive foramina just anterior to the postero-lateral corners and, in LIT'59 125, runs more laterally, rather than postero-laterally as in the Recent species. The edges of the palatal groove are sharp, overhang slightly and leave slight hollows in the side of the rostrum just anterior to pm^4 and ventral to its alveolus. Between the toothrows the bony palate forms a median ridge that continues as a slight posterior process when the bony palate ends level with the anterior lobe of m^2. The posterior palatal foramina are apparently on the maxilla-palatine suture at the level of pm^4/m^1 although occasionally they may be further posterior and wholely in the palatine. There are

two small anterior accesory foramina in the maxilla level with the anterior lobe of pm^4. The toothrows are straight, converge anteriorly and are parallel to the zygomata. There are tiny posterior maxillary foramina posterior to m^3. The origin of m. masseter superficialis at the anterior end of the zygoma is as in Recent Pedetes.

The basicranial sutures are closed in the holotype. The presphenoid and basisphenoid are as in P. surdaster except that the median foramen in the basisphenoid is large. There is a large fenestra opening into the orbit on either side of the presphenoid as in the living species. The basioccipital has well developed lateral wings that are considerably more pronounced than in P. surdaster: there is a single large median opening. The bullae lock into the lateral edges of the basioccipital and between the tympanic and the latter bone there is a well developed groove running forwards from the jugular foramen, between the basioccipital and the bony ventral process at the mouth of the Eustachian tube. At the anterior end of this canal there is a small middle lacerate foramen, in the angle between the basisphenoid and the bulla. It is both smaller and positioned more posteriorly than in the Recent species where it is in the angle between the basisphenoid and the pterygoid fossa. Laterally, the foramen ovale seems to have been quite large. Bony pterygoid fossae are present and the hamulus of the pterygoid is reasonably well developed. The buccinator and masticatory foramina are confluent: the glenoid fossa is formed entirely by the squamosal.

Anterior aspect:- The nasal aperture is relatively less deep and less wide than in Recent Pedetes. The preorbital bar appears to be more nearly vertical and the jugal projects a little more laterally than in the living species making the zygoma appear more robust. The infraorbital foramen is relatively larger than in living Pedetes: it is wider at the base due to the fossa in the lower part of the side of the rostrum; it is relatively higher, extending further dorsally, due to the reduction of the anteriorly facing plate of the maxilla at the dorsal end of the preorbital bar.

Posterior aspect:- This has been damaged in all specimens. It is generally like that of the living species but the foramen magnum appears to have been more oval without a pointed dorsal apex. The external occipital crest on the supraoccipital is well developed.

Upper dentition:- (Table 5.III). The upper incisors are as broad transversely as they are deep antero-posteriorly and are strongly opisthodont as in the Recent species. They are without anterior grooves or ridges and the enamel is stained a light buff. This is sometimes found in the living species but here it may be due to post-depositional staining as the enamel of the cheekteeth also shows a slight staining.

There are four cheekteeth with the apex of pm^4 curving anteriorly and the apices of m^1 - m^3 curving slightly posteriorly. In the holotype the right toothrow is exposed but the occlusal surface of the left is not. Right m^1 and m^2 show the typical pedetid pattern with two lobes, joined

on the lingual side, and separated by a narrow cement-filled buccal infold that extends most of the way across the tooth. In m^3 there is no buccal infold and the tooth consists of a plain enamel ring filled with dentine. The right pm^4 is almost reduced to the same state but there is still a very short buccal infold. Although the occlusal aspect of left pm^4 is not exposed the buccal aspect shows that a buccal infold is present but that it extends only a little way below the occlusal surface and further wear would soon obliterate it. The buccal aspect of left m^1 is similar but the infold extends further down the tooth below the occlusal surface.

Isolated cheekteeth and maxilla fragments including cheekteeth support the general description based on the holotype. Material of young individuals shows that, as in the living species, the two lobes are initially separate but the groove in the occlusal surface separating them is very much shallower on the lingual than on the buccal side. Thus wear produces the typical bilobed pattern with a buccal infold, found in the holotype in m^1 and m^2 and also in Recent Pedetes. This infold does not widen to any significant extent at its open end as does the lingual infold in the lower teeth (Fig. 5.2B). The posterior lobe is larger than the anterior except in m^3 in which the anterior lobe is the larger. As the roots close in older animals further wear eventually removes the typical pattern and reduces the teeth to simple enamel rings filled with dentine. The rate with which the typical pattern is lost depends on how far the

buccal infold extends through the height of the tooth. This is greater in m^1 and m^2 than in pm^4 and m^3, but it does not extend through the whole height of any tooth as it does in the living species. Thus, as shown in the holotype, m^1 and m^2 retain the typical pattern longest and m^3 is the first tooth to lose this pattern and be reduced to a simple ring.

Mandible:

(Table 5.II ; Fig. 5.1B ; Plate 7). Most of both rami are present in the holotype and there are a number of other pieces although in no case is the angle preserved. The lower masseteric tubercle, just antero-lateral to pm_4, is relatively better developed than in Recent Pedetes. Passing back horizontally from it is a pronounced shelf forming the insertion of m. masseter medialis: it curves a little dorsally at its posterior end. Also beginning at the lower masseteric tubercle is the masseteric crest which curves postero-ventrally across the lateral face of the ramus and which is relatively better developed, especially ventrally, than in the modern species. Ventrally it curves into the angle which arises from the posterior surface of the incisive alveolus and does not have a distinct anterior process. The foramen mentale has two openings – a dorsal one just anterior to pm_4 and a second one on the lateral face of the ramus over the posterior edge of the incisor. The diastema has a ridge along the medial edge. It appears that the symphysial region is as in modern Pedetes with the bone pierced by many small foramina. The insertion of m. digastricus is well developed.

The coronoid process arises at the level of m_2/m_3 and is similar to the living species. The condyle is relatively a little wider while the posterior edge of the ascending ramus is more distinctly concave so that the posterior process of the angle may have been more pronounced. The incisive alveolus curves up high into the ascending ramus, as in Recent Pedetes, and produces a distinct, broad, ridge in the lateral face. In the lateral face of the horizontal ramus there are no pronounced tubercles marking the ends of the cheekteeth as there are in the living species although, especially in younger animals, there may be slight tubercles over the ends of some of the teeth. The roots of the cheek-teeth extend down to the level of the incisor and pass laterally to it.

Lower dentition:- (Table 5.IV). The lower incisors are similar to the upper ones and arise high in the ascending ramus of the lower jaw.

There are four lower cheekteeth (Figs. 5.2C - E). In the holotype the left m_1 and both fourth premolars are exposed. The former is as in Recent Pedetes with a narrow, cement-filled, lingual infold passing almost across the tooth and separating two lobes that are joined on the buccal side. The two premolars have each worn a little differently. The right pm_4 consists of a dentine-filled enamel ring which has a slightly triangular form with the apex anteriorly: in the lingual wall a slight notch marks the position of the lingual infold. The left pm_4 is similar but, in addition, in the centre of the tooth there is a small enamel ring forming a

central island. This presumably represents the remains of a slightly deeper section of the lingual infold.

The teeth in other mandibular fragments such as Laet.'76 3864 show the pattern found in younger animals. They consist of two separate lobes with the groove between them shallower on the buccal than on the lingual side so that wear will produce the typical bilobed pattern of two lobes joined on the buccal side and separated by a lingual infold. The lingual infold generally widens out distinctly at its open end in contrast to the upper teeth in which this is not so pronounced.

In the lower fourth premolars the posterior ridge of the anterior lobe has a median fold passing anteriorly as is normal in P. capensis but which is not found in P. surdaster. Laet.'76 3593, an isolated right pm_4, shows replacement of a deciduous tooth by the permanent one (Davies, in prep.). This is the best evidence yet available for premolar replacement in the genus Pedetes.

Vertebral column:

In the holotype fragments from all regions of the vertebral column, except the sacrum, are present. The sacrum is only preserved in an unnumbered fragment, probably collected in 1959, amongst the material in TILLMIAP. A number of fragments of caudal vertebrae are preserved but none of these show any features that are not found in the holotype.

Cervical vertebrae:- (Table 5.V). There are remains of all

the cervical vertebrae except for the atlas and, in all of them, the transverse processes and the neural spines have been damaged or are missing completely. The axis is very similar to that found in the living species of Pedetes but the neural spine is less broad antero-posteriorly and hence a little less plate-like; it is angled very slightly posteriorly. In contrast to the position in P. surdaster the axis is not fused to Ce3 nor is there any trace of fusion in the more posterior members of the series. In this feature the species resembles P. capensis.

The remaining cervical vertebrae are all generally similar to Recent Pedetes. In Ce3 the prezygapophyses are flat and the neural spine is angled slightly posteriorly. The zygapophyses of the other cervicals are vertical. Only in Ce5 is a significant portion of the neural spine still present: it is vertical and was probably quite well developed. Ce6 had pronounced ventral processes which suggests that there was a well developed m. longus colli. There appears to have been a vertebrarterial canal in Ce7 and rib 1 just articulated with the postero-lateral corner of this vertebra.

Thoracic vertebrae:- (Table 5.V , 5.VI). There are four fragments from this region in the holotype: of these one is a tiny fragment of neural arch; one a complete centrum and two are relatively complete vertebrae. The latter three pieces are all from the anterior half of the series, the position of the neural arch fragment cannot be determined.

There are two pieces from the extreme anterior end of

the series: the more posterior and more complete one is probably Th3. The centra are broad, thin and flat. In Th3 the transverse process arises from the lateral edge of the prezygapophysis and not from the neural arch immediately posterior as it does in all the anterior thoracics of the living species. A distinct ridge runs along the antero-dorsal edge of the transverse process in contrast to Recent Pedetes: also the anterior edge of the neural arch is more square rather than smoothly U-shaped and the arch is relatively deeper antero-posteriorly. The zygapophyses of Th3 are flat and the neural spine is almost vertical with only a slight posterior tilt. The rib hemifacets at the anterior end of the centrum are much larger than those at the posterior end.

The remaining reasonably complete piece is probably Th6. The centrum is deeper than in the more anterior vertebrae with the dorsal surface slightly concave transversely and the ventral surface sharply convex transversely and slightly concave antero-posteriorly. Both transverse processes are broken off: they arose at the junction of the pedicle and lamina of the neural arch, level with the posterior edge of the prezygapophysis. The zygapophyses are flat: the neural arch is relatively deeper longitudinally than in Recent Pedetes: the neural spine is angled posteriorly. Both anterior and posterior rib hemifacets are about the same size.

Lumbar vertebrae:- (Table 5.V , 5.VI). Three vertebrae remain in the holotype: two are articulated and the third

was probably the vertebra immediately anterior to these two. They appear to be Lu4 - Lu6 and are generally similar to the lumbars in Recent Pedetes. The centra are about as broad as they are long and are quite shallow with a transversely concave dorsal surface and a ventral surface that is convex transversely and concave longitudinally. In the anterior half of the ventral surface there is a distinct median ridge. The transverse processes are missing except in Lu6 where only the tip is missing: initially they are directed laterally and slightly ventrally and then they turn antero-laterally and ventrally. Anapophyses are present and it was their development relative to Recent Pedetes that was used to fix the position of these vertebrae. On the pedicle of the neural arch, between the bases of the anapophysis, transverse process and prezygapophysis, there is a large, shallow fossa which probably formed part of the origin of m. psoas. Metapophyses were present but all are broken off: the neural spines are inclined anteriorly and do not appear to have had pronounced grooves on their posterior surfaces. The posterior vertebral notch is much better developed than the anterior.

Sacrum:- The only preserved fragment shows that the sacrum was formed from three fused vertebrae and includes a complete Sa3, Sa2 with the anterior part of the centrum missing and part of the neural arch of Sa1. The piece is quite badly damaged and it is impossible to tell whether the tips of the transverse processes were fused. Sa1 probably

expanded anteriorly to articulate with a relatively wide Lu7; the centra of Sa2 and Sa3 are narrow as in the Recent species. The neural spine of Sa2 is the stoutest as in the living species but, in contrast to their development in Recent Pedetes, the zygapophyses form prominent tubercles. Sa3 has two small postero-ventral tubercles that provide the base for the first chevron bone

Caudal vertebrae:- (Table 5.VII). In the holotype there are remains of 16 vertebrae: probably Ca11 - Ca26. They are all made up, principally, of a cylindrical centrum with a number of processes, not usually well developed, and they are similar to the caudal vertebrae of Recent Pedetes showing that the animal had a similar long tail.

Towards the proximal end of the series the processes are better developed than they are more distally and this is especially true of the remains of the neural arch which is restricted to the posterior end of each vertebra. On the dorsal surface of each centrum there is a pronounced median ridge running from the remains of the neural arch, anteriorly, between the paired anterior, dorsal processes, to the anterior end of the centrum. This ridge is not present in Recent Pedetes.

The development of processes at the anterior and posterior ends of the vertebrae results in each vertebra appearing to have a pinched-in waist. Transverse processes are very reduced in all the vertebrae and consist of a slight horizontal flange or even just a ridge in the middle of either side. The other processes are also very reduced

especially more distally in the tail, but the ventral processes at the anterior end of each vertebra are the best developed: the anterior dorsal processes are also quite well developed. Towards the tip of the tail the vertebrae become very small and are strongly compressed transversely: they are less elongated than in Recent Pedetes. The transverse compression of the vertebrae is much less pronounced at the proximal end of the series.

In Laet.'75 2932 there are four pieces from a more proximal region of the tail than that preserved in the holotype. These pieces are similar to vertebrae from the same region in the living species.

In Laet.'75 446 there are also vertebrae from the proximal end of the tail. In these the neural arch is at the anterior end of the vertebra so that the anterior vertebral notch is very small and the posterior notch is large. The centrum is wider than it is deep and the ventral surface is concave longitudinally. In Ca7 - Ca8 the transverse process forms a flat sheet; the neural arch is elongated and low; the metapophysis is large; the neural spine is low and elongated antero-posteriorly and the centrum is the dominant element.

Ribs, sternum, clavicle and scapula:

There are no known remains of these parts of the skeleton, except for a proximal rib fragment, in the holotype. This rib fragment is probably from the left side and about the middle of the series (i.e. around the region

of rib 6): it is as in the modern species. A rib fragment in LIT'59 125 has a similar morphology to the Recent species but is smaller and more delicate.

Humerus (Table 5.VIII ; Fig. 5.3A, B):

In the holotype the distal humerus is preserved from both sides articulated with the ulna and radius. In addition there is an uncatalogued fragment of the distal left humerus and a complete left humerus (LIT'59 125 in TILLMIAP) that confirm those features shown in the holotype.

The proximal humerus is only preserved in LIT'59 125 and from this specimen the length is found to be 69% of the length in Recent Pedetes. The head is relatively larger compared to the length of the bone than in the living species and the delto-pectoral crest is less well developed.

As in Recent Pedetes the medial epicondyle ends in a dorsal hook-like process and an entepicondylar foramen is present. The lateral epicondyle and the supinator crest are less well developed than in the living species: the upper end of the supinator crest merges more gradually with the shaft. In the distal articular surface the capitulum is more bulbous and the trochlea is relatively deeper than in the Recent species. Along the medial edge of the trochlea there is a pronounced crest. The olecranon fossa is small but is deeper than the anterior supratrochlear fossa. There is no supratrochlear foramen. In LIT'59 125 the epicondylar width is 32% of the humeral length which is almost exactly the same as the mean in P. surdaster.

Ulna (Table 5.IX ; Fig. 5.3C, D, E, F):

This is smaller than the ulna in Recent Pedetes but is otherwise very similar. The coronoid process is relatively a little narrower transversely but is more convex to fit the deeper humeral trochlea. Towards the proximal end of the shaft the postero-medial edge forms a distinct ridge whereas in the living species there is no ridge and the edge is more smoothly curved.

Radius (Table 5.IX ; Fig. 5.3C, D, E, F):

The radius is also similar to the modern species in nearly all its features and is smaller. The distal end is much less wide transversely relative to its depth: the styloid process is not especially well developed but there is a longitudinal ridge on its anterior surface that is more pronounced than in Recent Pedetes and edges a groove on the medial half of the anterior surface of the bone. The distal facets for the scapho-lunar and cuneiform are as in the Recent species.

Manus:

There are no remains of the manus preserved.

Innominate bone (Table 5.X ; Fig. 5.4A):

In the holotype only the right ilium is preserved but there are also a number of other fragments although there are no remains of most of the pubis or much of the posterior and ventral portions of the ischium. The innominate bone is

smaller than that of the living species but is generally similar. The lateral surface of the ilium is divided into a larger dorsal and a smaller ventral plate by a broad, low, horizontal ridge: the anterior tip curves out laterally. Just anterior to the acetabulum the fossa marking the origin of m. rectus femoris is about as well developed as in the living species but the ventral edge forms a pronounced ridge. The dorsal edge of the acetabulum is a little more concave than in Recent Pedetes and there is a well developed acetabular notch. The ischial spine is level with the posterior edge of the acetabulum. Immediately posterior to this the dorsal surface of the bone begins to curve up into the ischial tuberosity which was probably well developed. In one of the unnumbered specimens in TILLMIAP the posterior corner of the ischium is preserved: the ischial tuberosity is as in the Recent species, the section below it is more robust than in the living species along the edge of the obturator foramen. The pubis has a slightly better developed pectineal tubercle than in the Recent species.

Femur (Table 5.X , 5.XVI ; Fig. 5.4B, C):

The complete right femur and the proximal end of the left femur are preserved in the holotype: there are also a number of other fragments, especially distal ends. The bone has a generally similar appearance to that in Recent Pedetes but is shorter and more slender. The right femur of the holotype is 82% of the mean femoral length in P. surdaster. At the proximal end the trochanter major

rises high above the head but relatively less than in the modern species: the trochanter minor and intertrochanteric crest are well developed, the trochanteric fossa is deep. On the anterior face of the trochanter major, at the level of the head, there are three ridges: the medial ridge is very poorly developed while the lateral one is quite distinct and both are similar to the ridges found in the Recent species. The middle ridge is very well developed with the central section forming a large tubercle, it is much better developed than in the living species. The neck of the femur is shorter than in the modern species so that the head is brought closer to the shaft: there is a large fossa in the head for the ligamentum teres and the articular surface overlies the postero-dorsal surface of the neck.

The shaft has a slight anterior bow and, especially towards the distal end, is compressed a little antero-posteriorly. At the upper end the ridges marking the muscle insertions are a little better developed than in Recent Pedetes.

The distal end is essentially as in the living species. The medial condyle projects down below the lateral while the lateral condylar facet is continuous with the broad, shallow patellar groove which is set slightly obliquely to the longitudinal axis of the shaft. On the posterior surface of the shaft, just medial to the lateral condyle, there is a low roughened tubercle marking the origin of m. plantaris. Above each condyle there is a facet for the sesamoid in the tendon of origin of the respective head of m. gastrocnemius.

There are three fossae in the lateral face of the lateral condyle with the fossa for the tendon of origin of m. extensor digitorum longus well developed. In the distal femur of a juvenile (Laet.'75 864) in which the distal epiphysis is unfused the down-curves of the epiphysial line on the lateral and medial surfaces are broader and less sharply curved than in Recent species.

Patella (Table 5.X):

This is triangular with a sharp dorso-lateral corner and a more rounded dorso-medial one. The ventral corner is sharply pointed. The patella is a robust bone and in the holotype the right patella is preserved.

Tibia (Table 5.X , 5.XVI ; Fig. 5.5A, B):

This bone is also shorter and more slender than in Recent Pedetes and its length, in the holotype, is just under 82% of the mean tibial length for P. surdaster. The difference in lengths is largely a result of a shorter distal section (i.e. the section below the point where the tibia and fibula become closely joined) in P. laetoliensis. In posterior aspect the bone has a slight S-shaped curvature that is more pronounced than in the Recent species, especially in the distal half.

At the proximal end the lateral facet is larger and extends a little further anteriorly than the medial and is edged by a small bony shelf whereas the medial facet extends to the edge of the bone. The facets are not joined

anteriorly, are concave transversely and convex antero-posteriorly; the medial edge is higher than the lateral. Immediately anterior to the lateral facet there is a slight notch in which the tendon of origin of m. extensor digitorum longus ran. The tubercle at the proximal end of the cnemial crest is relatively better developed than in the living species. On the postero-lateral corner of the head there is a small concave facet for the head of the fibula.

On the shaft the crest on each of the three corners is very distinct proximally: the postero-medial and postero-lateral crests can be traced for the whole length of the shaft; the former the more easily. The cross-section of the shaft changes about halfway down from triangular, with convex antero-medial and concave antero-lateral and posterior faces, to quadrilateral, slightly compressed antero-posteriorly toward the distal end. In the upper third of the bone there is a distinct vertical ridge down the middle of the antero-medial face marking the insertion of mm. gracilis and semitendinosus. This ridge is more pronounced than in the living species.

The distal articulation is obscured in the holotype by the astragalus but other material shows that it is as in the living species. There is a well developed medial posterior process with a pronounced ridge down either edge: the medial ridge being continuous with the postero-medial ridge of the shaft. On the anterior face at the distal end there are three ridges of which the middle and lateral ones are well developed: there is a slight fossa on the antero-medial

corner. The lateral anterior process is not well developed but there is a well developed anterior notch between the two facets distally. The medial tubercle behind which the flexor tendons run is elongated to form a short ridge as in Recent Pedetes, neither it nor the groove in which the tendons run is well developed. Just posterior to the fibula there is a slight tubercle and a groove in which the peroneal tendons run: both of these are a little further posterior than in the living species and the ridge down the posterior edge of the groove is a little better developed.

Fibula:

The proximal end of the bone is not preserved but it articulated with the postero-lateral corner of the head of the tibia where there is a slightly concave facet. The bone is very thin and about halfway down becomes closely associated with the tibia. In the holotype, almost certainly an old animal on the basis of its teeth, partial fusion may have occurred between the two bones but a distinct fibula can be traced for its whole length. In other specimens there is no fusion. At the distal end the fibula becomes free and articulates with the astragalus as in the living animal.

Tarsus (Fig. 5.5C):

The tarsus is shorter than in modern Pedetes but the basic construction is similar. The individual bones of the tarsus are similar to those in Recent Pedetes but there are

some differences in detail and all are smaller.

Astragalus:- (Table 5.XII , 5.XVI). The length of the astragalus is 75% of the mean length in P. surdaster and as in this latter species 60% of this is made up by the neck and head. The lateral condyle of the body is better developed than the medial and the groove of the trochlear surface is displaced toward the medial side. The lateral face of the body articulates with the fibula.

The sulcus tali is quite well developed, appearing more open than in Recent Pedetes, but is closed at the medial end by a distinct ridge. The neck and head are angled medially more than in the living species, in which the bone is straighter, and resemble Megapedetes. There is quite a well developed tubercle on the dorso-lateral surface of the neck. On the dorso-medial surface of the head there is a distinct tubercle; there is no contact between the dorso-lateral corner of the head and the calcaneum. The distal facets for the navicular and the cuboid process are either confluent or are separated by a very slight ridge: there is a distinct facet for the proximal end of the first cuneiform on the distal ventro-medial corner.

Calcaneum:- (Table 5.XI , 5.XVI). The mean length of this bone is 72% of the mean length in P. surdaster. The tuber calcis and the central eminence are as in the living species but the disto-dorsal portion of the primary astragalar facet is a little better developed. The sustentaculum is poorly developed and offset to about the same amount as in the

living species: there is quite a pronounced groove on its ventral surface for the tendon of m. flexor hallucis longus.

At the distal end the facet for the cuboid is similar to that in the Recent species but the lateral edge is a little more convex and medially the portion curving round onto the medial face of the bone and articulating with the base of the proximal process of the cuboid is less well developed. There is a slight overhang of the dorsal edge of the facet especially medially. The distal dorso-lateral groove is less well developed than in the Recent species but the distal dorsal tubercle is well developed and a ridge runs proximally from it.

The tuber calcis accounts for 45% of the total length of the bone: this is the same proportion as in P. surdaster.

Navicular:- (Table 5.XIII). The distal facet for the third cuneiform is more oblique than in the Recent species and truncates the disto-lateral corner: the facet for the second cuneiform is more markedly convex and is not split into two separate facets, one facing distally and one dorso-distally. On the lateral face the facets articulating with the cuboid are less well developed than in the living species. On the proximal face the ventral edge of the facet for the astragalus is straight and not downcurved. On the medial face there is a facet for the first cuneiform and there is a tubercle present on the disto-medial edge of the bone. As in the Recent animal there is a well developed horizontal plantar process directed distally: the length of the plantar surface, including this process, is 80% of the

mean length in P. surdaster.

Cuboid:- (Table 5.XIV). In the holotype the length of the cuboid is 69% of the mean length in P. surdaster. The distal end articulates with Mt.IV and the disto-lateral edge also articulates with Mt.V: this contact with Mt.V is better developed than in Recent Pedetes in which it is often absent. At the dorsal disto-medial corner there is an articulation with the dorsal proximo-lateral process of Mt.III. On the lateral surface the peroneal tubercle is similar to that in the living species but is less hook-like and the groove on the dorsal surface running back from it is shorter with the edging ridges, especially the medial, much better developed. The proximal facet for the calcaneum is of the same form as in Recent Pedetes but, as might be expected from the less developed disto-medial facet on the calcaneum, it does not extend to the end of the proximal process which is otherwise similar to the living species. On the large ventral tubercle the ventro-lateral ridge is well developed but there is no vertical groove in the distal face.

First cuneiform (C1):- (Table 5.XV). The length of this bone is about 83% of the mean length in P. surdaster but it is similarly reduced to a thin splint. There is a dorsal median expansion and the dorsal edge from this to the distal end is straight rather than concave so that the median expansion appears to be a more integral part of the whole bone rather than a dorsal process as in Recent Pedetes. The distal end of the lateral face articulates with Mt.II; the

median expansion articulates with the second cuneiform laterally and, by a small facet near its apex, with the medial sesamoid medially. The proximal end is broken off in the holotype but presumably articulated with the astragalus (see above) as in the Recent species. In the medial face of the bone, just ventro-distally to the facet for the medial sesamoid, there is a pronounced oval fossa.

Second cuneiform (C2):- (Table 5.XV). The second cuneiform is 77% of the mean length in P. surdaster. The distal edge is S-shaped and more distinctly curved than in Recent Pedetes. There is a facet on the medial face of the bone articulating with the median expansion of the first cuneiform. Halfway down the disto-medial edge it is more hollowed out than in the living species so that the distal facet is more visible in medial aspect. This hollowing is partly responsible for the increased curvature of the distal edge. The ventral half of the bone is relatively narrower than in the Recent animal.

Third cuneiform (C3):- (Table 5.XV). This bone is also 77% of the length in P. surdaster. On the distal face there is a flat facet articulating with the proximal end of Mt.III. The distal third of the medial side is attached to the overlapping portion of Mt.II while the proximal two-thirds of this side articulates with the second cuneiform. The proximal half of the lateral side faces slightly proximolaterally and articulates with the cuboid. Proximally the facet for the navicular is aligned more obliquely, facing

proximo-medially, than in the living species so that the angle between it and the facet for the cuboid is much sharper and this results in the proximo-lateral corner appearing to project proximally. Most of the dorsal surface is occupied by a low tubercle.

Metatarsus (Table 5.XVII , 5.XVIII):

There is no hallux and digit 3 is the dominant digit. In the holotype the proximal ends of the metatarsals are largely obscured by matrix. Morphologically the metatarsals are very similar to those of the living species but they are shorter and more slender. Metatarsal III is a little smaller and metatarsal V is a little larger relatively than in P. surdaster.

The proximal end of Mt.II is more concave than in the modern species in order to fit the more convex second cuneiform. Its proximo-medial corner is not flat but appears to project medially. On the medial face, at the end of an area roughened for a ligamentous attachment, there is a facet for the distal end of the first cuneiform. There are proximal dorsal and ventral facets for the third cuneiform on the lateral face and for about 6mm distally the lateral surface is roughened for the ligamentous attachment to Mt.III. From what can be seen the remaining metatarsals do not appear to differ significantly from Recent Pedetes except that in Mt.IV the proximal tubercle for Mt.III on the medial face is set a little further distally than is normal in the living species.

Phalanges (Table 5.XIX , 5.XX , 5.XXI):

Both first and second phalanges (Ph.I and Ph.II) have

the same morphology as in the Recent animal but are more slender. However, in both cases, they are relatively slightly longer compared with the metatarsals than in the Recent species. In Ph.I the distal facet is slightly concave transversely whereas in the living species it is flat. The tubercles on the ventral surface, just proximal to the distal facet, are a little better developed than in the Recent species.

Two examples of the third phalanx (Ph.III) are found in the holotype and in both the distal end is missing. They are similar to but smaller than the Ph.III in the Recent animal. Both appear to be symmetrical about the midline which suggests that they are from digit 3. At the proximal end the tubercles on either side are relatively better developed than in Recent Pedetes.

CHAPTER 6

Fragmentary pedetids.

In addition to the material of the better known pedetid species there is also material that either provides very little information about the species concerned or is so fragmentary that it is difficult to assign. Much of this material comes from Southern Africa but there is also material from the Kenyan Miocene sites and Beds I and II at Olduvai Gorge. More recent material has been found in the Ngaloba Beds at Laetoli and at a number of sites subfossil material of the Recent species has been found. The material described in this chapter is listed in Appendix VI.

c.f. Parapedetes namaquensis.

Amongst the material in the South African Museum there is a fragment of left mandible, isolated teeth and assorted post-cranial bones, probably from a single individual, catalogued as SAM-PQ 2121. This specimen was collected at Elisabethfeld in Diamond Area No.1 by G. Corvinus: it comes from the Red Sands. The site is that from which the type material of Parapedetes namaquensis was collected (Stromer, 1926) but this material shows an important difference in the cheekteeth which makes it difficult to ascribe it to Pa. namaquensis with any degree of certainty.

Fragment of left mandible (Table 6.I) :

This is complete except for the posterior part and is less massive than SAM-PQ-AD 1745 (see below). The lower masseteric tubercle is relatively well developed but, although better developed than in Pedetes, it is less well developed than in Megapedetes. The insertion of m. masseter medialis is high up the ramus, it is slightly curved and, posteriorly, it is continuous with the anterior edge of the coronoid process which arises at the level of the middle of m_2. There is a relatively pronounced masseteric crest that is a little better developed than in the living genus, especially close to the lower masseteric tubercle; it passes below the level of the incisive alveolus posterior to the position in Megapedetes. Most of the angle is missing but the base of the ventral edge is relatively thick: there does not appear to have been a distinct anterior process.

There are two openings of the foramen mentale: a small dorsal one near the medial edge of the ramus and a lateral one over the incisive alveolus. The symphysis is not produced below the incisive alveolus and does not produce any ventral protuberance in contrast to the small one found in Pedetes.

The coronoid process is S-shaped and rises slightly less steeply than in P. capensis, at the top it curves back to pass smoothly into the condyle. This is as in the Recent genus but there is less of a lateral overhang.

The cheekteeth all show a pattern of two separate lobes, which, with further wear, would join on the buccal side

leaving a lingual infold as in Pedetes and not a buccal infold as in Parapedetes (Stromer, 1926 ; also see Chap. 4). In each tooth the anterior lobe curves towards the posterior lobe which is straight. The teeth do not form tubercles in the lateral wall of the ramus, which is smooth.

Three incisor fragments (Table 6.II) :

These comprise the right lower and the two upper incisors: the lower one has a much greater radius of curvature than the uppers. In all three the enamel covers just less than half of the sides. In the lower incisor the antero-medial corner is sharper than the antero-lateral; on the anterior face, just on the medial edge, there is a tiny ridge that is closer to the edge than is the antero-lateral ridge in Megapedetes. On the anterior face of the upper incisor there is no trace of any ridges but as in the lower incisor the antero-medial corner is more sharply curved than the antero-lateral.

Isolated cheekteeth (Table 6.III) :

There are ten isolated cheekteeth which probably represent most of the remaining cheekteeth of this individual. Two upper premolars are present: they have a single root which curves anteriorly as in Pedetes. The occlusal pattern is bilobed with the anterior lobe smaller than the posterior: the lobes join on one side and the infold between them splays out slightly at the open end.

The right lower premolar is present; the anterior lobe is sharply convex anteriorly and is smaller than the posterior

lobe. This tooth appears to have had two roots, one anterior and one posterior, close together at their bases but separating towards their apices. The roots are closed. There is also a tooth that is probably a third molar: the posterior lobe is distinctly smaller than the anterior and the tooth has a single root that narrows to an apex and is closed. The remaining six teeth have roots like that in the third molar but they cannot be accurately placed in the jaws.

All these teeth show normal occlusal patterns. In some of them the adult pattern has been achieved: the occlusal surface is bilobed with the lobes, which are dentine-filled, joined on one side and the infold, which does not splay out significantly at the open end, filled with cement. Some of the teeth still show a more juvenile pattern with two separate lobes: each lobe is a dentine-filled ring; one is straight and the other curves toward the first on the side on which the median infold between the lobes is much shallower; the infold is cement-filled.

Vertebral column :

The remains of the centrum and part of the neural arch of a thoracic vertebra are preserved (Table 6.IV). It is similar to but smaller than in Pedetes and is probably from the posterior end of the series. The ventral surface of the centrum is concave antero-posteriorly: there is no transverse process visible; the zygapophysis is flat and the matapophysis is well developed. This all suggests that this vertebra is from the region of Th8 or Th9.

Five fragments of lumbar vertebrae remain but they are very small and damaged. These fragments probably come from the anterior end of the series; the two preserved fragments of centra, probably from a single vertebra, have a slight ventral median ridge: the base of the transverse process suggests that it was not well developed.

There are two main pieces from the tail: an isolated centrum (from the region of Ca3) and a complete vertebra (from the region of Ca7) (Table 6.IV). The more anterior centrum is relatively flattened and at the posterior end of the ventral surface there are two well developed tubercles providing a base for the chevron bone. There are two foramina in the dorsal surface of the centrum and these pass through to emerge on the ventral surface. In this vertebra the transverse processes are relatively robust and horizontal, they are aligned slightly posteriorly.

In the more posterior caudal vertebra, which is very similar to Pedetes, the neural arch is present but is low and elongated: the neural spine is vestigial. Both anterior and posterior zygapophyses are present as are metapophyses. On the ventral surface of the centrum there are two pronounced parallel ridges with a well developed tubercle at the anterior end of each. The transverse process forms a flat sheet that is indented in the middle almost to the centrum so that there are, effectively, separate anterior and posterior processes as in the living species.

Ribs :

There are 12 rib fragments which are essentially similar to those in Pedetes with flattened anterior and rounded posterior surfaces.

Clavicle (Table 6.V) :

A complete left clavicle is preserved as is the scapular end of the right clavicle. The clavicle is similar to Pedetes but the scapular end curves relatively further posteriorly and bears a distinct, lateral, facet for articulation with the acromion. The sternal end is as in Pedetes but is longer relative to its depth. The initial section of the bone is flat whereas in Pedetes there is a slight downcurve before the bone turns dorsally.

Humerus (Table 6.V) :

The proximal and distal ends of the right humerus are preserved but the distal end of the shaft is missing. This bone is similar to Pedetes. The lesser tuberosity is much better developed than in the living genus and from it a distinct ridge runs down the shaft. The delto-pectoral crest is well developed but is slightly narrower at the distal end than in the living genus. There is a well developed bicipital groove. Of the distal portion only the extreme end is preserved and it shows no special features.

Ulna :

The only remains of the ulna is the proximal end of the

right one. The olecranon process does not have a medial process but the medial edge is prolonged back to form a proximal process. Overall this end is like that of Pedetes except that the facet for the head of the radius is relatively not so hollowed out.

Radius (Table 6.V) :

A complete left radius and the proximal end of the right radius remain. This bone is generally like Pedetes. The proximal articulation for the humerus is oval rather than circular as in Pedetes: there is a well developed bicipital tuberosity which is set a little further distally than in the Recent genus. The shaft is curved and is flattened distally as in the living species. There is a groove towards the distal end as there is in Pedetes but in this animal the bounding ridges are more pronounced so that the groove does not seem so like a notch as in the living animal. The styloid process is as in the Recent species.

Manus :

The left scapho-lunar (Table 6.V) and centrale are preserved. Both are very similar to Pedetes. The centrale is minute and is still attached to the scapho-lunar on which the facets for the other carpals are indistinct. There is a well developed bar on the medial edge of the scapho-lunar and this bears a medial facet suggesting that a radial ossicle was present as in the living genus.

Metacarpals:- Two metacarpals were preserved: a right Mc.I (Table 6.V) and a left Mc.V; the latter is no longer extant but had proximal and distal articular surfaces as in Pedetes. Mc.I is very similar to the living genus: the distal articular surface is convex dorso-ventrally and narrower along the dorsal surface than along the ventral. Proximally there is a rounded ventro-lateral facet for the trapezoid and medial to this there is a longer facet and a proximo-medial tubercle with a small facet on its medial face.

Phalanges:- A first phalanx and a third phalanx also remain. In the first phalanx (Table 6.V) the proximal articulation has a median groove for the distal keel on the metacarpal and the bone bulges out on one side whilst it is straight on the other. Halfway down the shaft there are two tubercles on the ventral surface. The distal articulation is convex dorso-ventrally and very slightly concave transversely; it resembles the first phalanx in the pes of Pedetes rather than the manus. It is not known from what digit either this bone or the third phalanx come.

The third phalanx is very like that of Pedetes. There is a relatively pronounced proximal palmar process with a groove along the base on either side. The upper edge of the proximal facet is produced proximally, the facet is concave dorso-ventrally and flat transversely. The distal end of the bone curves down ventrally but the tip is broken off so that the detailed form is not known: on the palmar surface a slight ridge runs distally from the proximal process.

Distal left femur (Table 6.VI) :

This is very similar to the Recent genus, as far as can be seen, but it is very badly damaged. There was a sesamoid present above the lateral condyle, in the tendon of origin of m. gastrocnemius caput laterale.

Patella (Table 6.VI) :

This bone is isolated but is interpreted as a left patella, although this cannot be certain. It is triangular and more symmetrical than in Pedetes with the proximal corners more equally curved although the proximo-lateral is a little more angular than the proximo-medial. The bone is shorter compared with its breadth than in the living genus.

Tarsus :

Left calcaneum:- (Table 6.VI). The tuber calcis is as in Pedetes as is the primary astragalar articulation or central eminence although the lateral side is a little more hollowed out. There are facets on both the distal and medial faces of the central eminence. The dorsal part of the facet, passing distally from the central eminence, is relatively extensive. The sustentaculum is well offset from the main body of the bone and has the secondary articulation for the astragalus on its dorsal surface. The distal facet for the cuboid is as in the Recent genus and extends round onto the medial surface. The distal end is slightly damaged but there may have been a dorsal tubercle.

Right navicular:- (Table 6.VI). The general form is as in Pedetes. There is a cup-shaped facet proximally for the astragalus; the facet does not extend to the medial edge which is wide, projecting a little medially: the lateral edge is hollowed out and bears a facet where the proximal process of the cuboid fits. On the distal surface there are two large facets separated by a ridge: the concave lateral facet is for the third cuneiform, the flat medial facet is for the second cuneiform and is the longer dorso-ventrally.

The lateral face bears a large facet for the proximal process of the cuboid and, more distally, just adjacent to the distal facet for the third cuneiform, there is another small facet for the cuboid. At the ventral end of the distal facet for the third cuneiform there is a small tubercle which bears a very small lateral facet for the cuboid and a dorso-medial facet that is, in effect, a continuation of the distal facet for the third cuneiform. The medial wall of the navicular is well hollowed out below the level of the astragalar facet, presumably for the first cuneiform, but there are no facets visible. The plantar process is less well developed than in Pedetes and there is a plantar-lateral facet for a tendon.

Metatarsus :

Proximal right Metatarsal II (Mt.II):- (Table 6.VII). The lateral surface of the shaft is flattened as is the proximal part of the medial surface. There is no sign of a facet for

the distal end of the first cuneiform such as is found in Pedetes. The proximal end is set slightly obliquely and extends back to overlap the third cuneiform. Proximally on the lateral face there are dorsal and ventral facets articulating with the third cuneiform. Distal to these the lateral surface is roughened for a ligamentous attachment to Mt.III.

A proximal plantar process was evidently present but was not well developed and is damaged. The proximal facet is triangular, concave transversely and slightly convex dorso-ventrally. The lateral edge forms a slightly concave curve. The shaft has an axial twist.

Proximal Metatarsal:- (Table 6.VII). The shaft is strongly compressed transversely with one side very flat. The proximal plantar process is well developed, projecting beyond the articular facet proximally. This proximal facet is concave dorso-ventrally and convex transversely. The dorsal corner on the rounded side forms a slight tubercle and there appears to be a facet on the face of the plantar process on this same side. At the proximal end of the flattened side a ligamentous attachment seems to have been present but there is no tubercle.

This bone was originally assumed to be the right Mt.V but at that time it was noted that it resembles the Mt.I of Megapedetes pentadactylus very closely in that it lacks evidence of the normal articulation with an Mt.IV and has a clear proximal facet. Also the absence of a facet for the

distal end of the first cuneiform on Mt.II resembles the state in Megapedetes. On examination of the type material of Parapedetes namaquensis it was found that the articulated Mt.V are not at all similar to this bone (see Chap. 4). All the evidence suggests that this bone is a Mt.I.

Phalanx I (Ph.I) (Table 6.VII) :

This is possibly from left digit 5 and resembles similar bones in Pedetes but is smaller and more delicate. The shaft is curved and there is a pronounced proximo-dorsal tubercle.

Sesamoids :

A) in the tendon of origin of m. gastrocnemius caput laterale: this is as in Pedetes.

B) in the flexor tendon at the end of the metatarsal: similar to Pedetes but relatively quite deep.

Megapedetes c.f. pentadactylus :

Material collected at Arrisdrift includes three fragments that are pedetid. They come from Pit 2/AD8 and are ascribed by Corvinus (1978) to Parapedetes or Megapedetes. It is stated that this material is from an animal that is larger than the one still living. According to Corvinus (1978) the site at Arrisdrift is Late Lower Miocene with an age based on faunal dating of 14 - 18 million years b.p. The deposits were laid down by a river and are found in the old river channel

with the state of some fossils implying that they have not been extensively transported. This suggests that the site, at least in part, is sampling the fauna that was found in the area at the time. The large herbivores that were present at the time are predominantly browsers and not grazers which implies that there was more vegetation present than is now the case and it is suggested that riverine woodland was present (Corvinus, 1978). 27 species of mammal, all extinct, have been found at Arrisdrift with Prohyrax being the commonest form. The three pedetid fragments are described below and their measurements are given in Table 6.VIII. They are housed in the South African Museum.

SAM-PQ-AD 1745 : Left mandibular fragment :

The lower masseteric tubercle is large and is situated antero-laterally to the socket for pm_4. There is a well developed masseteric crest that runs postero-ventrally across the face of the ramus and passes below the level of the incisive alveolus anterior to the position in Pedetes. The foramen mentale has two openings that are positioned as in Megapedetes with the upper one near the lower masseteric tubercle and the lower one just above the incisive alveolus. The symphysis is well developed and forms a pronounced ventral process below the incisive alveolus.

The incisor has a sharp antero-medial angle and a more smoothly curved antero-lateral one. There is a slight ridge on the anterior face toward the lateral side but none on the medial edge. Enamel covers less than half of the sides and

covers rather more of the lateral face than of the medial.

SAM-PQ-AD 1746 : Isolated molar crown :

The crown pattern consists of two separate lobes. One lobe is straight while the other curves toward the first on one side of the tooth. The groove in the occlusal surface separating the two lobes is shallower on the side on which the lobes approach closely than it is on the other side. The tooth has been slightly worn so that any underlying cusp structure is not visible.

SAM-PQ-AD 1747 : Isolated molar :

This tooth is well worn but still has an occlusal pattern consisting of two separate lobes. As in SAM-PQ-AD 1746 the two lobes curve towards one another on one side of the tooth and the groove separating them is shallower on this side. Both lobes are simple, dentine-filled, enamel rings with no cusp structure. The median infold is not filled with cement.

The roots are damaged but there appear originally to have been three arranged triangularly with a single root in the middle of the side on which the two lobes converge and the other two roots, in line, on the other side of the tooth. All three roots are positioned close together and narrow toward their apices.

Gen. et sp. indet. :

Material of a second species of pedetid from the Lower

Miocene of Kenya was first described in Lavocat (1973). This material consisted of three cheekteeth from Rusinga Island which are described as being just like the teeth of Megapedetes pentadactylus but much smaller. Consequently they were ascribed to Megapedetes sp.. Van Couvering & Van Couvering (1976) lists this species as being present at Rusinga, Maboko and, questionably, in South West Africa but it does not specify the source of the information in the case of the latter two sites. There is some undescribed material in TILLMIAP that confirms the presence of a small pedetid in the Lower Miocene of East Africa. This material comes from sites at Rusinga and Maboko with one questionable piece from Fort Ternan. It can probably be ascribed to the same species as Lavocat's three teeth, which have not been seen, but the material is such that no definite allocation to genus is really possible.

KNM-Mb 429 : Small rooted cheektooth (Table 6.IX ; Fig. 6.1A) :

Collected 1973. The crown is complete and is made up of two transverse lobes that are completely separated by the groove which runs across the occlusal surface and which is very much shallower on one side than on the other. One lobe is made up of two cusps but the other shows no pattern. There are three roots: on one side there is a broad plate-like root while on each of the remaining two corners there is a tubular root.

KNM-Mb 431 : Half of a cheektooth crown (Table 6.IX) :

Collected 1973. There is one lobe and one enamel ridge

of the second lobe present. It is possible that both lobes were originally composed of two cusps but the wear and damage make it impossible to be certain. The groove between the two lobes is marginally shallower on one side than on the other.

Ru 362'52 : Incisor fragment with a small piece of bone attached :

The incisor is longer (antero-posteriorly) than it is wide (transversely) (Table 6.IX) and bears a slight ridge down one side of the anterior face. The attached bone is very badly damaged and it is impossible to tell whether it represents a piece of premaxilla or of mandible.

Ru 741'59 : Fragment of left upper incisor with a piece of the premaxilla attached (Table 6.IX) :

The fragment of the premaxilla includes the base of the zygoma which seems to be set relatively slightly further back than in Pedetes, more as in Megapedetes pentadactylus. The position of the zygomatic root, thrown so far anteriorly, suggests that the fragment is either pedetid or idiurine. However, the incisor is quite unlike any of those described in Lavocat (1973) for the anomalurids and the piece is identified as pedetid. Part of the incisive foramen is visible on the corner of the break: it is somewhat posterior to the incisive alveolus and was probably not set in a palatal groove. Internally, it opens into a groove that passes anteriorly, with a median ridge separating it from the groove on the right side. The base of the zygoma appears to have

been hollow internally.

Ru 700'56 : Two right calcanea (Table 6.X : Fig. 6.1B, C, D, E) :

In both of these specimens the distal end is broken off but in one (I) the break is much closer to the distal end than in the other (II). The tuber calcis is long with a process continuing the medial surface at the posterior end. This and the form of the primary astragalar articulation are almost identical to Pedetes. The sustentaculum is broken off in both specimens but it appears that it may have been offset rather more than in Pedetes thus resembling M. pentadactylus. On the plantar surface the groove for the tendon of m. flexor hallucis longus is slight. Distal to the primary articulation for the astragalus the bone is broader and less deep dorso-ventrally than in the living genus. On the dorsal surface the continuation of the facet for the astragalus is better developed than in Pedetes. The calcanea are about 60% of the size of the same bone in Pedetes and between 45% and 50% of the size in M. pentadactylus. Apart from the greater width across the sustentaculum the proportions appear to have been very similar to those in the living genus.

Ru 514'47 : Articulated proximal ends of right Mt.III and Mt.IV (Table 6.XI ; Fig. 6.1F, G, H, I) :

The triangular proximal facet of Mt.III is inclined slightly disto-medially to the shaft and extends to the tip of the well developed proximal plantar process, in contrast to the living genus. On the medial face of the shaft the

surface is roughened for the ligamentous connection to Mt.II and the slight tubercle is a little better developed than in Pedetes; the proximal ventro-medial corner of the plantar process bears a distinct tubercle. Most of the lateral surface is obscured by Mt.IV but it obviously bears a fossa for the tubercle of the latter. Proximal to the end of Mt.IV the dorsal corner of Mt.III forms a small process with a facet for the cuboid at its end.

Mt.IV bears a tubercle that articulates with the fossa on the lateral wall of Mt.III, and this tubercle is well separated from the proximal facet. It is thus relatively more distal than is usual in Pedetes and resembles M. pentadactylus. This positioning results in the transverse width of the bone appearing to be relatively less than in Pedetes in proximal view because the tubercle is not included in the width. The proximal plantar process curves medially and appears to articulate with that of Mt.III but the matrix in this region makes it uncertain. On the lateral surface of the shaft there is a fossa into which the proximal end of Mt.V fitted. The shaft appears to have an axial twist but is broken off too close to the proximal end for this to be certain.

Maboko, no number : Complete right Mt.II (Table 6.XI ; Fig. 6.2A, B, C, D) :

As in Pedetes the shaft has an anticlockwise axial twist when viewed from the distal end and it curves medially. It is basically cylindrical but has a flattened lateral surface.

Due to the curvature of the shaft the distal articulation is set obliquely, disto-laterally, to the longitudinal axis of the foot. The distal articulation is barrel-shaped with a median plantar ridge that continues onto the shaft for a short distance, proximal to the facet, curving medially and almost reaching the medial edge whereas in Pedetes it is straight. In dorsal view this ridge is just visible on the end of the facet. On the dorsal surface the proximal edge of the facet is marked by a transverse groove.

The proximal facet for the second cuneiform is concave transversely and very slightly convex dorso-ventrally. There is a proximal plantar process which is slightly wider than in Pedetes. The proximal part of the lateral face of the shaft is roughened and slightly hollowed for the ligamentous attachment to Mt.III. There is a proximo-plantar facet on the lateral face of the plantar process and the proximo-dorsal corner of the bone overhangs slightly and bears a facet on its underside: these two facets probably articulated with the medial surface of the third cuneiform as do the corresponding facets in Pedetes. On the medial surface there is a roughened area with a terminal facet: such a facet is found in Pedetes where it articulates with the end of the elongated first cuneiform. This suggests that the hallux may have been suppressed as in the living genus. There are two facets on the medial surface of the plantar process. Proximally, on the dorsal surface, a wide shallow groove runs disto-medially and results in the proximo-medial corner forming a ridge. This is not found in Pedetes.

Fort Ternan, no number, labelled FT/67 Level 4 : Phalanx I, probably from right digit 2 or left digit 4 (Table 6.XI) :

This bone is generally similar to Pedetes. The shaft is slightly flattened transversely and curves to one side distally. The distal facet is sharply convex dorso-ventrally with a very slight transverse concavity; it just extends onto the dorsal surface of the bone. Dorsally the transverse width narrows slightly and there is a slight fossa just proximal to the facet: on the ventral surface, just proximal to the facet, there are two pronounced tubercles; these are not at all well developed in Pedetes. The proximal facet is saucer-shaped with a deep median groove for the ridge on the metatarsal; the dorsal surface overhangs slightly. This bone would fit a bone such as the Maboko metatarsal but it is evidently from a slightly smaller animal.

Pedetes c.f. surdaster :

Material belonging to one of the Recent species of Pedetes has been found in Tanzania at both Olduvai Gorge and Laetoli. At both sites the material is very fragmentary and not sufficient to enable which of the Recent species is represented to be determined.

Olduvai Gorge:-

According to the notes made by Lavocat (Leakey, 1965 : 17 - 19) Pedetes is present in Upper Bed I at FLK N1.

However the accompanying Table (Table 2) lists the genus as present at FLK NN1 and not FLK N1. The genus is represented by only a few specimens. Material from other sites shows that the genus is also present in Bed II. There is one isolated molar from HWK, collected in 1962; 3 molars and 3 premolars from BK, collected in 1963, and 7 molars and 1 premolar from MNK, collected between 1963 and 1965: these teeth are all housed in TILLMIAP. In the BM(NH) there is a fragment of left mandible with pm_4 - m_2 that is labelled "Rabbit Tooth, Olduvai Bed II", there is no information about the site from which this piece comes.

Left mandibular fragment with pm_4 - m_2 (Table 6.XII) :

The ventral edge and all of the ramus posterior to m_2 are missing. Overall it is very similar to Recent specimens. The lower masseteric tubercle is quite small: the masseteric crest begins at this tubercle and is a little more pronounced than in the living animal, especially as it passes over the tubercle formed by m_1. The coronoid process arises at a level between m_1 and m_2 and its anterior edge is continuous with the distinct horizontal shelf, running posteriorly from the lower masseteric tubercle, that forms the insertion of m. masseter medialis. There are the usual two openings of the foramen mentale.

The cheekteeth form tubercles in the lateral wall of the ramus and are worn to the normal, bilobed pattern with the lobes joined buccally and the cement-filled lingual infold passing almost across the tooth. The anterior lobe of pm_4

is shorter bucco-lingually and longer antero-posteriorly than the posterior lobe: in this tooth the infold has a distinct buccal bifurcation. In m_1 and m_2 the lobes are subequal.

Isolated cheekteeth (Table 6.XII) :

These are just like the teeth of Recent Pedetes. The only pm_4 (067/517 from BKII) has a fold, anteriorly into the lobe, in the posterior enamel ridge of the anterior lobe.

Post-cranial bones (Table 6.XIII) :

There are two post-cranial bones in TILLMIAP: a left calcaneum (068/6547) and a left navicular (068/6550) both of which are labelled FLK.NN.TTII.VG. The left calcaneum has OLD 1960 560 written on it; the left navicular, OLD 1960 569. Both of these bones are very like those of living Pedetes.

Laetoli:-

There are two springhares specimens from the site of Hominid 18 at Laetoli. Material at this site is taken from the Ngaloba Beds, dated at 120,000 $\pm$ 30,000 years b.p. (Day et al., 1980). The two specimens are: Laet.'76 3907, the body of a left astragalus, and Laet.'76 3908, a right navicular (Table 6.XIV). Both of these pieces are the same size as in living animals and are also morphologically almost identical except that in the left astragalus the sulcus tali is a little less distinct than normal while in the right navicular the notch for the proximal process of the cuboid is less well developed and the ventral edge of the astragalar

facet is not down-curved. These two specimens are assigned to Pedetes c.f. surdaster as it is almost impossible on the basis of isolated post-cranial elements to distinguish the two modern species of the genus Pedetes. A more accurate identification is, therefore, not possible.

Laet.'75 1310 : Left mandibular fragment with pm_4 - m_3 (Table 6.XIV) :

This specimen is from Locality 8 and although supposedly from the Laetolil Beds it is unusually large for Pedetes laetoliensis.

The lower masseteric tubercle is not well developed but the insertion of m. masseter medialis is quite pronounced. The coronoid process arises level with the anterior lobe of m_2. There is no medial ridge in the diastema but the dorsal opening of the foramen mentale is large. The symphysis menti is massive with a well developed ventral process. On the lateral face of the ramus the masseteric crest is relatively well developed and the apices of the cheekteeth form distinct tubercles. Pm_4 does not possess an anterior invagination of the posterior enamel ridge of the anterior lobe.

This specimen is assigned to Pedetes c.f. surdaster because the general morphology especially the size and the presence of distinct tubercles over the apices of the cheek-teeth preclude its being P. laetoliensis. Unless further material of like type is found in the Laetolil Beds it seems more reasonable to assume that this fragment is not contemporary with the deposition of these beds and is either intrusive or

surface material that has become admixed with material genuinely from the Laetolil Beds.

Pedetes hagenstadi Lyle, 1931 (in Dreyer & Lyle, 1931).

This species was described on the basis of eight isolated cheekteeth from the site at Floris Bad in the Orange Free State, 30 miles NNW of Bloemfontein (Dreyer & Lyle, 1931). Since there is no evidence as to the exact provenance within the site for this material, except that it was probably not excavated from the undisturbed beds, it is not possible to give an accurate age for it, but the site as a whole is dated as Middle Stone Age on the basis of the artefacts found there (Dreyer & Lyle, 1931 ; Clark, 1955). The original description, which was based on a collection made in November 1928, did not give any indication of where the material was housed nor did it give any reference numbers by which the material could be identified. Cooke (1952) states that there was, in the South African Museum, material of P. hagenstadi from the Floris Bad spring deposits. However it does not make clear whether the material to which it refers was the type or merely additional material ascribed to the species. The reference catalogues of the South African Museum do not contain any reference to Pedetes hagenstadi and no material identified as belonging to this species was found during an examination of the collections. There is a reference to five cheekteeth, described as belonging to Pedetes caffer, collected by Dr. T.F. Dreyer, possibly in

1915, at Hagenstad Bath, O.F.S. This forms part of the Floris Bad site and the material is now referenced as SAM-PQG 3292. This specimen may, in fact, have been collected in 1917, not 1915, as stated in the catalogue, and possibly forms part of the collection, made by T.F. Dreyer in 1917 at the request of the South African Museum, which, according to Dreyer & Lyle (1931 : 5), was made from the bath itself. Cooke (1952) probably refers to this material which is assigned to P. hagenstadi because it came from the same site as the type material of that species. The statement at the beginning of Dreyer & Lyle (1931) that that paper was written on the basis of the 1928 collection means that this South African Museum material cannot be part of the type of P. hagenstadi and consequently the current whereabouts of the type is not known.

The teeth in the South African Museum consist of a left pm^4 ; a left m^2 ; a right pm_4 ; a right m_3 and a tooth that may be either a left m^1 or a right m_1 (Table 6.XV). They are all of the same order of size as the corresponding teeth in Pedetes capensis and have the simple bilobed structure with a deep median infold that is found in both of the living species. In m^2 and m_3 the posterior lobe is smaller than the anterior; in the other teeth the anterior lobe is the smaller.

There are some minor differences from P. capensis. In pm_4 the anterior lobe does not have a small anteriorly directed infold in the posterior enamel ridge as is normally the case in P. capensis. Since this is not found in every specimen of that species, only the vast majority, but is

never found in the other living species, P. surdaster, the significance of its absence in this single tooth is doubtful. In each tooth there is a slight vertical groove down the face that does not bear the deep infold; such a groove is often found in P. capensis but in the m1 it is much better developed than in the latter species. In this tooth it arises because the enamel covering this face does not form a complete sheet but has a gap in the middle as though it had developed from the anterior and posterior ends and had not quite joined in the middle. In this respect this is the only one of these teeth to resemble the description of the type of Pedetes hagenstadi.

Pedetes gracilis Broom, 1930.

Synonymy:

1930	Pedetes gracilis	Broom R. Nature 125 814
1934	Pedetes gracilis	Broom R. S. Afr. J. Sci. 31 476 - 477
1939	Pedetes gracilis	Broom R. Ann. Transvl. Mus. 19 316
1961	Pedetes gracilis	de Graaf G. S. Afr. J. Sci. 57 192
1963	Pedetes gracile	Cooke H.B.S. Table 6 (part), p. 92 In : Howell F.C. & F. Bourliere [Eds.] African Ecology and Human Evolution.

1967 Pedetes gracilis Cartmill M. Quaternaria 9 178

1978 Pedetes gracile Lavocat R. Table 5.1, p. 73
In : Maglio V.J. & H.B.S. Cooke
[Eds.] Evolution of African Mammals.

This species is known from a single specimen (Broom, 1939), the holotype, from Taungs in the Cape Province, 80 miles north of Kimberley. The holotype consists of a broken cranium which was found in a block of cave breccia together with four other species of mammal, all described as new by Broom (1930, 1934). This breccia was described as being associated with the type specimen of Australopithecus africanus, the Taungs child, but doubt has since been cast on whether the fauna in fact comes from the same level as the hominid (Howell & Bourliere, 1963 : 562). The original descriptions did not say where the material was housed but it is, in fact, in the Albany Museum, Grahamstown, where the P. gracilis holotype is catalogued as AM4194C.

Some doubt has been cast on whether P. gracilis is a valid name. Hopwood & Hollyfield (1954) state that they are of the opinion that it is definitely a nomen nudum. The initial mention of the name (Broom, 1930) simply stated: "Then we have remains of a small spring-hare which is quite a distinct species from the living one. This is being called Pedetes gracilis." Subsequently (Broom, 1934) the species was more fully described. The name is valid and takes the original date and authorship if the statement quoted above is considered to be a sufficient diagnosis. It can be argued that this was the case at the time of publication on the basis

that to ascribe the material to the genus Pedetes assumes that it possesses the characters of that genus and being the only form then known, apart from the living species, to describe it as smaller was sufficient to differentiate it from all other members of the genus. Thus the name will here be used with its original date and authorship – Broom, 1930.

Description (Fig. 6.2E):

The holotype cranium, AM4194C, is badly broken and almost entirely embedded in matrix. Much of what remains is in the form of a natural mould. The remaining bone is stained black but the enamel of the cheekteeth is still white. Measurements of this specimen are given in Table 6.XVI.

The enamel of the incisors is bright orange on the anterior face and the anterior part of the sides: this is probably not due to post-depositional staining as the enamel on the posterior edges of the sides of the incisors and the enamel of the cheekteeth has not been affected. Immediately behind the incisors the incisive foramina are set in a palatal groove. The lower maxillary root of the zygoma arises just posterior to the incisive alveolus: the posterior palatal foramina are set on the maxilla-palatine suture and appear to be much longer than in P. capensis. The cheekteeth are hypsodont and, apparently, rootless. They show the normal bilobed pedetid pattern but are narrower antero-posteriorly than in the living species.

Possible taxonomic relationships are discussed below.

CHAPTER 7

Family Pedetidae : Taxonomic considerations.

In any taxonomic consideration of a family there are two aspects that can be investigated: the intrafamilial relationships and the relationship of the family, as a unit, to other families within the same, higher-ranked, taxon. The present discussion will relate principally to the intrafamilial taxonomy of the Family Pedetidae and will involve diagnosis of the various species and genera and consideration of the evidence relating to their possible interrelationships. A short discussion of the possible relationships of the family to other rodents is also presented.

As mentioned in the introduction the Family Pedetidae forms a morphologically closely-knit group. It can be diagnosed by a suite of characters although many of these, individually, are found in other rodent families. The diagnosis of taxa, especially of relatively highly ranked taxa such as families, on the basis of individual diagnostic characters is at best difficult and generally proves to be impossible as has been shown in most classifications of rodents. Using a "diagnostic" character implies the belief that the character concerned has been uniquely derived in the taxon in question and is not subject to any parallelism or convergence (i.e. in cladistic terminology it is believed to be an autapomorphy of the taxon). Such characters may be found, and some examples will be given below, but in higher ranked taxa they are relatively uncommon and the

characterisation of such groups must normally be by the possession of a unique suite of characters. Thus the diagnosis of a higher taxon will normally be polythetic rather than monothetic. Polythetic diagnoses have the advantage of focussing attention on the organisms as complete biological entities whereas the use of monothetic diagnoses can easily result in the formation of a classification of characters rather than of organisms: this latter type of classification is, nevertheless, of great value as a key.

In the case of the fossil members of the Family Pedetidae their incomplete preservation means that the state of some characters may be unknown in some of the taxa. Such characters should, preferably, not be used in the formal taxonomic diagnoses but, in practice, it is not possible to ignore these characters and consequently where the character state is unknown in a taxon it is usually assumed to be the same as in the other taxa in the immediately higher ranked taxon. Examples of this will appear below. Because of this the formal diagnoses of the taxa must be subject to continual revision as new evidence comes to light and are to be considered as summaries of the more important characters of the taxa and not as definitions of those taxa. Similarly, only osteological characters have been used in the formal taxonomy because, as explained in Chapter 1, the state of characters of the soft anatomy cannot be known for the majority of pedetids and so the contrasts and similarities in these characters cannot be determined.

Family Pedetidae Owen, 1847 : new diagnosis.

Large, bipedal, saltatorial rodents. Cranium morphologically hystricomorph; mandible sciurognath. Nasals large (ratio of mean length of nasals : mean length of frontals > 75%); post-orbital process, temporal fenestra and origin of m. temporalis all very reduced; when present post-orbital process mainly composed of squamosal with only a small contribution from frontal; interparietal distinct; both parietal and inter-parietal contact mastoid bulla; auditory bullae inflated and appearing on dorsal surface of cranium; zygoma robust with large jugal that makes contact with lachrymal in preorbital bar; simple posterior process of squamosal runs in groove across mastoid; bony palate short, ending about level with m^2; posterior palatal foramina on maxilla-palatine suture; basioccipital with distinct ventro-lateral wings; incisors opisthodont, apex extending back to level of infraorbital foramen, enamel without grooves in anterior face; cheekteeth pm1/1, m3/3; pm molariform; all cheekteeth simplified with an occlusal pattern of two sub-equal lobes separated by a narrow transverse infold that penetrates from one side of the tooth almost to the other.

Vertebral column :- Ce7, Th12, Lu7, Sa2 - 3, tail long for balancing. Vertebrarterial canal present in Ce7; anti-clinal vertebra Th10 or Th11.

Forelimb shortened; humerus with well developed delto-pectoral crest.

Femur without trochanter tertius; tibia elongated; fibula very reduced but not normally fusing with tibia; metatarsals elongated but not fused.

Type genus : Pedetes Illiger, 1811

Included genera : Megapedetes MacInnes, 1957

Parapedetes Stromer, 1924

The Family Pedetidae, as discussed in Chapter 1, is morphologically distinct but of uncertain relationships within the Order Rodentia. A number of rodent groups have developed a bipedal, saltatorial mode of locomotion but the large size of the pedetids separates them from these other groups. Formerly the pedetids were associated taxonomically with a number of other groups of saltatorial rodents but it is now generally accepted that the similarities on which this grouping was based are adaptive similarities which do not provide good taxonomic information (Sclater, 1901). The development of saltation has involved changes in a number of characters and these may be examined separately: when this is done, and providing that care is taken, some taxonomic information may be obtained. Other characters, that are not directly related to adaptations for saltation, are also available for consideration and some of these can be used to support hypotheses of relationship.

Hystricomorphy of the cranium is an apomorphy that is shared with a number of other rodent groups. However there is considerable evidence that this apomorphy has arisen several times independently. Development of a hystricomorph cranium can be observed occurring within the Family Pseudosciuridae (Wood, 1974) which is but one example of an independent derivation of this character state. Given such

evidence the sharing of the apomorphy of hystricomorphy provides dubious evidence of relationship because the amount of parallelism is not known. Many authors (e.g. Lavocat, 1974; Wood, 1974) believe that those hystricomorphous rodents that are also hystricognathous are all relatively closely related on the basis of the synapomorphy of hystricognathy, in addition to other characters. These same authors accept that the hystricomorphous rodents that have sciurognathous mandibles are not closely related to the hystricognathous rodents. Sciurognathy is a plesiomorphy and can, therefore, provide no evidence of relationship and so, using only this evidence, there is no basis for believing that sciurognathous, hystricomorphous rodents are closely related to each other although the evidence does not preclude this.

The presence of nasals that are large relative to the frontals is very common amongst rodents, although comparatively rare amongst the Sciuromorpha. The pedetids display this condition which is the plesiomorphous state in rodents: consequently the character provides no help in elucidating possible relationships.

The presence of a post-orbital process in mammals is an advanced feature (Romer, 1966 : 188) and not a primitive retention of a post-orbital bar. Members of the early rodent Family Paramyidae possess an incipient post-orbital process of the frontal that is considered to be the homologue of the post-orbital process in sciurids (Wood, 1962b). The process is well developed in the sciurids but is reduced or absent in most forms: the absence of a distinct process is considered to be plesiomorphous. In Parapedetes there is no post-orbital

process while in Pedetes and Megapedetes a small post-orbital process is present but it is mainly formed from the squamosal with only a small contribution from the frontal. This state is considered to be apomorphous and the distribution of the states of this character is discussed below, in the section on subfamilies.

Both the temporal fenestra and the origin of m. temporalis, and thus, presumably, the muscle itself as well, are reduced in the pedetids. According to Wood (1962b) m. temporalis was large and an important jaw muscle in paramyids and the reduction of this muscle in pedetids can be considered as apomorphous. However this character may to some extent be correlated with the expansion of the auditory bulla which has restricted the space available for m. temporalis. The information on relationships that can be provided by this reduction of the temporal fenestra and m. temporalis must therefore be carefully considered to ensure that it is not simply acting as another means of expressing the fact of expansion of the bulla.

In the Family Pedetidae the interparietal remains distinct throughout life which by comparison with other mammals is shown to be plesiomorphous whilst fusion of the sutures resulting in the loss of a distinct bone, which occurs in a number of rodent groups, is apomorphous. Amongst groups in which the apomorphous state is found are the sciurids, hystricids, anomalurids and spalacids; this state is also found in some, but not all, bathyergids and this suggests that it may have arisen independently in several

families and thus not provide particularly sound evidence for possible relationships.

An inflated condition of the auditory bullae is an apomorphous state compared with the uninflated bullae normally found in rodents and other mammals. Inflation of the bullae is commonly found in rodents living in arid areas with very little vegetation (Oaks, 1968) and so has also come to be associated with a saltatorial mode of locomotion. Often only the tympanic bulla shows a pronounced degree of inflation and the extreme inflation of the mastoid bulla found in pedetids is more restricted in occurrence. The inflation of the bulla in pedetids results in the parietal and the interparietal both making contact with the mastoid. Contact between the interparietal and the mastoid bulla is not found in either the dipodids or gerbillines; there is contact between the parietal and the mastoid in dipodids and some gerbils (e.g. Pachyuromys). The presence of a squamosal process passing back across the inflated mastoid bulla is also a character correlated with the expansion of the bulla. In pedetids the process is simple in contrast to the position in dipodids in which the process is T-shaped. This process is believed to represent the remains of that portion of the squamosal that is positioned between the parietal and the auditory bulla in those forms in which the bulla is not inflated. Although these characters are correlated with the inflation of the bulla it is suggested that the contact of the bulla with both parietal and interparietal is apomorphous compared to contact with only the parietal and also that, if

the proposed origin of the squamosal process on the bulla is accepted, the simple process, as found in the pedetids, represents the apomorphous state. This can be explained if it is believed that the mastoid bulla expands and separates the suture of the squamosal and parietal anteriorly first and gradually separates these bones further back, the cross-bar on the process of the dipodids would then represent the posterior edge of the squamosal which made contact with the parietal dorsally. A simple process of the squamosal onto the mastoid bulla is also found in some dipodids (e.g. Cardiocranius) (Walker, 1975).

The presence of a large jugal in the zygoma is plesiomorphous as is the presence of contact between the jugal and the lachrymal in the preorbital bar (Gregory, 1920). This character cannot therefore provide any evidence on the probable relationships of the pedetids. A short bony palate is an apomorphy and the extremely short palate in the pedetids is very unusual amongst rodents but more closely resembles the position in lagomorphs. A comparison with other rodents shows that the palate normally terminates level with m^3 as it does in the paramyids (Wood, 1962b) or further posteriorly. The ending of the hard palate level with m^2 in pedetids is considered to be one of the most characteristic apomorphies of the family. The position of the posterior palatal foramina, on the maxilla-palatine suture, is apomorphous but is also very common in rodents except for a few of the most primitive (Wahlert, 1977 : 6).

Lateral wings of the basioccipital are found in a number

of rodents and seem to be common in the Sciuromorpha: they were also found in paramyids (Wood, 1962b) although the lateral wings referred to in that paper are different from what is meant by the term here where it refers to the prominent lateral processes of Wood. Gregory (1910) states that the feature is quite common and is correlated with enlargement of the bulla which would suggest that it is apomorphous; on the other hand the presence of lateral basioccipital wings in paramyids would suggest that their presence may be plesiomorphous. The difficulty in determining the polarity of the morphocline in this character is less serious than it might appear since the presence of distinct lateral wings of the basioccipital is sporadically distributed amongst the rodents suggesting that the character is subject to parallelism and consequently that it would be difficult to erect a hypothesis of relationship on it.

The upper incisors are strongly opisthodont in pedetids and arise at the level of the infraorbital foramen, the anterior enamel is without grooves except in foetal material of the modern species. Opisthodont incisors are apomorphous being derived from the slightly pro-odont incisors found in a number of rodents including the most primitive (Landry, 1957). The degree of opisthodonty is very high in pedetids. Incisors extending back into the maxilla to arise at the level of the infraorbital foramen are found in many rodents and this character state is therefore considered to be plesiomorphous: only in a small number of species (e.g. some bathyergids) has an apomorphous state evolved (the extension

of the incisor back into the pterygoid). Pedetids do not have any grooves in the enamel of the incisor and this state would normally be considered to be plesiomorphous but Parsons (1898) states that there are grooves present in the incisor enamel of a foetal specimen of P. capensis that he examined. Confirmation of this observation comes from specimen BP97 (an almost full-term foetus of P. capensis collected in Botswana) in which the upper incisors bear two faint grooves in the centre of the anterior faces. The presence of these grooves is of dubious taxonomic significance but may mean that pedetids are derived from a form in which the incisor enamel was grooved. However, it may also be nothing more than a developmental feature related to the way the incisor enamel is formed. Detailed embryological work would be required to determine which situation is the more likely.

The primitive number of upper cheekteeth in rodents is generally believed to be five, two premolars and three molars (Wood, 1962b). In many species this number is reduced and any reduction represents an apomorphy so that the presence of only four cheekteeth in pedetids is apomorphous. Nevertheless this provides little information of phylogenetic value since all the rodents in which there has been further reduction in the number of cheekteeth presumably passed through a stage in which there were four cheekteeth: this character, therefore, serves only to unite all those groups that show some reduction in the number of cheekteeth. There is also the problem that even in the most primitive rodents the most anterior tooth is very much smaller than the others

and consequently its loss may well have occurred a number of times independently. Likewise the molarisation of the premolar is an apomorphy that is found in most rodents and appears to have begun early in the evolution of the order.

The pattern of the cheekteeth in the pedetids, with each tooth made up of two lobes and little cusp structure present except in unworn teeth, is apomorphous. This type of pattern is found in the geomyoids and in the Upper Eocene genus Protoptychus although Wahlert (1973) states that in the latter genus the principal transverse infold (the mesoflexus) is formed in a different way from that in Pedetes. This is true on first observation but the description given of the mesoflexus in Protoptychus suggests that it is formed in the same way as in Megapedetes. According to Wahlert (1973) the teeth of Protoptychus can be readily compared with paramyid teeth suggesting that a form of cheekteeth similar to that in the pedetids can be derived relatively easily from the type of cheekteeth found in paramyids. However it seems unlikely that the pedetids are closely related to Protoptychus since there are detailed differences in the cheekteeth and the latter genus is apparently hystricognathous (Wahlert, 1973) : similarly it seems unlikely that the pedetids are closely related to the sciuromorphous geomyoids. It thus seems most reasonable to assume that the simplified tooth patterns seen in these three groups are independently derived from a primitive, possibly paramyid-like, tooth pattern.

The vertebral column does not provide very much taxonomic information as it is subject to considerable functional

selection in relation to the development of a saltatorial mode of locomotion. Similar vertebral columns can be seen in a number of other saltatorial forms (Hatt, 1932). As in all mammals, with the three exceptions usually quoted, there are seven cervical vertebrae and all, including the seventh, possess a vertebrarterial canal. This canal is present in the seventh cervical vertebra only in marsupials, Procavia, Cynocephalus, the hippopotamus and some rodents (Saunders et al., 1969). The presence of this feature might be thought to be primitive and its sporadic occurrence in mammals to be due to its retention in a small number of forms. However, Kielan-Jaworowska (1977) states that the absence of a vertebrarterial canal in Ce7 is plesiomorphous in therian mammals and so those groups in which such a canal is found must have acquired it secondarily and independently several times. The presence of a vertebrarterial canal in pedetids is thus apomorphous and might provide evidence of possible relationships but, unfortunately, the occurrence of this feature in rodents is not well reported.

The presence of 19 thoracico-lumbar vertebrae divided into 12 thoracic and 7 lumbar is stated in Hatt (1932) and Wood (1962b) to be plesiomorphous in rodents. This is the state found in pedetids. The anticlinal vertebra is Th10 or Th11 which is slightly anterior to the position given in Hatt (1932) and corresponds to the position found in quadrupedal rodents. This also is the plesiomorphous state for this character and means that the pedetids have not undergone modification in these features of the vertebral

column. Pedetids have a variable number of sacral vertebrae and the significance of this variation can best be considered in relation to the division of the family into subfamilies (see below). A long tail is required in saltatorial mammals to act as a balancing organ but is also found in paramyids (Wood, 1962b) and consequently must be assumed to be plesiomorphous in rodents. However the tail in pedetids is heavily built as well as being long and this latter is believed to be apomorphous and adaptively determined by the large size of the pedetids which would require a heavy balancing organ. This character thus does not provide information on the relationships of the pedetids since it is not known whether the tail could be said to be different in build, relative to the size of the animal, to the tail found in other saltatorial rodents.

The forelimb in pedetids, in common with other ricochetal mammals, has been relatively shortened and this state is considered to be apomorphous. However since this state has arisen in several rodent groups as well as a number of non-rodent groups it is assumed that it is subject to considerable convergent evolution and consequently the shared presence of this character state does not provide good evidence for possible relationships. The very large delto-pectoral crest found in pedetids is also an apomorphy but is adaptively determined by the requirements of burrowing. It is, therefore, probable that this character can provide little phylogenetic information at this level. Finally in the forelimb the presence of a radial ossicle in the carpus may

prove to be a characteristic feature of the Family Pedetidae but until it can be shown to occur in the fossil species this cannot be said. Pocock (1922) stated that the arrangement of the carpal pads, including the radial ossicle, in Pedetes was probably unique in living rodents. A similar arrangement of the carpus was probably found in the fossil species represented by specimen SAM-PQ 2121 on the basis of the evidence of the preserved scapho-lunar but until more is known of the carpus in other fossil pedetids it is not possible to use features of the radial ossicle as taxonomic characters within the family.

The greatly elongated hindlimbs of pedetids are a further apomorphy that is adaptive and related to the requirements of ricochetal locomotion. The principal elements elongated are the tibia and the metatarsals. In the femur, which is not greatly elongated, the trochanter tertius is absent and this is an apomorphy. In the lower leg the reduction of the fibula is an apomorphy and although found in all pedetids is more advanced in Pedetes and Parapedetes than it is in Megapedetes. This suggests that this reduction has occurred at least twice within the Family Pedetidae and is therefore subject to parallelism. Pedetids possess a linear astragalus which contrasts with the marked angle between the body and the head and neck in other rodents including paramyids (Wood, 1962b). This feature is considered to be an apomorphy of pedetids. The absence of fusion between the metatarsals is plesiomorphous and contrasts with the position in the dipodids.

The discussion above shows that while the morphological

characters given in the diagnosis of the Family Pedetidae serve together to distinguish the family from other rodents many of them provide little help in determining the possible relationships of the family. Some of the characters used in the diagnosis of the pedetids are plesiomorphies which cannot be used to determine phylogenetic relationships. Of the apomorphies used in the diagnosis a number can be shown, with some degree of certainty, to be the subject of convergence or parallelism and both of these restrict the phylogenetic information content of the characters although the former does so very much more than does the latter (Simpson, 1961). There are, therefore, only a few characters left that may contain useful phylogenetic information at the family level. Partly this is due to the fact that the fossil forms are not completely preserved: thus many characters cannot be used because it is not known whether they possess a single state at the family level. Also the value of characters from the post-cranial skeleton is reduced because so little information is available on the distribution of these characters amongst other rodents and other mammals so that morphocline polarities are difficult or impossible to determine and the range of taxa sharing particular apomorphous states cannot be ascertained. The failure of mammalogists to make proper use of the characters in the post-cranial skeleton has been noted by Szalay (1977) and Lavocat (1974) has pointed out the paucity of information on the post-cranial osteology of rodents.

On the basis of the characters given in the diagnosis of the Family Pedetidae there seems to be no basis for classifying

the pedetids as particularly closely related to any other rodent group. Further knowledge of fossil forms, especially pre-Miocene forms, may enable an analysis of comparative osteology to produce a clearer view of possible pedetid relationships. On the present evidence there seems to be no basis for arguing against the belief that the pedetids evolved directly from the most primitive of rodents independently of other later groups of rodents.

A number of characters, mainly of the Recent species, have been used by other authors in an attempt to determine pedetid relationships and many of these have already been outlined in Chapter 1. These characters have not been used here because their state is either unknown or unknowable in the fossil species and the practice of taking modern species as representative of a family that contains a majority of fossil forms is considered to be of dubious value. However given this caveat these characters can now be considered to see if they can provide any clues to possible pedetid relationships.

Characters in the reproductive system have been considered by several workers and produce equivocal results. Fischer & Mossman (1969) believed that the structure of the foetal membranes suggested that the pedetids are highly specialised sciuromorphs but that there seemed to be no reason to believe that they were closely related to the anomalurids. Luckett (1971) investigated the foetal membranes of the anomalurids and pointed out that there are a number of similarities with pedetids but suggested that these were plesiomorphies which would mean that they do not imply a close relationship. As

discussed in Chapter 1 Wood (1974) has pointed out the care that must be used in interpreting the phylogenetic information that may be available from foetal membranes. Coe (1969) examined the reproductive system of Pedetes and suggested that there were similarities with the anomalurids but also pointed out that further work was required on both groups, this suggestion has not been taken up to any extent. Work on the chromosomes has also not, as yet, provided any evidence for the possible relationships of pedetids (George, 1980).

Guthrie (1963 & 1969) examined the carotid circulation in a number of rodent groups including the pedetids (using the Recent Pedetes as representative) but did not examine any anomalurids. The pattern of the vessels found in Pedetes was unique amongst those rodents examined but it was suggested that a similar pattern might be found in anomalurids. Bugge (1974) has criticised some of this work on the grounds that it concentrated too much effort on the origin of the internal maxillary artery and contained a number of mis-interpretations. Both pedetids and anomalurids are investigated in Bugge (1974) and the cephalic arterial supply is found to be very similar in both groups and to support a relatively close relationship of these two families but also suggests that this group, of anomalurids plus pedetids, had an independent origin from the paramyids. George (1981), in an examination of post-cranial blood vessels in rodents, states that the conclusions of Bugge (1974), in respect of the anomalurids and pedetids, are not contradicted.

The work on the middle ear discussed in Parent (1976) also supports a close relationship of the pedetids and anomalurids although it is stressed that it could not be claimed that one family was the ancestor of the other. The structure of the incisor enamel has been examined in Pedetes but not in the fossil forms, although there is no reason why this should not eventually be done. In Pedetes the enamel is multiserial whilst in anomalurids the enamel is uniserial (Wahlert, 1968 : Table 5). Both these types of enamel are believed to be derived from the pauciserial type of enamel, found only in primitive rodents, and consequently this character provides evidence against a close relationship of pedetids and anomalurids. Lavocat & Michaux (1966) also states, on the basis of the structure of the unworn cheek-teeth, that there is no evidence for a close relationship of pedetids and anomalurids.

Finally Hoogstraal (1972) examines the ticks of the genus Haemaphysalis found on Pedetes. It concludes that the ticks on Pedetes represent a new species, restricted to the genus, and that they appear to be more closely related to one of the Palaearctic groups of ticks than to the more recent group that is now found in the Ethiopian region.

To conclude it thus seems that the situation, with regard to the possible position of pedetids within the rodents, is only a little improved over that found in Simpson (1945). However, work since that time has provided further evidence suggesting that there is a closer relationship between the pedetids and the anomalurids than there is between the pedetids and any other rodent group: this is not to say that

the pedetids and anomalurids have only recently separated. Rather it would appear that the two families have been long separated and their common ancestor was probably little advanced from the primitive paramyid state. Only by such a view of the evolution of the two groups can the apparent contradictions of, for example, the incisor enamel structure and the cephalic arterial system be explained with the former character showing divergence along two different pathways from the primitive state and the latter character showing evolution along the same specialised pathway. Some morphological characters, such as the anteriorly displaced zygoma in some pedetids and anomalurids, are then explained as parallelisms rather than convergences which is also a more satisfactory view since parallelism is to be expected in groups sharing a common ancestry (Szalay, 1977). Information from the post-cranial skeleton cannot be properly fitted into the scheme as the detailed information on the skeleton in all anomalurids is not known and so the distribution of character states cannot be determined. Hopefully further evidence from the fossil record will be forthcoming which will enable an idea to be formed of the pre-Miocene evolution of both the pedetids and the anomalurids. Only with such evidence does there seem to be much chance of providing a soundly based conclusion on the relatedness of pedetids and anomalurids.

Subfamilies :

The Family Pedetidae appears to be comprised of two evolutionary lines and so can be formally subdivided,

taxonomically, into two subfamilies. These two subfamilies can be diagnosed as below.

Subfamily Pedetinae Owen, 1847 : new diagnosis.

Pedetids in which the lower maxillary root of the zygoma is displaced anteriorly and positioned close to the incisive alveolus; incisive foramina positioned closer to incisors than to cheekteeth; sides of external nares either open or enclosed by lateral wings of the nasal bones; cranium broad across frontals without a pronounced interorbital constriction; frontals with median depression in dorsal surface; small post-orbital process present, composed mainly of squamosal bone with only a small contribution from the frontal; origin of m. masseter lateralis extending onto lateral surface of zygoma; jugal not extending posterior to squamosal root of zygoma; external acoustic meatus ossified; vertical foramina present in basisphenoid and/or basioccipital; cheekteeth with transverse infold penetrating from lingual side in lower jaw and from buccal side in upper jaw.

In mandible foramen mentale with two openings, a dorsal one anterior to pm_4 and a lateral one just behind incisor; ventral edge of angle not especially thickened.

Lesser tuberosity of humerus without pronounced ridge running ventrally from it; innominate bone with well developed ischial tuberosity; femur with very high trochanter major; pes mesaxonic (digit 3 dominant); Mt.V not reduced to a thin splint as in Parapedetinae; phalanx I of pes not curved, longitudinally concave, ventrally; ungual phalanx of pes short and hoof-like.

Type genus : Pedetes Illiger, 1811

Included genus : Megapedetes MacInnes, 1957

Subfamily Parapedetinae subfam. n. :

Pedetids in which the lower maxillary root of the zygoma arises just anterior to pm^4; incisive foramina set in a slight palatal groove and positioned slightly closer to cheekteeth than to incisors; sides of external nares enclosed by wings of the premaxilla bones; premaxillae edge nares but do not overlap them; cranium with pronounced interorbital constriction; frontals without median depression in dorsal surface; post-orbital process absent; groove for m. temporalis very reduced; lachrymal forms preorbital process; origin of m. masseter lateralis almost completely restricted to ventral edge of zygoma; posterior maxillary notch well developed; bony pterygoid fossae absent; foramen ovale small; external acoustic meatus unossified; no vertical foramina through either basisphenoid or basioccipital; incisors deep antero-posteriorly and narrow transversely, uppers with medial ridge on anterior face; cheekteeth semi-hypsodont with transverse infold penetrating from the same side, the buccal, in both upper and lower teeth; roots of cheekteeth open but eventually closing in old animals.

In mandible foramen mentale single with only a lateral opening present; masseteric crest relatively well developed; angle of mandible projects well posterior of condyle and has very thick ventral edge.

Cervical vertebrae not fused; sacrum made up of three fused vertebrae; acromion of scapula of equal width through-

out its length; lesser tuberosity of humerus well developed with distinct ridge running ventrally from it; entepicondylar foramen present; olecranon process of ulna with distinct medial process.

Innominate bone with poorly developed ischial tuberosity; femur with trochanter major lower than in Pedetinae; trochanter major with large tubercle on anterior face; fibula reduced; in calcaneum sustentaculum tali well developed and distinctly offset medially; plantar process of navicular short and rounded; pes paraxonic (digits 3 & 4 about equally developed); Mt.III not articulating with cuboid; Mt.V very reduced, to a thin splint; phalanx I of pes curved longitudinally concave ventrally; ungual phalanx longer and more claw-like than in Pedetinae.

Type and only included genus : Parapedetes Stromer, 1924

The diagnoses of the two subfamilies clearly show the major differences between these two taxa. For the purposes of a key further comment would not be necessary but for a formal taxonomy that is intended to represent the phylogeny of the taxa some evolutionary consideration should be given to the character states. In the case of the Subfamily Pedetinae it is necessary to show that the two included genera possess synapomorphies that they do not also share with Parapedetes while in the case of the Subfamily Parapedetinae it is necessary to show that Parapedetes possesses autapomorphies within the Family Pedetidae. The important characters and their states are summarised in Tables 7.I & 7.II.

The position of the lower maxillary root of the zygoma, arising just anterior to pm^4, in the parapedetines contrasts with the position in the pedetines in which the root is displaced anteriorly. An outgroup comparison with other rodents suggests that the character state in parapedetines is plesiomorphous. Pedetines possess a synapomorphy in the anterior displacement of this root and this is only paralleled amongst living rodents in the anomalurid genus Idiurus in which a similar anterior displacement occurs. This synapomorphy supports the uniting of Pedetes and Megapedetes in a single taxon: Idiurus is not included in this taxon and its possession of this apomorphy in the zygoma is believed to be due to parallelism. In the case of the incisive foramina the character state distribution is similar to that for the lower maxillary root of the zygoma with the relatively more posterior position in the parapedetines being plesiomorphous and the more anterior position in the pedetines being a synapomorphy. Within the Subfamily Pedetinae both the zygomatic root and the incisive foramina can be further considered in the separation of the genera and this is discussed below.

The development of premaxilla wings above the incisive alveolus and enclosing the sides of the external nares in parapedetines is believed to be plesiomorphous although the determination of this morphocline polarity is suspect and consequently undue weight should not be given to this character at this stage. In the pedetines there are no premaxilla wings and in Megapedetes the sides of the external nares are open while in Pedetes lateral wings of the nasal

bones are found. Both these conditions are considered to be apomorphous at this level and the loss of premaxilla wings is, thus, felt to be a synapomorphy of the pedetines. Further discussion of this character can be deferred as it can be used in the separation of genera within the Subfamily Pedetinae. The proposed character state distribution at this level suggests possible support for the hypothesis of relationship shown in Fig. 7.1.

In the pedetines the cranium is very broad across the frontals and this state is contrasted with the narrow inter-orbital region in the parapedetines. The character state in the pedetines is believed to be plesiomorphous and that in the parapedetines is apomorphous. This distribution supports the distinction of the parapedetines as a separate taxon but provides no basis for the formation of a Subfamily Pedetinae. As a contrast, the presence of a depression in the frontals is considered to be a synapomorphy of the pedetines and the absence of such a depression in parapedetines is believed to be plesiomorphous.

Within the Family Pedetidae the presence of a post-orbital process made up largely from the squamosal is considered to be apomorphous and, being found in the pedetines, is a synapomorphy of the Subfamily Pedetinae. The absence of a post-orbital process in the parapedetines is considered to be plesiomorphous being similar to the position in a number of paramyids. The incipient post-orbital process found in a number of paramyid genera is considered to be the homologue of the sciurid post-orbital process which is made up of the frontal bone (Wood, 1962b) and not the squamosal bone.

According to Wood (1965b) the primitive origin of m. masseter lateralis in rodents was a fossa occupying the ventral third of the zygomatic arch. In the pedetines this origin is essentially unmodified in extent but in the parapedetines the origin is more restricted and m. masseter lateralis arises only from the ventral edge of the arch except for a small slip at the posterior end of the zygoma. The position in parapedetines is thus considered to be apomorphous and derived from the more primitive arrangement still found in the pedetines. The character state distribution is, therefore, in support of the distinction of the parapedetines.

In the pedetines the posterior end of the jugal does not extend posterior to the squamosal root of the zygoma. This is the state in most living rodents and also the paramyids (Wood, 1962b) and is, consequently, interpreted as the plesiomorphous state. The jugal in parapedetines extends beyond the squamosal root of the zygoma in a manner that resembles lagomorphs and thus displays an apomorphy that, within the Family Pedetidae, is an autapomorphy of the Subfamily Parapedetinae.

The presence of an unossified external acoustic meatus in parapedetines may represent a plesiomorphy but it is found that the external acoustic meatus is ossified in most living rodents and also in the other pedetids. However, in most paramyids the bulla itself is not ossified (Wood, 1962b) although this is not the case in Reithroparamys which is believed to have been ricochetal. Also the degree of ossification is less in Megapedetes, which is more primitive

in a number of other characters, than it is in Pedetes. It therefore seems most reasonable on the basis of present evidence to accept the suggested morphocline polarity with the unossified state in the parapedetines being considered plesiomorphous and the state in the pedetines being apomorphous. The fact that an ossified external acoustic meatus is found in most living rodents suggests either that the state evolved early in rodent evolution or that it has arisen independently in a number of lines; it may well be that there has been a combination of the two.

Neither Hill (1935) nor Wahlert (1974) in their work on the cranial foramina of rodents describe any midline foramina in the basisphenoid or the basioccipital. Foramina are not present in this region in parapedetines but are found in one or both of these bones in the genera in the Subfamily Pedetinae. Median foramina in these bones do not appear to be common in either living or fossil rodents which would suggest that the absence of such foramina is plesiomorphous and their presence is apomorphous. Assuming this polarity for the morphocline the presence of a median foramen in the basioccipital is a synapomorphy of the genera in the Subfamily Pedetinae: a second synapomorphy may exist in the presence of a foramen in the basisphenoid but since this bone is not preserved in Megapedetes this cannot be determined.

The pattern of the cheekteeth is normally reversed in the lower jaw as compared to the upper (Stehlin & Schaub, 1951) and this is considered to be the primitive arrangement. Thus the pattern of the cheekteeth displayed by the pedetines is plesiomorphous in this feature as the transverse infold

penetrates from the opposite side in the upper and lower teeth. The state in parapedetines with the transverse infold penetrating from the same side in both jaws is an apomorphy and clearly distinguishes the parapedetines from the pedetines. However a similar apomorphy is found in a few other rodents (Stromer, 1926) although given the weight of evidence associating the parapedetines with the pedetines it must be assumed that other rodents also displaying this apomorphy in the cheekteeth have acquired the character independently. Within the Family Pedetidae the non-reversed pattern of the cheekteeth found in the Subfamily Parapedetinae must be considered an autapomorphy of the subfamily.

In the mandible the foramen mentale is usually single in rodents and this is believed to represent the plesiomorphous state. However Wood (1962b) states that some specimens of Paramys possess two openings for the foramen mentale while others possess one. When two foramina are present they are both lateral with one below pm_4 and the other further anterior, often the posterior opening is very small. The anterior of the two lateral openings of the foramen mentale in these paramyids probably corresponds to the lateral opening found in all the pedetids. The dorsal opening of the foramen in the diastema anterior to pm_4 which is found in the pedetines would not seem to be homologous with the small posterior lateral opening in the paramyids and so should be considered an apomorphy. This apomorphy probably characterises the Subfamily Pedetinae but since the mandible in Parapedetes is poorly preserved it is not possible to be certain that this genus did not also possess two openings for the foramen

mentale and if this were to prove the case then the character would be an apomorphy of the Family Pedetidae rather than just one of the subfamilies. The value of this character must, therefore, remain uncertain on the basis of available evidence.

Also in the mandible the ventral edge of the mandibular angle is extremely thick in the parapedetines. This edge forms the insertion of m. pterygoideus internus medially and of m. masseter superficialis laterally and is, to some extent, thickened in all rodents. The degree of thickening in the parapedetines is exceptional and is considered to be apomorphous whilst the pedetines possess a normally thickened edge and thus display a symplesiomorphy.

In the humerus of the parapedetines there is a well developed ridge running ventrally from a relatively well developed lesser tuberosity. This ridge is not found in the pedetines but is present in SAM-PQ 2121 (see below) and it is considered to be an apomorphy characterising the Subfamily Parapedetinae. Its presence is related to the development of m. teres major (see Chap. 8) and forms the insertion for this muscle: in the pedetines, in place of this ridge, there is a low tubercle and this is the plesiomorphous state within the Family Pedetidae.

The ischial tuberosity is well developed in the pedetines and this probably is, at least in part, related to functional considerations (see Chap. 8). However this character can also be used as a taxonomic character at this level and the condition in the pedetines would then represent an apomorphy. A poorly developed ischial tuberosity such as is found in the

parapedetines is the plesiomorphous state of this character and is found in most rodents. The distribution of character states in this case supports the uniting of Pedetes and Megapedetes within a single taxon.

A high trochanter major of the femur is another character that has a significance in functional terms but that can be used as a taxonomic character. The very high trochanter major in pedetines is apomorphous and represents a synapomorphy that unites the two genera that have been placed in the Subfamily Pedetinae. The lower trochanter major of the parapedetines more closely resembles that found in other rodents and is considered to show a plesiomorphous state within the Family Pedetidae. In the pes, however, a reversed character state distribution is found with the pedetines possessing a symplesiomorphy in the presence of a mesaxonic foot. The dominance of digit 3 in the pes is found in many rodents as well as in many other groups of mammals and so must be considered plesiomorphous. A paraxonic pes such as is found in parapedetines is, therefore, to be considered apomorphous and in this case is an autapomorphy characterising the Subfamily Parapedetinae

Some reduction of digit 5, and especially of Mt.V, is found in all pedetids but the extent of this reduction is very much greater in the parapedetines than it is in the pedetines. This extreme reduction is apomorphous within the family whilst the state in the pedetines is plesiomorphous. The character state distribution therefore supports the separation of the parapedetines from the other pedetids but does not provide evidence in favour of the creation of the

Subfamily Pedetinae.

Finally two other characters are also found in the pes and these involve Ph.I and the ungual phalanges. In the pedetines Ph.I is not curved longitudinally and concave ventrally but is flat and this is believed to be the apomorphous state. Parapedetines have a curved Ph.I and thus display the plesiomorphous state. The same distribution is found in the ungual phalanges in which the hoof-like form of the pedetines is apomorphous and the more claw-like form of the parapedetines is plesiomorphous. Both these characters thus serve to unite the two genera that have been placed in the Subfamily Pedetinae by the possession of a synapomorphy.

Of the characters discussed above 10 are synapomorphies possessed by the two genera in the Subfamily Pedetinae but not by the Subfamily Parapedetinae and they serve to support the hypothesis of intrafamilial relationships proposed in Fig. 7.1 at the level of the first dichotomy. A further eight characters are autapomorphies of the Subfamily Parapedetinae and these support the validity of a separate taxon at this level for the genus Parapedetes. Finally a further three characters provide information the value of which is suspect because in two of them the state of the character in one of the genera is unknown or uncertain and in the other one there is considerable doubt about the polarity of the morphocline or even whether a true morphocline exists (this is the character of the enclosure of the sides of the external nares). The most parsimonious way of explaining these character distributions is according to the phylogeny of Fig. 7.1 and so this phylogeny must be preferred

on the basis of this evidence. However, the characters discussed above are those in which the Subfamily Pedetinae is known to possess a common state and thus it should be expected that all the synapomorphies supporting the creation of the Subfamily Pedetinae will have been discussed. In addition to the above characters there are many others the distribution of which must be considered to see whether they contradict the hypothesis of pedetid phylogeny proposed. Some of these characters are of importance in the analysis of the relationships of the genera Pedetes and Megapedetes within the proposed Subfamily Pedetinae and the discussion of these characters is postponed to the section on genera below: others of these characters can be discussed here and these are those characters which either are not preserved in one of the genera or are unable to provide useful taxonomic information. These characters and their states are summarised in Table 7.I.

The first of these characters is the presence of a posterior maxillary notch, which is plesiomorphous (Wahlert, 1978 : 12), in the parapedetines. Such a notch is not found in Pedetes although some specimens may possess a small posterior maxillary foramen: the state in Pedetes is apomorphous. In Megapedetes this region of the cranium is not preserved in any known specimen and so the character cannot provide any evidence on relationships. If Megapedetes resembled Parapedetes then the character state distribution would be such that the character is of no value at the subfamily level but would be of value within the Subfamily Pedetinae. If Megapedetes resembled Pedetes on the other

hand the synapomorphy thus displayed would support the hypothesis of a valid Subfamily Pedetinae.

In the pterygoid region the presence of distinct pterygoid fossae is believed to be plesiomorphous since such fossae are found in most rodents and were present in paramyids although in Paramys they were less well developed than in later rodents and the lateral edge was not always clearly delimited; the medial pterygoid process is, however, well developed (Wood, 1962b). Pterygoid fossae are found in Pedetes but not in Parapedetes in which even the medial pterygoid process is extremely reduced and the state in the latter genus is considered to be apomorphous. The state of this character in Megapedetes is not at present known as this region is not preserved in any of the known fossils but if there were pterygoid fossae in this genus then the character would support the separation of the parapedetines but provide no information on the relationships of the pedetines. The absence of pterygoid fossae in Megapedetes would be a synapomorphy with Parapedetes and would be inconsistent with the proposed hypothesis of relationships within the Family Pedetidae.

Also in the pterygoid region the presence of a small foramen ovale is plesiomorphous and this state is found in the parapedetines. Pedetes possesses a large foramen ovale which is apomorphous but once again this region is not preserved in Megapedetes. As with the posterior maxillary notch the possession by Megapedetes of a small foramen ovale would provide no information on the phylogeny at the level of the subfamily while its possession of a large foramen

would creat a synapomorphy supporting the validity of the Subfamily Pedetinae.

The presence of ridges on the anterior face of the incisor is considered to be apomorphous and consequently in this character both Megapedetes and Parapedetes possess an apomorphy while Pedetes shows the plesiomorphous state. However Megapedetes possesses a lateral ridge on the incisor while Parapedetes possesses a medial ridge and it is therefore unlikely that the ridges are homologous in the two genera. This suggests that within the family incisor ridges have developed independently in Megapedetes and Parapedetes and while the character suggests that the acceptance of three genera is justified it provides no evidence on their interrelationships since there is no synapomorphy to be found.

A well developed mandibular angle that projects posterior to the condyle is found in many rodents and is believed to be plesiomorphous: this is the state found in parapedetines. Pedetes has a very reduced angle which is apomorphous but the angle is not completely preserved in Megapedetes. From the remains known the angle in the latter genus would appear to have been better developed than in Pedetes but not to have projected beyond the condyle. If this proves to be the case then this character would be further evidence in favour of the validity of the proposed hypothesis that there are two subfamilies.

In the post-cranial skeleton the development of the scapular acromion is different in the pedetines, in which it broadens out at the level of the glenoid, from in the parapedetines, in which it is more rod-like. As Lavocat

(1974) points out the post-cranial osteology of rodents is not particularly well known and consequently there is insufficient information available on this feature to make the determination of the morphocline polarity at all certain. However Wood (1962b) states that in some paramyid genera the acromion is large with a well developed metacromion and the illustrations in this paper suggest a resemblance to the acromion in the pedetines which is, therefore, considered to represent the plesiomorphous state within the Family Pedetidae. The parapedetines then possess the apomorphous state of this character which supports their distinction from the other pedetids but cannot provide evidence on their position within the family.

Of these additional characters three may turn out to be synapomorphies supporting the existence of the Subfamily Pedetinae and cannot provide evidence against this subfamily: one may turn out to be of no value at the subfamily level when the morphocline polarity is more definitely determined: one may contradict the hypothesis of relationship or provide no evidence and the last, the presence of incisor ridges, can provide no useful phylogenetic information. This means that there is still no positive contradictions of the proposed phylogeny and its taxonomic equivalent which provides the most parsimonious way of explaining the evolution of the character state distributions.

Genera :

The Subfamily Parapedetinae contains only a single genus

namely the type genus Parapedetes Stromer, 1924 and this genus, in turn, is monotypic and only contains its type species Pa. namaquensis Stromer, 1924. Thus it is not possible to differentiate specific, generic and subfamilial characters and all the characters to be considered are included in the diagnosis of the subfamily. The discovery of further taxa within this subfamily would necessitate extensive modification of the diagnosis since it would become possible to determine whether some of the characters used are valid at the subfamily level. Until this occurs the taxonomic discussion of the Subfamily Parapedetinae fixes the taxonomic position of the taxa included in the subfamily without need for further consideration.

The Subfamily Pedetinae contains two genera and, therefore, the subfamilial diagnosis only refers to characters that have a common state in these genera. The two genera can be separately diagnosed as below.

Genus Pedetes Illiger, 1811 : new diagnosis.

Pedetines in which the premaxillae edge but do not overlap the nasals; nasal bones with lateral wings enclosing the sides of the external nares; median depression in frontals restricted to anterior half; groove for m. temporalis shallow; anterior edge of preorbital bar straight; lachrymal not forming a significant preorbital process; jugal not contributing to glenoid fossa; lower maxillary root of zygoma arising immediately posterior to incisors and passing back more horizontally than in Megapedetes; incisive foramina set in a palatal groove and positioned immediately posterior to

incisors; incisors without ridges on anterior faces and about as wide transversely as they are deep antero-posteriorly; cheekteeth semi-hypsodont or fully hypsodont.

In mandible lower masseteric tubercle not well developed; masseteric crest not pronounced; slight bony ventral projection below symphysis menti.

Humerus with medial epicondyle having dorsal hook-like process; entepicondylar foramen present; olecranon process of ulna with distinct medial process.

Sacrum composed of three fused vertebrae; fibula reduced; astragalus with sulcus tali not continuous with median groove of trochlear surface; sustentaculum tali of calcaneum reduced; plantar process of navicular elongated; first cuneiform reduced; metatarsal III articulates with cuboid; proximal facet of metatarsal III does not extend to ventral tip of plantar process; hallux absent.

Type species : Pedetes capensis (Forster, 1778)

Included species : Pedetes surdaster Thomas, 1902

Pedetes gracilis Broom, 1930

Pedetes laetoliensis sp. n.

Genus Megapedetes MacInnes, 1957 : new diagnosis.

Pedetines in which the premaxillae overlap the edges of the nasals; nasal bones without lateral wings; median depression in frontals extending whole length of bone; groove for m. temporalis relatively deep; anterior edge of preorbital bar concave; lachrymal forms distinct preorbital process; jugal contributes to lateral edge of articular surface of glenoid fossa; lower maxillary root of zygoma arising a

little further posteriorly than in Pedetes and inclined distinctly postero-ventrally; incisive foramina not set in palatal groove and positioned a little further posterior than in Pedetes; incisors with lateral ridge on anterior face, narrow transversely and deep antero-posteriorly; cheekteeth rooted and brachyodont.

In mandible lower masseteric tubercle pronounced; masseteric crest well developed; well developed bony projection below symphysis menti.

Humerus with medial epicondyle without dorsal hook-like process; entepicondylar foramen normally absent; olecranon process of ulna without distinct medial process.

Sacrum composed of two fused vertebrae; trochanter major of femur with large tubercle on anterior face; fibula relatively robust; astragalus with sulcus tali continuous with median groove of trochlear surface; calcaneum with large sustentaculum tali; plantar process of navicular short; first cuneiform well developed; metatarsal III does not articulate with cuboid; proximal facet of metatarsal III extends to ventral tip of plantar process; hallux present.

Type species : Megapedetes pentadactylus MacInnes, 1957

Included species : Megapedetes augaeus Sen, 1977

The generic diagnoses provide a list of characters that serve to distinguish these two genera: these characters and their states, both in these two genera and in Parapedetes, are summarised in Table 7.III. The characters in which Pedetes and Megapedetes resemble each other have already been discussed as they form the basis on which the two genera

are classified together in a single subfamily. In addition to the characters listed there are a number of other characters that are only known in the Recent species and which may be of taxonomic value: these have been discussed at the family level because of the light that they may shed on the relationships of the Family Pedetidae. Other characters of the skeletal system that are only known in some of the forms have been discussed above at the subfamily level and more of them will be discussed at this level.

The position of the dorsal portion of the premaxilla, lateral to the nasals, in Pedetes is considered to be plesiomorphous and thus provides no evidence to support the unity of the genus Pedetes. In Megapedetes the overlapping of the edges of the nasals by the premaxillae is an autapomorphy that supports the distinction of the genus Megapedetes. The state of the character in Parapedetes resembles Pedetes but being plesiomorphous does not provide evidence for relationships at the subfamily level. Although the state of this character in Pedetes has been referred to the state in P. gracilis is unknown: because of the poor preservation of this species this is actually true of most characters. In the following discussion reference will be made to the character state in the genus Pedetes without qualification but it should be borne in mind that normally this will only apply to three of the species with P. gracilis not included.

Within the Subfamily Pedetinae the absence of any bone enclosing the lateral edges of the external nares is believed to be plesiomorphous and this is the state present in Megapedetes. In Pedetes the nasal bones have developed

lateral wings and these are apomorphous. This apomorphy is considered to be one that is probably characteristic of the genus and supports the validity of its creation.

The presence of a median depression in the frontal bones is plesiomorphous within the pedetines but it differs in its extent between the two genera. In Megapedetes the depression extends for the whole length of the frontals and this is considered to be apomorphous: a pronounced depression in the frontals seems to be uncommon amongst rodents and it is assumed that it developed at the anterior end of the bones between the frontal sinuses and then gradually enlarged by spreading posteriorly. On this basis the state in Pedetes would be plesiomorphous and the character would support the validity of a genus Megapedetes. However, since the determination of the morphocline polarity for this character is so dependent on assumption, undue weight should not be given to the evidence it provides.

In Megapedetes there is a well developed groove in the cranium for m. temporalis and this implies that the muscle was relatively well developed. Although much less developed than in the paramyids (Wood, 1962b) a well developed m. temporalis must be considered plesiomorphous in Megapedetes and the reduction of the groove and presumably the muscle in Pedetes is an apomorphy. This supports the unity of the genus Pedetes but a reduction of m. temporalis is also found in Parapedetes which means that the latter genus displays a synapomorphy with Pedetes and this is inconsistent with the proposed phylogeny. However a reduction of m. temporalis is common in rodents as the dominant jaw muscle has switched to

m. masseter and considerable reduction from the paramyid condition of m. temporalis has occurred even in Megapedetes. The evidence, therefore, supports the view that reduction of m. temporalis is one of the basic changes that have produced the characteristic rodent jaw structure and should be found commonly within the order. Consequently the reduction of this muscle in both Parapedetes and Pedetes would not seem to be a sufficiently weighty synapomorphy to warrant rejection of the proposed phylogeny.

The preorbital bar displays two characters that can be considered at this level. The first is the shape of the anterior edge of the bar which is concave in Megapedetes and straight in Pedetes. It is believed that the latter state is plesiomorphous and the former is apomorphous. This distribution of character states supports the distinction of Megapedetes and means that Pedetes and Parapedetes have a symplesiomorphy in this character which is consistent with the proposed phylogeny. The basis for determining this morphocline polarity needs some explanation since many hystricomorphs have the anterior edge of the preorbital bar concave and so it might be thought that this should be considered plesiomorphous. However, as discussed at the level of the family, hystricomorphy is believed to have evolved independently in several lines of rodents and the plesiomorphous state of detailed characters need not be the same in each line. Thus for an outgroup comparison only those hystricomorph rodents that are on the same evolutionary line as the pedetids can be considered and this restricts comparison to the anomalurids. In this group the anterior

edge of the preorbital bar is generally straight as it is in two of the three genera of pedetids which suggests that in the line of evolution that produced the hystricomorphous condition in pedetids and anomalurids the anterior edge of the preorbital bar was primitively straight rather than concave. This analysis depends on the assumption that the pedetids are more closely allied to the anomalurids than to any other rodent group; the evidence for and against this view has already been discussed and it has been suggested that this interpretation is, on the basis of the present evidence, the most likely.

The second character in the preorbital bar concerns the preorbital process of the lachrymal. This is absent in Pedetes and this is considered to be apomorphous; both Megapedetes and Parapedetes possess such a process and thus have a symplesiomorphy. Such a character state distribution is consistent with the phylogeny already proposed.

More posteriorly in the zygoma the jugal contributes to the formation of the lateral edge of the glenoid fossa in Megapedetes but does not do so in Pedetes. The state in the former genus is considered to be apomorphous. According to Marshall (1979) a contribution by the jugal to the anterior edge of the glenoid fossa is plesiomorphous in therian mammals and is found in a number of rodents but there is no reason to assume that the state in Megapedetes represents this plesiomorphous state rather than a secondarily derived contribution of the jugal to the glenoid. Assuming the state in Megapedetes to be secondarily derived the position in Pedetes and Parapedetes is that they possess a symplesio-

morphy in the absence of any contribution by the jugal to the articular surface of the glenoid fossa. This character state distribution is consistent with the hypothesised phylogeny and the autapomorphous state in Megapedetes supports the distinctiveness of this genus.

The anterior displacement of the zygoma found in both Pedetes and Megapedetes is an apomorphy at the level of subfamilies but can be further subdivided so that within the Subfamily Pedetinae it can be considered to possess two states. The lesser displacement found in Megapedetes is plesiomorphous at this level and the more anterior position in Pedetes is apomorphous. This character is one of the few that can be determined in all the known members of the genus Pedetes including P. gracilis and represents a synapomorphy uniting the four species and providing evidence for the validity of the genus Pedetes. The alignment of the lower maxillary root is horizontal in Pedetes which is considered thereby to possess the plesiomorphous state of the character with the postero-ventrally inclined root of Megapedetes being apomorphous. The distribution of both these characters is consistent with the phylogeny of Fig. 7.1.

Development of a pronounced palatal groove is another apomorphy that is known to occur in all the forms that are ascribed to the genus Pedetes. The incisive foramina are set in this groove and are positioned immediately posterior to the incisors, this too is an apomorphy and is known in all four species of Pedetes. In Megapedetes there is no palatal groove, which is plesiomorphous, while in Parapedetes there is a trace of a very shallow groove in which the

incisive foramina are set. It would seem that Parapedetes possesses a synapomorphy with Pedetes in this character.

The position of the incisive foramina has already been used at the subfamily level but as with the lower maxillary root of the zygoma the Subfamily Pedetinae shows two states. The far anterior position in Pedetes has already been stated to be an apomorphy and the more posterior position in Megapedetes is plesiomorphous within the pedetines. The anterior displacement of the foramina in the latter genus is much less than in Pedetes and results in the foramina being only a little nearer to the incisors than to the cheekteeth: they are thus only a little displaced from the plesiomcrphous position.

The absence of ridges on the anterior face of the incisor is considered to be plesiomorphous and is found in all four species ascribed to Pedetes. An anterior ridge is found in Megapedetes; this is an apomorphy that supports the distinctiveness of Megapedetes. It is only at this level that this character provides useful taxonomic information as was discussed above.

A further character of the incisors is their length (= antero-posterior depth) relative to their transverse width. In both Megapedetes and Parapedetes the incisors are narrow and this is believed to be the plesiomorphous state. By contrast Pedetes has wide incisors and this is an apomorphy that is found in all four species and characterises the genus. The symplesiomorphy possessed by the other two genera does not provide any information on their possible relationships and the character states are distributed in a manner that is

consistent with the proposed relationships.

Megapedetes possesses rooted, brachyodont cheekteeth; this can be considered as two characters in both of which Megapedetes possesses the plesiomorphous state. The acquisition of some degree of hypsodonty in Pedetes is an apomorphy that is found in all the species ascribed to this genus. However the acquisition of rootless teeth does not occur at the same time as that of hypsodonty since Pedetes laetoliensis possesses semi-hypsodont cheekteeth that are rooted; the other species of Pedetes all have rootless cheekteeth. The acquisition of hypsodonty supports the hypothesis of distinction between Megapedetes and Pedetes and the unity of the genus Pedetes. The possession of rooted as opposed to rootless cheekteeth provides no information at this level and is further considered below. Parapedetes closely resembles P. laetoliensis in both of these characters and the significance of this is also discussed below.

In the mandible Megapedetes possesses a relatively well developed lower masseteric tubercle and masseteric crest. Both of these states are believed to be plesiomorphous and in both cases Pedetes possesses the corresponding apomorphy of less well developed features. The development of the masseteric crest in Parapedetes is better than it is in Pedetes implying that the former genus possesses a symplesiomorphy with Megapedetes; the degree of development of the lower masseteric tubercle is not properly known so the distribution of states for this character cannot be determined.

Also in the mandible the large ventral process below the symphysis menti in Megapedetes is apparently apomorphous.

Wood (1962b) states that paramyids commonly have a small bony projection which is considered to be plesiomorphous and is the state found in Pedetes. The position in Parapedetes, in which there is no bony ventral projection, is considered to be encompassed within the plesiomorphous state as it corresponds with those paramyids that do not possess incipient ventral projections.

The post-cranial skeleton possesses a number of characters that can be considered at this level. In the humerus of Pedetes there is a distinct dorsal hook-like process on the medial epicondyle; this is an apomorphy and is not found in Megapedetes. The state of this character is not known in Parapedetes so that while it supports the distinction between the two pedetine genera it cannot provide any information on the proposed phylogeny at the subfamily level. Also in the humerus the absence of an entepicondylar foramen in most specimens of Megapedetes is an apomorphy. This foramen is present in both Pedetes and Parapedetes as well as in most other rodents including the paramyids (Wood, 1962b): presence of this foramen is, therefore, considered plesiomorphous. The fact that this foramen is not absent in all Megapedetes but only the majority suggests that its loss is still evolving and consequently that it forms an autapomorphy of Megapedetes.

According to Wood (1962b) the medial surface of the olecranon process of the ulna in paramyids is very rugose which means that the presence of a distinct medial process on the olecranon in both Pedetes and Parapedetes can be considered plesiomorphous. The state in Megapedetes is with a less well developed medial process but this surface is

still rugose and therefore while the character can be used for the practical task of distinguishing Pedetes from Megapedetes it is questionable whether it can be properly regarded as showing a genuine morphocline with different character states.

There are only two vertebrae in the sacrum of Megapedetes and according to Hatt (1932) this is the primitive condition in rodents. However Wood (1962b) claims that the most primitive arrangement encountered is a sacrum of three vertebrae, found in Paramys and Ischyromys, which are interpreted as one sacral and two pseudosacral. Both Pedetes and Parapedetes possess a sacrum made up of three fused vertebrae and, following Hatt (1932), this is considered to be a synapomorphy of these two genera. Since this particular apomorphy is very common in rodents there is reason to believe that it has arisen several times particularly as the developmental path leading to the fusion of the first caudal vertebra to the sacrum is relatively simple. Thus the fact that the distribution of character states in this case is inconsistent with the proposed hypothesis must be treated with care and not be given undue weight.

Reduction of the fibula is an apomorphy found in a number of rodent groups and within the Family Pedetidae it is a synapomorphy of the genera Pedetes and Parapedetes. In Megapedetes the fibula is relatively robust and this is the plesiomorphous state within the family. This character state distribution contradicts the hypothesised relationships within the family as shown in Fig. 7.1.

The astragalus of Megapedetes has the sulcus tali

continuous with the central groove of the trochlear surface; this is believed to be plesiomorphous since it is apparently found in paramyids as far as can be told from the illustrations in Wood (1962b). There is a contrasting state in Pedetes in which the two grooves are separated by the primary articular surface for the calcaneum and this state is thus apomorphous. The unity of the genus Pedetes is supported by this character state distribution: the state of the character in Parapedetes is not known.

In the calcaneum the reduction of the sustentaculum tali in Pedetes is an apomorphy and is an autapomorphy of this genus within the Family Pedetidae. Both Megapedetes and Parapedetes possess large, offset sustentacula and thus show a symplesiomorphy. Again this supports the validity of the genus Pedetes but provides no information on relationships at the subfamily level. Also in the tarsus the length of the plantar process of the navicular and the presence of an articulation between the cuboid and Mt.III display the same distribution of character states as with the sustentaculum. In both cases the state in Pedetes, a long plantar process and the presence of an articulation, is apomorphous. Both Megapedetes and Parapedetes possess the plesiomorphous short plantar process of the navicular and no contact between the cuboid and Mt.III.

A second character in Mt.III that displays a difference between Pedetes and Megapedetes is the ventral limit of the proximal facet for the third cuneiform. In the former genus this facet does not extend to the ventral tip of the plantar process of the metatarsal whilst in Megapedetes it does.

Because this character has not apparently been reported in the literature for other rodents it is difficult to determine a polarity for the morphocline. There is at present no basis for preferring one polarity to the other and so while pointing out that this character serves to distinguish the two pedetine genera from each other its wider significance in terms of evidence of relationship must be left unstated. The state of this character is not known in Parapedetes.

Finally there is a pair of correlated characters concerning the first digit to be considered. This pair is the presence or absence of a hallux and the associated development of C1. In Pedetes the hallux is absent and C1 is reduced to a thin splint; this is the apomorphous state. Megapedetes possesses a hallux and consequently C1 is relatively robust: the situation in Parapedetes is somewhat equivocal but certainly C1 is relatively robust and as discussed in Chap. 4 there is some evidence that the hallux was present. It would thus seem that in this case Megapedetes and Parapedetes possess a symplesiomorphy and Pedetes has an autapomorphy that serves to characterise the genus within the Family Pedetidae.

Of the characters discussed above 18 are apomorphies that, within the Subfamily Pedetinae, are only possessed by the genus Pedetes. This supports the validity of this genus as distinct from other pedetids. Of these apomorphies four are known to be synapomorphies with Parapedetes and thus are inconsistent with the hypothesis that the Family Pedetidae can be subdivided into two subfamilies in the manner

discussed above. However, some of these characters are of dubious weight and anyway should not be considered to outweigh the 11 characters that are believed to be synapomorphies of Pedetes and Megapedetes and that support the proposed hypothesis; there are also a further three characters which as mentioned above may turn out to provide additional support for the validity of the Subfamily Pedetinae. The weight of evidence now considered certainly supports the hypothesis proposed that the primary division of the Family Pedetidae is between Parapedetes and Megapedetes plus Pedetes. In two characters of the 18 the state in Parapedetes is uncertain but the evidence points to it not being a synapomorphy with Pedetes while in another two characters of the 18 the state in Parapedetes is completely unknown. This means that in 10 of the characters considered Pedetes possesses an autapomorphy. Megapedetes possesses seven autapomorphies amongst the characters considered and this supports the belief that the genus Megapedetes is a valid taxon. Two of the remaining four characters, although useful in distinguishing Pedetes from Megapedetes, do not, at present, provide any information on relationships at any level. The third of these four, namely incisor ridges, displays an apomorphous state in Megapedetes but again cannot provide any information on relationships whilst the last character, which can be considered as two, is the state of the cheekteeth and it provides information of use at the level of the species and is, therefore, discussed below.

A couple of characters that are known in the Recent

species of the genus Pedetes may prove to be of value at this or some other level but unfortunately their state is not known in any of the fossils. The first of these characters is found in the cranium and is the absence of an alisphenoid canal. In Pedetes this canal appears to be represented by a shallow groove in the floor of the braincase, running from the middle of the anterior edge of the foramen ovale antero-medially to the sphenoidal fissure. According to Bugge (1974) this groove carries the infraorbital branch of the carotid arterial system. The absence of a true alisphenoid canal is considered to be an apomorphy but it is uncertain at what level it may represent a synapomorphy. The second character concerns the overall structure of the manus which in the Recent species has five digits equally well developed. Since the manus is not fully preserved in the fossils it is not known how any character state differences may be distributed, but on the evidence available from Megapedetes and SAM-PQ 2121 it seems possible that the manus was essentially similar in all pedetids. If this is so then this character can provide no information on possible relationships since the state in Recent Pedetes is the plesiomorphous state for rodents.

In a similar manner to that discussed above in relation to the genus Pedetes and P. gracilis the character states of the genus Megapedetes are those of M. pentadactylus. The species M. augaeus is known only from teeth and consequently the state of most of the characters considered is not actually known in this species: the species is further

discussed below.

Species :

Because Parapedetes is monotypic the possible relationships of Pa. namaquensis have already been discussed. In the case of the genus Megapedetes the species M. augaeus is known from such fragmentary remains that its relationship to M. pentadactylus is difficult to determine. Discussion of M. augaeus is deferred to the section discussing the other fragmentary pedetid remains. The characters given in the generic diagnosis are based on M. pentadactylus and it is, therefore, not possible to separate generic characters from characters that more properly apply just to the species M. pentadactylus. Thus only in the case of the species in the genus Pedetes can separate diagnoses be prepared for the species and the relationships of these species be discussed. The species of Pedetes may be diagnosed as below.

Species Pedetes capensis (Forster, 1778) : new diagnosis

Pedetes with relatively long nasal bones (mean length 103% of mean frontal length); incisive foramina relatively long (mean length 37% of diastemal length); interforaminal septum robust; palatal groove deep (more than 4.5mm); median foramen in basisphenoid normally large; lateral wings of basioccipital relatively well developed; cheekteeth hypsodont with persistent pulps; pm_4 with posterior enamel ridge of anterior lobe normally possessing anterior fold; lower cheekteeth forming distinct tubercles in lateral wall

of mandibular ramus; no fusion between any of the cervical vertebrae; tubercles on anterior face of trochanter major of femur small.

Species Pedetes surdaster Thomas, 1902 : new diagnosis

Pedetes with relatively short nasal bones (mean length 77% of mean frontal length); incisive foramina relatively short (mean length 29% of diastemal length); interforaminal septum thin; palatal groove shallow (less than 4.1mm); median foramen in basisphenoid normally small; lateral wings of basioccipital not well developed; cheekteeth hypsodont with persistent pulps; pm_4 without anterior fold in posterior enamel ridge of anterior lobe; lower cheekteeth forming distinct tubercles in lateral wall of mandibular ramus; Ce3 and axis fused, other cervical vertebrae may show some degree of fusion; tubercles on anterior face of trochanter major of femur small.

Species Pedetes gracilis Broom, 1930 : new diagnosis

Small Pedetes with incisors having orange enamel; cheek-teeth hypsodont with persistent pulps.

Species Pedetes laetoliensis sp. n.

Small Pedetes about 85% of the size of the living species of the genus Pedetes; cheekteeth with pulp cavities remaining open into adult life but closing in older animals with the loss of the bilobed pattern found on the occlusal surface, lower cheekteeth not normally producing pronounced tubercles in the lateral wall of mandibular ramus; cranium less deep than in the Recent species of the genus Pedetes; nasals 92%

of frontal length; infraorbital foramen enlarged, extending further dorsally and having a relatively wider base than in living Pedetes; fossa in side of rostrum below incisive alveolus; shallow palatal groove; incisive foramina relatively long (about 35% of diastemal length); basisphenoid with large median foramen; lateral wings of basioccipital well developed; pm_4 with posterior enamel ridge of anterior lobe possessing anterior fold.

No fusion in cervical vertebrae; large tubercle on anterior face of trochanter major of femur.

Species Pedetes hagenstadi Lyle, 1931 (in Dreyer & Lyle, 1931)

The type material has not been examined since its present location is not known. The original description is short but does not list any characters that would distinguish this species from Pedetes capensis. Since the cheekteeth in the three species of Pedetes that have persistent pulp cheekteeth are almost identical the erection of a new species solely on the basis of minor cheektooth differences is not considered to be warranted. It is, therefore, felt that there is no justification for the retention of this species and the name is considered to be a junior subjective synonym of Pedetes capensis (Forster, 1778).

Pedetes gracilis is the least well preserved of the Pedetes species considered to be valid and its position within the genus can only be determined with some degree of uncertainty as it is based on a very small amount of evidence. The presence of orange incisor enamel in P. gracilis makes it

clearly distinct from other species in the genus. Orange incisor enamel, on the basis of the evidence available, is considered to be an apomorphy in the Family Pedetidae: the other species of Pedetes have white or slightly buff-stained enamel; Parapedetes, as preserved, has buff-stained enamel but this is probably due to post-depositional staining and is sufficiently light in colour that it seems most probable that it represents staining of previously white enamel. The state of this character in Megapedetes is not known since, as preserved, the incisor enamel is darkly stained, probably post-deposition because the enamel of the cheekteeth is also stained. If the incisor enamel in Megapedetes were originally white then it would argue strongly for the hypothesis that orange incisor enamel in P. gracilis is an autapomorphy. The cheekteeth in P. gracilis are rootless and hypsodont which is a synapomorphy shared by this species and the two living species of the genus Pedetes that suggests that P. gracilis is more closely related to the two living species than it is to P. laetoliensis. Because the type and only known specimen of P. gracilis is so poorly preserved it is impossible to determine the state of many characters in this species. Consequently the position of P. gracilis within the genus can be hypothesised only tentatively on the basis of the two characters that are available.

Pedetes laetoliensis possesses the apomorphies that characterise the genus Pedetes but is more primitive than the two living species in a number of features. The cheek-teeth, semi-hypsodont with pulp cavities remaining open for a considerable time but without persistent pulps, represent

a plesiomorphy within the genus Pedetes. This character state distribution supports the hypothesised relationship (Fig. 7.1). The presence of semi-hypsodont cheekteeth is a character state that might be expected in the ancestor of the other Pedetes species but since ancestors are logically unknowable (Hennig, 1966; Cracraft, 1974) it is not possible to say that P. laetoliensis is indeed such an ancestor. Semi-hypsodonty is the first stage of a morphocline from brachyodont cheekteeth to the sort of cheekteeth found in the other species of Pedetes. Coupled with the presence of semi-hypsodont cheekteeth P. laetoliensis does not possess pronounced tubercles in the lateral surface of the mandibular ramus: this character state is plesiomorphous but being a correlated character of the form of the cheekteeth it can provide no additional taxonomic information. The evolution of cheekteeth hypsodonty in P. laetoliensis is at the same stage as in Parapedetes although the former is Plio-Pleistocene and the latter is Lower Miocene. Although semi-hypsodonty is plesiomorphous within the genus Pedetes it is apomorphous within the Family Pedetidae and thus Pedetes laetoliensis and Parapedetes share an apomorphous character state. A phylogeny based on this character is contradicted by the distribution of a large number of other characters (see discussion, above, of the differences between Pedetinae and Parapedetinae) so the sharing of this apomorphy must be assumed to be due to parallel evolution. Thus semi-hypsodonty has apparently evolved twice in the pedetids: on the first occasion in the parapedetines which eventually became extinct; and on the second occasion in the genus Pedetes it lead to the

evolution of full hypsodonty.

Enlargement of the infraorbital foramen is plesiomorphous within the Family Pedetidae and the significance of the relatively greater enlargement in P. laetoliensis is uncertain. A possible functional significance for this character is discussed (Chap. 8) and this argument can be held to imply that the relatively smaller foramen in the two living species of Pedetes represents a synapomorphy. The changes in this character are correlated with changes in the overall size of the skull and demonstrate allometric changes.

A shallow palatal groove is considered plesiomorphous in the genus Pedetes and can thus provide no evidence for the relationships of P. laetoliensis and P. surdaster. The presence of a deep palatal groove in P. capensis is an autapomorphy and supports the hypothesis that this species is distinct from P. surdaster. Relatively long incisive foramina are an apomorphy (Wahlert, 1978 : 12) but the values shown in Pedetes of the ratio "length of the incisive foramina":"length of diastema" are all low when compared to other rodents which suggests that the state of this character is plesiomorphous in Pedetes. The mean value of the ratio is different in the three species, P. capensis, P. surdaster and P. laetoliensis but the ranges show considerable overlap. For the purpose of distinguishing the two Recent species from one another this character can prove helpful but it is not considered to show sufficient variation for useful interpretation in terms of a transformation to be possible.

The presence of an anterior fold in the posterior enamel ridge of the anterior lobe of pm_4 in P. capensis and

P. laetoliensis is considered to be plesiomorphous and probably represents the division between two cusps. P. surdaster does not possess a fold and this is an autapomorphy that provides support for the distinction of P. surdaster as a separate species. A similar character state distribution is found in the cervical vertebrae with P. surdaster possessing an autapomorphy in the fusion of the axis and Ce3 and, sometimes, other vertebrae. The other two species in which this character is known share a symplesiomorphy in the absence of fusion in the cervical vertebrae.

Neither Recent species of the genus Pedetes possesses a large tubercle on the anterior face of the trochanter major of the femur. Such a tubercle is present in all other known pedetids and this is, consequently, considered to be the plesiomorphous state within the family. A synapomorphy is, thus, shared by the two Recent species which is further support for the proposed hypothesis of relationship.

In the basicranial region the presence of a large median foramen in the basisphenoid is believed to be a plesiomorphy and is the character state found in P. capensis and P. laetoliensis. The presence of a small median foramen such as is found in P. surdaster represents the apomorphous state and supports the distinctiveness of this species. More posteriorly the larger lateral wings of the basioccipital found in P. laetoliensis and P. capensis are considered to be plesiomorphous compared to the flatter lateral wings present in P. surdaster which represent the apomorphous state.

When considering the three better known species of the

genus Pedetes there is a clear size gradation although there does not appear to be any way to determine whether this represents a true morphocline. With regard to the cranium there is a general trend that P. capensis is the largest and P. laetoliensis is the smallest with P. surdaster between the other two but more similar in size to P. capensis than to P. laetoliensis.

In the recent past it has been argued that there is only a single living species of the genus Pedetes. This view has not been accepted and on the basis of the characters discussed above it is felt that the retention of P. surdaster as a species distinct from P. capensis is justified. On the basis of distribution evidence currently available the boundary between the two species would appear to be at about Latitude $04^{o}00'S$ but it cannot be said whether the two distributions are discrete or whether they overlap since this region has not been sufficiently well collected.

Subspecies :

Only in the case of the Recent species is there a sufficient number of specimens from a wide enough geographical range to make the consideration of subspeciation possible. Even within the living species clear-cut osteological differences are not generally found between subspecies and many of the named Recent forms are described on the basis of slight differences in coat colour. Both of the living species have been oversplit into subspecies: a total of 13 have been described (see Chap. 2) However Allen &

Loveridge (1927) suggests that as Pedetes lives in widely separated colonies this may result in the development of local and characteristic variations.

Pedetes surdaster Thomas, 1902.

This species was divided into three subspecies when two new subspecies – P. surdaster larvalis and P. surdaster currax – were described in 1918 (Hollister, 1918). The second of these subspecies is known only from the type specimen and no specimens that could be attributed to it have been seen nor have any further references to it been found apart from Hollister (1919), which again only mentions the type specimen, and its listing in synonymies (e.g. Ellerman, 1940). The original description of P. surdaster currax mentions slight cranial differences and coat colour differences from other members of the species. Of all the characters in the skull only the greater breadth of the mastoid seems to represent a genuine difference from other P. surdaster specimens: the measurement given in Hollister (1918) is outside the range found in specimens examined (Table 2.I). Since the type specimen has not been examined the significance of the coat colour differences given in the original description cannot be properly assessed. On the basis of the skull characters, however, there is not considered to be sufficient justification for the retention of this subspecies since it is only represented by a single specimen.

P. surdaster larvalis and P. surdaster surdaster are differentiated mainly on the basis of cranial characters.

The main difference between the two subspecies is supposed to be the cranial profile with the dorsal surface flat in the former subspecies, due to the presence of well developed frontal sinuses which obscure the depression in the frontals in profile view; in the latter subspecies the frontal sinuses are less well developed which results in an uneven profile with a depression over the orbits. This difference in profile produces two quite distinct morphological groups. While less clear-cut there is also a definite trend in the possession of a bony strut in the sphenoidal fissure that divides off a small ventral portion from the larger dorsal part: this strut is commoner in P. surdaster surdaster than in P. surdaster larvalis. However, although these characters result in two morphological groups, these cannot be described as subspecies because it appears that they show overlapping distributions. In the specimens examined there also seemed to be no consistent differences in the other characters mentioned in Hollister (1918), namely the anterior portion of the cranium and the form of the fronto-parietal suture. There is, thus, no basis for retaining P. surdaster larvalis as a separate subspecies and consequently Pedetes surdaster must be considered a monotypic species.

Pedetes capensis (Forster, 1778).

Ten subspecies have been described for this species (see Chap. 2) and, as stated in Ellerman, Morrison-Scott & Hayman (1953), this seems to be an excessive number. Most of these subspecies are based on minor differences in coat colour although some also include osteological characters.

One of the named subspecies is not valid as the name is a nomen nudum: this is P. capensis bradfieldi Ellerman, 1940. When this name was first published it was stated that no previous reference to it could be traced although there are specimens labelled with the name in the British Museum (Natural History). There are also specimens bearing this name in the Transvaal Museum and in both cases they were collected by the Vernay-Lang Kalahari Expedition (1930). Descriptions of the mammals collected by this expedition are published in Roberts (1935) in which the pedetids from Kroonstad are ascribed to P. capensis orangiae while all the others are ascribed to P. capensis damarensis. An examination of the specimens shows that those from Kroonstad are indeed labelled P. capensis orangiae and it appears that the specimens labelled P. capensis bradfieldi were intended to be used as the basis for a new subspecies but that subsequently it was decided that they were not, in fact, sufficiently distinctive for this.

The distribution of the other subspecies described reflects collecting effort with all but one of them coming from Tanzania, South-West Africa or the Republic of South Africa. The species is found throughout southern Africa but the shortage of available material from central southern Africa (the region of Rhodesia, Zambia and Malawi) makes it difficult to be certain of the status of animals from this area. Ansell (1960, 1964, 1965, 1969 & 1973) provides information on distributions in Zambia but does not make clear whether this is based mainly on sight records or systematic collection nor where any material is housed.

However, even with the absence of data from this region it is still probable that there are only three subspecies and most of southern Africa is occupied by a single subspecies, the type subspecies, P. capensis capensis which extends over much of the Republic of South Africa, Botswana, South-West Africa and into Angola and Mozambique; it probably also extends up through central southern Africa. It thus includes the following named forms: P. capensis angolae, P. capensis damarensis, P. capensis fouriei, P. capensis orangiae and P. capensis salinae. The last two subspecies and P. capensis damarensis are described solely on the basis of slight variations in coat colour and an examination of a large number of skins shows that similar degrees of variation in colour can be found amongst specimens from a single locality. These variations cannot therefore be considered sufficient to differentiate these subspecies from P. capensis capensis and since there is no other evidence to support the retention of these subspecies it is considered that the names P. capensis damarensis, P. capensis orangiae and P. capensis salinae should be considered as junior subjective synonyms of P. capensis capensis.

P. capensis fouriei is also based principally on coat colour but is, in addition, described as being smaller than normal. The only specimen certainly attributable to this subspecies is the type (TM 8213) from Itota Pan but a specimen in the British Museum (Natural History) (BM(NH) 25.12.4.207) that comes from Etosha Pan may also be considered as belonging to it. Both of these specimens are of about average size for P. capensis. Since neither skull size nor

the slight variation in coat colour distinguish P. capensis fouriei it is felt that there is insufficient justification for the retention of this subspecies.

The final named form in this group is P. capensis angolae: the only material from Angola that has been examined is housed in the British Museum (Natural History) and, except for a single skin without a specific locality, it is all from either Cholinde or Capango. On the basis of the skin characters given in the original description (Hinton, 1920) there is no reason to retain this subspecies. The skull characters given are also of dubious value as many are also found in specimens of P. capensis capensis. Two characters do, however, provide some degree of differentiation for P. capensis angolae: these are the absence of an inferior process of the jugal, which is also found in a few P. capensis capensis crania, and the development of the maxillary portion of the preorbital bar. These are relatively minor differences and are not felt to be sufficiently important by themselves to make the retention of this subspecies certain and so it is felt to be best on present evidence to consider P. capensis angolae as a synonym of P. capensis capensis. This decision must be provisional and it is quite possible that when further evidence is available from Angolan specimens it will have to be reconsidered.

P. capensis albaniensis was described from the Eastern Cape region and is based on skin characters (Roberts, 1946). It was a specimen of this subspecies (BM(NH) 97.11.5.85) that formed the basis for the anatomical work of Parsons (1898). As with the other subspecies minor differences in coat colour

are not held to be sufficient to justify retention of a subspecies. However, this subspecies may be considered valid on the basis of osteological characters not included in the original description. Specimens from the Eastern Cape have a tendency to possess crania that are larger and more robust than specimens from most of the remainder of southern Africa. If cranial lengths greater than 90mm are plotted then 49% of those found came from the South-East Cape and southern Orange Free State. This area occupies much less than 49% of the area from which the specimens of P. capensis that were examined came and also only contains 30% of the total number of specimens. Furthermore the Transvaal, Orange Free State, South-West Africa and Botswana have all been fairly well collected and consequently this concentration of larger animals in the South-East Cape and southern Orange Free State cannot be considered an artefact of collecting. Also when crania having lengths between 87.5 and 90mm are considered this same area includes 35% of the specimens giving a combined result that 39.5% of specimens with a cranial length equal to or more than 87.5mm are found in the relatively restricted region of the South-East Cape and Orange Free State from which only 30% of the total specimens come. It therefore seems reasonable to accept the possibility that P. capensis albaniensis is a valid sub-species: in this context it should be said that the evidence would not be considered sufficient to justify the naming of a new subspecies but it is felt that it precludes the suppression of a subspecies already named. As far as can be determined on the evidence available the range of this sub-

species would not seem to extend west of Longitude 23°E nor east of Longitude 28°E and extends from the coast north to about Latitude 29°S in the Orange Free State. The area of this subspecies thus appears to correspond to the area of the coastal plain of Albany and the high ground north of this coast up to about Bloemfontein. The exact boundaries of this distribution cannot be determined without more extensive collections along the hypothesised boundaries and it is possible that once such collecting is carried out it will be found that the form in question in fact occupies a position at the end of a cline. However, on the present evidence, there is no reason to believe that this is so and, consequently, the validity of a subspecies, P. capensis albaniensis, is accepted.

A third subspecies of P. capensis is found in the southern two-thirds of Tanzania. This subspecies is characterised by an extremely compressed interparietal which is almost triangular. Two subspecies of P. capensis have previously been described from Tanzania: P. capensis dentatus and P. capensis taborae. The former subspecies was the first described but the original description is very short and provides no characters that would clearly distinguish this subspecies. P. capensis taborae was described second and includes a much better description. Allen & Loveridge (1927) state that P. capensis dentatus has a normal interparietal, although Miller (1927) does not say this, while P. capensis taborae has a greatly compressed one. The type material of these two subspecies is in the U.S.A. and has not been

examined but it seems unlikely that there are two subspecies in Tanzania. There are two specimens of P. capensis from Tanzania in the British Museum (Natural History) and both display the strongly compressed interparietal. One of these specimens (BM(NH) 65.2908) comes from a locality that was reported as a locality of P. capensis dentatus in Swynnerton & Hayman (1951). It thus seems best at this stage to accept that in Tanzania there is a distinct subspecies that is most easily distinguished by a compressed interparietal bone which is almost triangular. This subspecies would occupy the ranges of the described forms P. capensis taborae and P. capensis dentatus and although distinguished by a character listed originally for P. capensis taborae this subspecies must be called P. capensis dentatus since this is the prior name and the type of the latter subspecies is assumed to be included in the hypodigm of the Tanzanian subspecies. In order to be certain that this conclusion is justified the form of the interparietal in the type of P. capensis dentatus must be known: if it is as assumed here and compressed then the conclusion stands but if it has a normal shape then it must be concluded that Tanzania contains a subspecies P. capensis taborae, with a compressed interparietal, and P. capensis dentatus is either a valid subspecies in its own right or a synonym of P. capensis capensis.

It is interesting to note here that the two specimens in the British Museum (Natural History) that have been attributed to P. capensis dentatus have a palatal groove that is on the shallow side for P. capensis. However, the depth of the

groove is still considerably greater than in specimens of P. surdaster from northern Tanzania.

Fragmentary fossil pedetids :

c.f. Parapedetes namaquensis (SAM-PQ 2121):

This material, from Elisabethfeld, closely resembles the type material of Parapedetes namaquensis but displays a number of key differences. The most important of these differences is that the lower cheekteeth have the transverse infold penetrating from the lingual side as in the pedetines rather than from the buccal side as in parapedetines. The character state in SAM-PQ 2121, however, is plesiomorphous and thus does not preclude a relationship between it and Pa. namaquensis: the apomorphous state in this latter may represent an apomorphy at the generic or specific level and not at the subfamily level. A second similarity between SAM-PQ 2121 and the pedetines is the presence of two openings to the foramen mentale rather than only one. This is an apomorphy but because of the poor preservation of the type material of Pa. namaquensis it is difficult to be certain of the character state in the latter although it has been described as a single opening for want of better evidence. Consequently the importance of this character state distribution is uncertain.

The cheekteeth in SAM-PQ 2121 are semi-hypsodont and do not produce tubercles in the lateral wall of the mandibular ramus. Semi-hypsodonty is apomorphous in the Family Pedetidae and, amongst Lower Miocene pedetids, is only found

in this material and Pa. namaquensis: this provides evidence for a close relationship. There is no ridge on the anterior face of the upper incisor but there is a slight medial one in the lowers: this is not found in other pedetids. Pa. namaquensis has an anterior medial ridge in the uppers but no ridge in the lower incisors. Also in the mandible there is no bony process below the symphysis menti and this is plesiomorphous; there is, however, a very thick ventral edge to the angle which is a synapomorphy with Pa. namaquensis. This latter character thus supports a close relationship with Pa. namaquensis while the symplesiomorphy of the ventral process of the symphysis menti can provide no evidence for relationship.

There are a number of characters in the post-cranial skeleton that also provide evidence for the possible relationships of SAM-PQ 2121. The preserved proximal end of the humerus shows the presence of a very well developed ridge, for the insertion of m. teres major and m. latissimus dorsi, below the lesser tuberosity. This is an apomorphy and very closely resembles the same feature in Pa. namaquensis: as in the latter it is evidence of an adaptation for burrowing. A well developed sustentaculum tali in the calcaneum; a short plantar process of the navicular and the probable presence of a hallux are all plesiomorphies in which this specimen resembles Pa. namaquensis. Because these characters are plesiomorphies they do not, however, provide evidence for relationship.

SAM-PQ 2121 includes the only fossil pedetid scapho-lunar

known. It provides good evidence that a radial ossicle was present. This would mean that in at least one line of pedetids the radial ossicle had already evolved in the Lower Miocene. Thus the presence of this bone may be an apomorphy characteristic of the Family Pedetidae but since its presence or absence in most pedetids is not known it cannot be used in the family diagnosis until further evidence becomes available.

The weight of evidence discussed above suggests that SAM-PQ 2121 is related to Pa. namaquensis. Of the characters considered to contain, potentially, good taxonomic information three are synapomorphies in this specimen and Pa. namaquensis; one questionable character is synapomorphous in SAM-PQ 2121 and the pedetines; the other characters are either plesiomorphous or, in one case, autapomorphous in SAM-PQ 2121. That SAM-PQ 2121 comes from Elisabethfeld, the type locality of Pa. namaquensis, also suggests that it may belong to the latter species. However the relationship between the exact site and level from which SAM-PQ 2121 comes and that from which the type material of Pa. namaquensis comes is uncertain. Stromer (1926) does not give a detailed breakdown of the localities within Elisabethfeld but merely states that the pedetid material was found in a slab of red rock: SAM-PQ 2121 was found in the Red Sands. A difference in the time of deposition of the two sets of material may explain many of the differences between them as changes over time within a taxon.

Megapedetes c.f. pentadactylus:

This small amount of material contains a number of characters reminiscent of M. pentadactylus from East Africa. In SAM-PQ-AD 1745 the lower masseteric tubercle and the masseteric crest are well developed; the foramen mentale has two openings and there is a pronounced ventral process below the symphysis menti. Of the latter two characters the first is interpreted as an apomorphy, although its value is uncertain, found in all pedetines; the second is a synapomorphy of this material and M. pentadactylus only. Another synapomorphy shared with M. pentadactylus is the presence of a lateral ridge on the anterior face of the incisor.

The preserved cheekteeth are typically pedetid. They are rooted and brachyodont and thus resemble M. pentadactylus. Since both these characters are plesiomorphies they do not provide evidence for relationship.

Although this material closely resembles M. pentadactylus it is too small to be included in this species. Comparison of Tables 3.IV and 6.VIII shows that the measurements of the cheekteeth, which are well worn, are no greater than in juvenile specimens of M. pentadactylus in which no wear has taken place and are very much smaller than comparably worn teeth in the East African material. The three specimens are interpreted as belonging to the genus Megapedetes but not to the species M. pentadactylus. However, the material is so incomplete that suggestions about its taxonomic status must be tentative.

If the above assignment of this material is accepted then

it implies that the pronounced ventral process below the symphysis menti and the presence of a lateral ridge on the incisor are apomorphies characterising the genus Megapedetes as a whole rather than an individual species. This provides a basis for beginning to construct separate generic and specific diagnoses in the genus Megapedetes but, unfortunately, the evidence is, at present, still insufficient to do this formally.

Gen. et sp. indet.:

This material is very incomplete but quite closely resembles M. pentadactylus and is definitely identified as pedetid. Anterior displacement of the lower maxillary root of the zygoma and the position of the incisive foramina are apomorphies implying that this material is pedetine: within the pedetines, however, it displays the plesiomorphous, more posterior, position found in M. pentadactylus. Similarly the presence of rooted cheekteeth, the absence of a palatal groove and the transversely narrow incisors are plesiomorphies: the first two shared with M. pentadactylus, the last also with Parapedetes.

In the post-cranial material the calcanea possess a general overall similarity to Pedetes and Megapedetes rather than to Parapedetes: the sustentaculum tali is broken off in both specimens but was probably well developed and thus showed a plesiomorphous state providing no information on relationships. Ru 514'47 shows that Mt.III was dominant in the metatarsus which is a similarity with the pedetines and contrasts with the parapedetines although, unfortunately, it

is a plesiomorphy. The dorso-lateral corner of the proximal end of Mt.III articulates with the cuboid and the proximal facet extends to the ventral tip of the plantar process: the latter character resembles Megapedetes but the polarity of the morphocline is uncertain; the former character resembles Pedetes and is a synapomorphy.

The best preserved fragment is the Mt.II from Maboko. This is very similar to, but smaller than, the same bone in the living species. On the medial surface towards the proximal end there is a facet for the end of C1 which, by comparison with other pedetid material, implies that the hallux was suppressed. This would represent an apomorphy shared with the genus Pedetes and argues strongly against identification of this material as Megapedetes.

The fragmentary and dispersed nature of this material means that it is not possible to be certain that it all belongs to a single taxon although the consistency of size suggests that this is so. All that can reasonably be said of this material is that it represents at least one species of small pedetid. This is a new species but there is not sufficient material of any single individual to designate a holotype specimen and so it cannot be named. The anteriorly displaced lower maxillary root of the zygoma implies that the material is pedetine rather than parapedetine, the position of the incisive foramina supports this conclusion. The only genus with which this material possesses synapomorphies at the generic level is Pedetes.

Megapedetes augaeus:

The type material of this species, as well as the other material that is ascribed to the species in Sen (1977), has not been examined so that any suggestions as to the validity or relationships of the species have to be based, at least partly, on the published descriptions. The only valid character given in Sen (1977) on which this species could be based is the size of the cheekteeth. The curvature of the lobes of the cheekteeth and the distinctiveness of cusps is variable in M. pentadactylus and the range of this variability would suggest that there is no clear distinction between M. pentadactylus and M. augaeus in these characters.

In terms of size the cheekteeth in M. augaeus are considerably smaller than those in M. pentadactylus and the measurements given show them to be about the same size as the cheekteeth in KNM-So 3909B which is the juvenile mandible described in Lavocat & Michaux (1966). The three molars from Rusinga described in Lavocat (1973) and ascribed to Megapedetes sp. as well as the molars from Maboko described above are a little smaller than those described in Sen (1977). However the teeth of M. augaeus seem to be of a similar size to the teeth of Megapedetes c.f. pentadactylus from Arrisdrift and the isolated molar from Beni-Mellal (Lavocat, 1961). Sen (1977) claims that the material from Chios closely resembles M. augaeus but the photograph in Tobien (1968) suggests that the Chios material is closer in size to M. pentadactylus.

In conclusion, therefore, the material on which M. augaeus

is based would seem to be too small to be included in M. pentadactylus but since the material is so limited it would probably have been better if formal naming of a new species had not occurred. The species M. augaeus may turn out to be valid but it is also possible that better knowledge of Megapedetes material may show that it merely represents the termination of a size cline in which there is a decrease in size as one moves north.

Pedetes c.f. surdaster:

Material from Olduvai Gorge, together with three fragments from Laetoli, represents one of the modern species of the genus Pedetes. The mandibular fragments show that the lower cheekteeth form distinct tubercles in the lateral wall of the ramus and this is an apomorphy shared with the two Recent species. Of the preserved pm_4 the specimen from Laetoli (Laet.'75 1310) does not display an anterior fold in the posterior enamel ridge of the anterior lobe; 067/517 from Olduvai Gorge does show such a fold while the mandibular fragment in the British Museum (Natural History) does not. The few post-cranial remains are just like those of the Recent species.

Although 067/517 resembles P. capensis the material is considered too fragmentary to be certain to which of the two living species it belongs. It is described as Pedetes c.f. surdaster on the basis that P. surdaster is found in the area today.

CHAPTER 8

Family Pedetidae : some functional and ecological considerations.

In the case of a number of characters in the skeletal system of pedetids an interpretation in functional terms can be usefully discussed: the taxonomic consideration of the characters has been given in Chapter 7. In the case of the Recent forms some functional evidence may be directly available but this is not the case with the fossils. The proposed functional basis of a character in a fossil thus depends on the comparison of the character in the fossil with the same character in Recent forms in which the way the character functions can be more accurately and directly determined. Recent forms involved in such comparisons need not be restricted to the living species of the genus Pedetes but can include any mammal that possesses an analogous structure. The functional analyses used to interpret the various characters are derived from the literature and there has been no attempt to carry out experiments on living animals to determine function directly.

In addition to considering function in an individual system, evidence from various systems can be used to suggest possible aspects of the ecology of the animals. This is especially useful in the case of the fossils, in which the ecology cannot be investigated directly, although some extrinsic evidence of probable ecologies can be obtained

from the type of deposit in which the fossil is found.

Skull :

Incisors:

All the pedetids have strongly opisthodont incisors and this suggests that they are not used to loosen the soil during burrowing. In those rodents that normally use their incisors in burrowing (e.g. rhyzomyids, spalacids and some bathyergids) the incisors are strongly pro-odont so that, when being used to loosen the soil, there is a reduced chance of soil getting into the mouth. It is also interesting that amongst the dipodids Allactaga, which does use its incisors in burrowing, has somewhat pro-odont incisors (Hatt, 1932 : 618 [but note the misuse of the species name which is common with Russian authors (Ellerman & Morrison-Scott, 1965 : 532)]).

The significance of the development of broad incisors in the genus Pedetes from the transversely narrow incisors found in the earlier pedetids is uncertain. Despite being relatively narrower, the incisors in Megapedetes are very robust and it is only in Parapedetes that the incisors could be described as delicate. The diet of Recent Pedetes includes very tough corms (Coe, pers. comm.) and it is possible that the development of the powerful incisors in Pedetes is related to the acquisition of this sort of diet. This would be consistent with the hypothesis, discussed below in relation to the cheekteeth, that the pedetine line underwent a change in its ecology and diet during the Upper Miocene

and Lower Pliocene at about the same time as the genus Pedetes seems to have evolved. This, however, still does not explain why Megapedetes should have had relatively robust incisors while the incisors in Parapedetes are more delicate. On the basis of the dietary hypothesis the reverse might be expected.

Cheekteeth:

The cheekteeth of the living species of the genus Pedetes and of Pedetes gracilis are hypsodont, have persistent pulps and an occlusal pattern, when worn, of two subequal lobes separated by a narrow infold and joined on one side of the tooth. The infold extends through the full height of the tooth so that, once established, early in the animal's life, the adult pattern persists unchanged until the individual's death. In contrast, in the Lower Miocene genus Megapedetes the cheekteeth are rooted and brachyodont. During wear they pass through a stage resembling the cheekteeth in adults of the modern species but in older animals this pattern is worn away and the occlusal surface becomes a simple dentine-filled enamel ring (MacInnes, 1957 : 12 ; pers. obs.). Pedetes laetoliensis represents a more advanced stage than Megapedetes and a stage through which the ancestors of the modern species must have passed during the evolution of their hypsodont cheekteeth. The initial wear is similar to that in both Megapedetes and the living species with two separate lobes becoming joined on one side of the tooth to give a bilobed pattern. As in the Recent animals this pattern was probably established early in life but the infold separating the two

lobes does not extend through the whole height of the tooth. However it is better developed than in Megapedetes so that the bilobed pattern must have persisted longer than in the latter genus but, in contrast to the living species, wear eventually obliterated the bilobed pattern and produced a simple enamel ring. In teeth worn to this advanced stage the pulp cavities are closed. The stages of wear of the cheek-teeth are, therefore, similar in both Megapedetes and P. laetoliensis but the teeth of the latter species are more hypsodont and the middle, bilobed, stage of wear lasts much longer. P. laetoliensis represents an early stage in the evolution of hypsodonty and the evolution of the modern form of the cheekteeth from the form found in P. laetoliensis would involve the extension of the infold so that it is present throughout the complete height of the tooth and also the delayed closing of the pulp cavity leading to its eventually remaining open permanently. This would result in the suppression of the third stage of cheektooth wear, namely the loss of the bilobed pattern and the attainment of a simple ring, and the persistence of the second stage from the time of its establishment until the death of the individual.

One possible explanation for the acquisition of hypsodont cheekteeth with persistent pulps is that a change occurred in the diet from predominantly soft or very nutritious food to predominantly tougher or less nutritious food. If the food retains the same nutritive content then the volume eaten will remain constant but an increase in toughness will cause increased wear of the cheekteeth; similarly a decrease in the nutritional content of the food, even without any change

in its texture, will result in increased wear of the cheek-teeth because a larger volume of the food material must be eaten for the same amount of nutrients to be obtained: a combination of the two factors may occur. Rensberger (1975) states that among geomyoid and muroid rodents those forms with brachyodont cheekteeth tend to eat seeds, fruit and insects while forms with hypsodont cheekteeth tend to eat more green vegetation and bark. In the case of the pedetines it is suggested that the principal change in the diet was an increase in the amount of grassy material, including grass roots, eaten. The Recent springhares feed on very tough grasses together with grass roots, corms, stems, tubers and seeds (Smithers, 1971 ; Butynski, 1973 & 1975) probably admixed with a certain amount of soil. Although the actual rate of cheektooth wear that this diet produces under natural conditions has not been measured it would seem to be a relatively abrasive diet and consequently hypsodont, ever-growing cheekteeth would be required to cope with the high rates of wear. An adaptation to a diet composed of highly abrasive vegetation might be expected in a form living in semi-arid or arid conditions in which relatively soft vegetation tends to be absent or restricted and the amount of mineral material, as dust deposited on the vegetation, included in the diet tends to be high. It seems unlikely that Megapedetes with its brachyodont cheekteeth could have fed on the same type of food as Recent Pedetes and this suggests that it may have lived under less arid conditions in which a diet of less abrasive foods was possible: the sites at which Megapedetes is found provide some evidence

for this. The Miocene sites of East Africa provide evidence that the climate at that time was much more moist than that of the areas in which Recent springhares are found. These sites have both a fauna and flora suggesting possible extensive forests (Walker, 1969 ; Van Couvering & Van Couvering, 1976 ; Andrews et al., 1979). Andrews & Van Couvering (1975 : 84) points out that Hypogeomys, a burrowing, ricochetal rodent, lives in forests in Madagascar; according to Walker (1975) this genus is restricted to thick, virgin forest and feeds mainly on fallen fruit, it is about half to two-thirds of the size of living Pedetes. Possibly Megapedetes may also have lived in forests, especially those with a reduced undergrowth, and have fed, like Hypogeomys, on a relatively soft diet for which its cheekteeth would be quite suitable.

The semi-hypsodont cheekteeth of P. laetoliensis suggest that its diet resembled that of the Recent springhares rather than Megapedetes. Leakey & Hay (1979) implies, in its description of the footprint tuff at Laetoli, that the ecological conditions in the area at that time were similar to those found there today. Since the Lower Miocene sites suggest a more moist climate the change to the drier conditions found at Laetoli must have occurred sometime during the Upper Miocene and Lower Pliocene. It seems likely that the pedetines underwent a switch in their diet to one containing an increasing amount of grass and sedge material in conjunction with this change in ecological conditions.

Parapedetes, like P. laetoliensis, possesses semi-

hypsodont cheekteeth with the roots remaining open relatively late into life and it represents an early stage in the evolution of fully hypsodont cheekteeth. Thus Parapedetes also probably had a diet similar to that of the Recent springhares although being Lower Miocene it was more nearly contemporary with Megapedetes. Stromer (1926) suggests that the environment at Elisabethfeld when deposition occurred was steppe. The presence of dry grassland would be consistent with the need for semi-hypsodont cheekteeth in Parapedetes as it would produce a relatively abrasive diet. Corvinus (1978) describes the area around Luderitz as having been more moist than it is today but does not specify how much more moist: the hypothesis that dry grassland was present in the area would be consistent with a slightly moister climate. In contrast to the cheekteeth found in Parapedetes the cheek-teeth found in the pedetid at Arrisdrift are brachyodont; it has been argued in Chapter 7 that the remains from this site suggest a pedetid taxonomically closely related to Megapedetes pentadactylus and the cheekteeth imply that the animal also had a similar diet to the East African species. The description given in Corvinus (1978) of the site at Arrisdrift implies that there were distinct ecological similarities to the East African sites of about the same age and it would seem that the pedetid present was more similar both ecologically and taxonomically to the more distant East African form than to the geographically much closer species Parapedetes namaquensis which apparently had a quite different ecology.

The small pedetid found at some East African sites and described as gen. et sp. indet. also has brachyodont cheek-

teeth which would imply that it, too, had a diet that was less abrasive than that of the Recent springhares. Thus, on the basis of the cheekteeth, it appears that a change from a relatively unabrasive diet to a diet composed of much more abrasive constituents has occurred on two separate occasions within the Family Pedetidae. The first such change occurred early in the evolution of the family in the line that gave rise to Parapedetes but, as far as can be determined on present evidence, it did not proceed as far as the evolution of fully hypsodont cheekteeth. In the other line of pedetid evolution, the Subfamily Pedetinae, the acquisition of more hypsodont cheekteeth occurred much later and is not apparent until the Pliocene. This implies that the change in diet that provided the selective pressure for the acquisition of hypsodont cheekteeth occurred at this time. The development of hypsodonty in pedetids is believed to be related to their becoming semi-arid forms which in turn resulted in their diet becoming more abrasive.

Jaw musculature:

The inferred jaw musculature shows changes parallel to those of the cheekteeth. The principal movements of the jaw during mastication in rodents are antero-posterior with an active anterior stroke and a passive recovery stroke (McN. Alexander, 1975). In early paramyids m. temporalis was a large and important muscle (Wood, 1962b) but in later rodents the importance of this muscle tended to be reduced. In the pedetids, this muscle is very small in Pedetes and apparently also in Parapedetes while in Megapedetes it is a little

larger although still very much reduced compared to the paramyid condition. The contribution made by m. temporalis to the functioning of the jaw is thus small but the muscle does serve to assist in closing the jaw and drawing it backwards.

The masseter muscles are especially important in jaw function and, in the pedetines, m. masseter medialis, which is enlarged and has a line of action that is forwards and upwards at about 45° to the occlusal plane, appears to be the principal muscle (Fig. 8.1). The size of m. masseter medialis cannot be determined in Pedetes gracilis but in each of the other three species of the genus Pedetes it is well developed and of about the same absolute size. As the cranium in Pedetes laetoliensis is considerably smaller than the cranium in the other two species the relative size of m. masseter medialis in the former species is greater. In order to subdivide food during mastication the pressure applied to it by the teeth must be above a threshold value that varies with the toughness of the food. Since the force that a muscle supplies can be considered, to a first approximation, proportional to its absolute size it might be expected that two animals with teeth of about the same size should have similar sized jaw muscles if they are feeding on a diet of similar toughness. The cheekteeth in Pedetes laetoliensis are about 80% of the size of the cheekteeth in the two Recent species of the genus Pedetes and so with a similar sized jaw muscle it should have been able to produce somewhat higher forces at the cheekteeth. The diet in living Pedetes species is known to be tough and the evidence of the

jaw musculature suggests that P. laetoliensis probably had a similar diet.

In Megapedetes m. masseter medialis is less well developed than in Pedetes and the cheekteeth are about 140% of the size of the cheekteeth in the living springhares. This means that the force that could be produced per unit area of cheekteeth in Megapedetes must have been considerably less than is the case in Pedetes and this in turn suggests that the food eaten was less tough.

The anterior displacement of the lower maxillary root of the zygoma in the pedetines results in the line of action of m. masseter superficialis becoming more horizontal. This muscle, however, is relatively small and it is suggested that the main selective pressure for the anterior displacement of the zygoma root was the need to increase the size of the infra-orbital foramen to accommodate a larger m. masseter medialis. M. masseter superficialis despite its small size contributes to mastication in drawing the jaw forwards and slightly upwards in conjunction with m. masseter medialis.

In Parapedetes (Fig. 8.2) the infra-orbital foramen, although enlarged, is relatively less so than in the pedetines; this results from the absence of an anterior displacement of the root of the zygoma. M. masseter medialis is therefore relatively smaller than in the pedetines although it still has a similar line of action; the origin of m. masseter superficialis is better developed than in the pedetines which suggests that this muscle was larger. Also the origin was further posterior so that the line of action is less horizontal and closer to that of m. masseter medialis.

The combined effect of mm. masseter medialis and superficialis in Parapedetes was probably sufficient to enable relatively tough food to be dealt with and the development of these muscles, especially of m. masseter superficialis, probably occurred in parallel with the development of increasing hypsodonty as an adaptation to more arid environments.

M. masseter lateralis also shows distinct differences in development between the pedetines and the parapedetines. In the former its origin extends over the lateral surface of the zygoma while in the latter group its origin is restricted almost completely to the lower edge of the zygoma. This suggests that the muscle was more powerful in the pedetines than it was in the parapedetines. M. masseter lateralis has a line of action that is predominantly vertical with only a relatively small horizontal component. It is probably less important than the other two divisions of the masseter since it produces a crushing action which is not so important in subdividing food as is a grinding action such as that produced by the other divisions of the masseter complex.

The remaining jaw muscles that need to be considered are mm. pterygoideus externus and internus. Both these muscles originate in the pterygoid fossa and insert into the mandible immediately below the condyle and on the ventral edge of the angle respectively. M. pterygoideus externus is a relatively small muscle and acts to draw the ramus on that side towards the midline and tends to pull the condyle out of the glenoid. In mammals that chew by means of lateral movements of the jaw this muscle is much more important than it is in rodents

in which lateral movements of the jaw are very limited but it probably helps in making minor positional changes of the jaw. M. pterygoideus internus is the larger of the two muscles and also acts to pull the jaw ramus toward the midline but in addition it acts to pull the condyle into the glenoid which may possibly be an important function in preventing the jaw being disarticulated. As with m. pterygoideus externus the inward pull of the muscle is resisted by the form of the jaw articulation. These two muscles would not seem to be particularly important when considering mastication and their development can only be properly ascertained in Pedetes. In Megapedetes the region of the cranium including the pterygoid fossae is not preserved so that the development of mm. pterygoidei in this genus cannot be determined: in Parapedetes pterygoid fossae are not present which suggests that these muscles were not well developed. The very thick ventral edge of the angle in this latter genus might be thought to suggest that m. pterygoideus internus was large but it is probable that this thickening was related more to the relatively large m. masseter superficialis and provided a secure insertion for this muscle

Summary:

In the pedetine line of the Family Pedetidae evolution in the jaw system has been towards increasing hypsodonty and apparently an increasing of the force produced by m. masseter medialis. In conjunction with this the line of action of m. masseter superficialis has been made more horizontal by the anterior displacement of the lower maxillary root of the

zygoma which probably occurred to further enlarge the infra-orbital foramen. The effect of these changes has been to increase the efficiency with which very tough food can be eaten and it is suggested that such a change was necessary because the pedetines underwent a shift in their ecology and moved from moist, possibly forested, environments into semi-arid areas where the vegetation was tougher, requiring the production of higher masticatory forces to subdivide the food, and was also less nutritious which would require the animals to eat more; both factors would mean that the animals would have to be able to withstand more rapid tooth wear as would an increase in the amount of dust and soil in the food. This too would be likely to occur with a shift in ecology such as that proposed.

In Parapedetes the presence of semi-hypsodont cheekteeth suggests a somewhat similar need to resist the effects of tooth wear and implies an abrasive diet. The relatively reduced size of the infra-orbital foramen when compared with the pedetines implies that m. masseter medialis was smaller and consequently suggests that, during the active forward stroke of mastication, the pressure that could be brought to bear on the food was less than in the other pedetids. To some extent this may have been balanced by a larger m. masseter superficialis with a line of action more parallel to that of m. masseter medialis but it is possible that Parapedetes, while living under dry conditions, did not eat such tough vegetation as Pedetes. It would seem that the pedetines and parapedetines both had to solve a similar problem but adopted slightly different solutions to it.

Vertebral column:

The functional anatomy of the vertebral column in ricochetal rodents has been discussed in some detail by Hatt (1932). This study of the Family Pedetidae does not provide any further information on possible function in the vertebral column.

Forelimb:

The forelimb has not been completely preserved in any of the fossil forms and is thus known entire only in the living species: the manus, especially, is very poorly known. It has been stated in Smithers (1971) that in Pedetes the forelimb is used to loosen the soil in burrowing and this use is also mentioned in Pocock (1922). However St. Leger (1931) used the presence of a forelimb not adapted for burrowing as a character for keying down Pedetes. MacInnes (1957) pointed out that the forelimb in the living species is rather weak and, quoting Cuvier (1827) which is itself a reference to Burchell (1822), suggested that it is of less importance in fossorial activities than it is in manipulating the animal's food; Pocock (1922) also mentioned this use of the forelimb.

The anatomy of the forelimb in pedetids displays a curious mixture of characters with the upper part displaying characters that might be expected in a fossorial rodent while the lower part does not show such characters. Lehmann (1963) and Goldstein (1972) have discussed a number of features to be found in the forelimb of a burrowing rodent and comparisons can also be made with other non-rodent burrowers.

According to Lehmann (1963) the development of a teres major process on the postero-dorsal corner of the scapula is an adaptation for a fossorial way of life. This process increases the size of the origin of m. teres major and is found in the living species of the genus Pedetes and, although rather less well developed, in Megapedetes; these are the only pedetids in which the scapular plate is preserved. Coupled with a well developed origin there is also a well developed insertion for m. teres major on the humerus directly below the lesser tuberosity. This insertion takes the form of a low tubercle in the pedetines but in Parapedetes and SAM-PQ 2121 it forms a prominent ridge. M. teres major was therefore, apparently, well developed in all the pedetids: this muscle is a medial rotator of the humerus and also draws it posteriorly. According to Lehmann (1963) the principal action of m. teres major is that of drawing the humerus posteriorly or flexing the shoulder joint and the action of flexing the limb against the resistance of the substrate is an important action in digging.

Inserting at the same point on the humerus as m. teres major is m. latissimus dorsi which has its origin on the neural spines of the posterior thoracic and anterior lumbar vertebrae and the lumbar fascia. These neural spines are well developed in all pedetids but it seems unlikely that the size of m. latissimus dorsi has been the major factor in determining the development of these structures. This muscle has a similar action to m. teres major and with the latter is the principal flexor of the shoulder joint. The evidence of its insertion on the humerus suggests that it was better

developed in parapedetines than in pedetines which would imply that the former were better adapted for digging than the latter. Overall the evidence suggests that as a combined muscle mass the shoulder flexors were well developed and it is probably unreasonable to make too detailed a separation of the respective contributions of m. latissimus dorsi and m. teres major, especially in the fossil forms.

Also in the scapula the presence of a well developed spine, an oval glenoid, a well developed coracoid process and an acromion process that projects well beyond the glenoid are all adaptations for a fossorial way of life (Lehmann, 1963). In Pedetes the glenoid is oval and the spine is quite well developed but the coracoid process is not particularly large and the acromion process is short. In both Megapedetes and Parapedetes the spine is also well developed, the glenoid is oval and the acromion is short. However both of these genera have, in addition, a quite well developed coracoid process.

The development of the scapular spine and acromion process is related to the development of mm. deltoidei. Although well developed in pedetids the scapular spine is really only comparable with the spine in non-burrowing rodents which suggests that mm. deltoidei were not greatly enlarged. The deltoid tubercle on the humerus is, however, large but since it forms part of a complex including the pectoral crest and tricipital line its size may be related to factors increasing other parts of the overall complex rather than to direct influence of mm. deltoidei. Thus it seems likely that while being sizeable mm. deltoidei were not unduly enlarged.

Lehmann (1963) states that the longer acromion process in fossorial rodents reduces the degree of lateral movement at the glenohumeral joint. This is an advantage in a forelimb adapted exclusively for digging but is less advantageous if other uses, requiring greater freedom of movement, are also important. This latter case applies to the pedetids in which the forelimb is important in feeding for carrying food to the mouth and holding it while the animal examines it. For such a use increased freedom of movement is required which may partly explain the fact that a long acromion process has not been evolved. Even in Megapedetes, in which the acromion process is better developed than in Pedetes, it is still relatively short.

The oval glenoid found in pedetids is elongated in the antero-posterior axis and although an adaptation of functional significance in burrowers it is also found in many other non-burrowing rodents. Consequently it provides little evidence of specific adaptation to a fossorial habit but at least it does not provide evidence against such a way of life. A poorly developed coracoid process is to be expected in non-burrowing rodents which suggests that Pedetes is less well adapted for burrowing than is either Megapedetes or Parapedetes both of which have well developed coracoid processes. One implication of this is that pedetids were apparently better adapted to burrowing in the Miocene than they are now which supports the idea that there has been a change in their ecology since that time.

In the humerus the head is rounded but is more oval in Megapedetes than it is in Pedetes. This too implies that

Megapedetes was better adapted for burrowing than is Pedetes (Lehmann, 1963). The development of the region of the delto-pectoral crest in the humerus in all pedetids has been mentioned above: this region is better developed in Recent Pedetes than in P. laetoliensis although the general proportions of the humerus do not differ within this genus; in Megapedetes the delto-pectoral crest is well developed but is narrower than in the living species. In both Parapedetes and SAM-PQ 2121 the delto-pectoral crest is also large. The variations in the development of this region suggest that there was some degree of variation in the development of the associated muscles but the general proportions imply some degree of adaptation for burrowing in all pedetids.

The supinator crest is relatively well developed in all the pedetids but is larger in the Recent species than in any of the others. Muscles originating from this crest and the lateral epicondyle immediately below are principally supinators and extensors of the forearm. The medial epicondyle is well developed and possesses a distinct dorsal hook-like process in Pedetes; in Megapedetes the medial epicondyle is less well developed than in the Recent animals whilst the situation in Parapedetes is uncertain. This region of the humerus provides origins for pronators and flexors of the forearm.

Goldstein (1972) produced a regression line correlating humerus length with epicondylar width and the measurements in both Pedetes and Megapedetes fall on the curve for generalised burrowers in having an epicondylar width that is

about 33% of the humeral length. The necessary measurements cannot be determined in Parapedetes so it is at present not possible to say whether this genus fits the same regression curve as the other two genera. It is also interesting that the relation between epicondylar width and humerus length in the two pedetine genera is almost the same as that in Orycteropus which is highly adapted for burrowing (MacInnes, 1956).

In the forearm Goldstein (1972) analysed the relationship between the length of the olecranon process of the ulna and the length of the ulna distal to the trochlear notch. In Recent Pedetes the olecranon length is about 14% of the ulnar length which is considerably less than that predicted from the ulnar length not only for a generalised burrower but even for a generalised rodent. P. laetoliensis has an olecranon process that is even shorter relative to the ulnar length than in the living species, the proportion being about 7%. In Parapedetes the olecranon process is not well developed but it was not possible to obtain a measurement of it so the exact proportions cannot be worked out. There are no remains of a complete ulna in Megapedetes so that this calculation cannot be carried out but on casual observation the proportions seem to be generally similar to Recent Pedetes.

The lateral surface of the shaft of the ulna bears a shallow fossa in all the pedetids and this is the condition found in generalised rodents. In fossorially adapted forms this fossa becomes deepened. The only sign of fossorial adaptation in the ulna of pedetids is the relatively robust nature of the bone in Megapedetes.

Lehmann (1963) states that the only features of the radius that differ between fossorial and non-fossorial forms are the degree of lateral curvature and the distal modification of the shaft. Although the radius is curved in all pedetids it is not greatly so and while it may be interpreted as showing an incipient fossorial adaptation it does not show a clear adaptation for this way of life. At the distal end the radius in pedetids does not show the development of a pseudostyloid process, which is found in some burrowing rodents (Lehmann, 1963).

Finally the manus in the living species is relatively weak with long, apparently quite delicate, claws although it is quite broad. The manus in Megapedetes is much more robust but is not fully preserved and the only other remains of this part of the body are the scapho-lunar and centrale in SAM-PQ 2121 which suggest a manus of similar construction and strength to that in the living species. Whilst the manus in the living species does not give the impression of being adapted for burrowing that of Megapedetes would have been much more suitable for this purpose.

A particularly interesting feature of the manus in the living species of the genus Pedetes is the possession of a well developed radial ossicle made up of two segments (see Chap. 2). This ossicle was discussed by a number of anatomists in the late nineteenth century (e.g. Bardeleben, 1889 & 1890; Parsons, 1898) particularly in relation to the possibility of its representing the remnant of a praepollex. Pocock (1922) discusses the radial ossicle (= inner carpal pad) and the outer carpal pad and suggests that they may

have importance in grasping food; the opinion is also stated that the carpal pad arrangement in Pedetes is unique although, in fact, a number of other mammals possess a radial ossicle but this is not often as well developed as in Pedetes. There are analogous, if not homologous, ossicles present, for example, in Dipus (Parsons, 1898), Talpa and Ailuropoda (Jones, 1940). In the absence of detailed work on behaviour in Pedetes the exact function and hence likely explanation for the development of a well developed radial ossicle must remain in doubt. Its most likely function is in connection with the manipulation of food and in the modern species food is certainly manipulated in the hands (Coe, pers. comm.; pers. obs. of specimens in London Zoo) although an analysis of the exact movements made has not been carried out.

With the exception of SAM-PQ 2121 there are no fossil remains of the proximal carpus. The scapho-lunar preserved in SAM-PQ 2121 is very similar to that of Pedetes and provides evidence of the presence of a radial ossicle. This would mean that the evolution of this feature occurred very early and that the manipulation of food items was found even in early pedetids; the possible taxonomic importance of this was discussed in Chapter 7.

Conclusions:

Evidence from the anatomy of the forelimb shows that in all pedetids there has been some adaptation of this limb for fossorial activity. Most of the characteristic fossorial features are found in the scapula and humerus rather than in the forearm and manus which, on the contrary, show signs of

not being particularly well adapted for fossorial activity. A number of the features considered to provide evidence of fossorial adaptation are better developed in Megapedetes than in Pedetes suggesting that the former genus may have been more fossorial than the more recent animal. Parapedetes displays the same sort of adaptations for fossorial life as the pedetines but the state of the Parapedetes fossils means that the features concerned are not so clearly visible.

Two non-anatomical sources of evidence also suggest that burrowing was important in the evolution of the group. The first of these lines of evidence involves the fossil species Pedetes laetoliensis and Parapedetes namaquensis. At both Laetoli and Elisabethfeld most of the faunal remains, even the remains of robust forms, are badly broken up and dispersed but at both sites the pedetid remains are exceptionally well preserved with articulated skeletons present. According to M.D. Leakey (pers. comm.) the way the remains of Pedetes laetoliensis were found suggests that the animals had been trapped in burrows by ash-falls which prevented these remains becoming broken up and dispersed by scavengers and weathering. Also at Laetoli other well preserved forms are also probable burrowers including the lagomorphs and some of the small carnivores; these were probably similarly trapped and killed in their burrows by a volcanic eruption. At Elisabethfeld the remains of Parapedetes are well preserved in a similar manner to the remains of P. laetoliensis at Laetoli. Stromer (1926) suggested that the animals had been trapped on a hillock and drowned by a flash flood as a possible explanation for the state of preservation but such a

mechanism might be expected to disperse the dead animals rather than keep them together. The idea that the Parapedetes individuals were killed by a flash flood is still a possibility but it is suggested that the flood trapped and drowned the animals in their burrows and this has been the cause of their good preservation. In both of these cases the suggested hypothesis implies that the relevant fossil species were similar to the Recent species in resting in burrows which, presumably, they had dug, as the living animals do. According to Smithers (1971) the forelimbs in living animals are used to dig the burrows as well as to dig up food: the hindlimbs are used to expel the soil during burrowing after it has been loosened by the forelimbs.

The second line of evidence comes from physiological investigations carried out on Pedetes surdaster (Müller et al., 1979). The animals used are actually described as Pedetes capensis but since the work was done in Kenya it was presumably carried out on P. surdaster. This work shows that physiologically P. surdaster is more similar to fossorial animals than to forms adapted for living in desert environments. This helps to explain why the Recent species are restricted to semi-arid areas and suggests that fossorial activity has been an important feature of life in pedetids.

Hindlimb:

In all pedetids the hindlimb is adapted for ricochetal locomotion and is much better preserved in the fossils than is the forelimb.

The innominate bone in the pedetines is robust and well developed but is less so in Parapedetes. This suggests that the upper leg muscles were better developed in members of the former group than in the latter but because of the poor preservation of the bone in Parapedetes some features cannot be seen.

The origin of m. rectus femoris is well developed in Pedetes and Megapedetes but cannot be seen in Parapedetes. This muscle was apparently large and powerful as would be expected in a ricochetal mammal. The areas of origin of mm. gluteus medius and gluteus minimus are large and are positioned anterior to their insertions due to the high trochanter major. This suggests that they could act as extensors of the hip joint and thus contribute to jumping.

In the pedetines there is a high ischial tuberosity implying that mm. quadratus femoris, biceps femoris, semitendinosus and semimembranosus were well developed. The first of these muscles extends the femur and thus contributes to jumping; it also rotates the femur laterally. The other three muscles can act as leg extensors as well but also act as flexors of the lower leg. It is considered more probable that it was the need of these muscles to act as leg extensors that selected for the development of a large area of origin on the high ischial tuberosity rather than other functions that they may have. In parapedetines the ischial tuberosity is poorly developed and this implies that the posterior leg extensor muscles were not particularly well developed and that, consequently, this group was less specialised for ricochetal locomotion.

The high trochanter major of the femur has been mentioned above in relation to the possible line of action of mm. glutei. In all pedetids, except the living species, there is a pronounced tubercle on the anterior face of this trochanter. This probably provided part of the origin of m. vastus intermedius and suggests that this muscle, part of m. quadriceps extensor, was strong. The reason why the origin of this muscle should be less well developed in the Recent species even though they are highly specialised for ricochetal locomotion is unclear.

At the distal end of the femur the origin of m. extensor digitorum longus is well developed as also are the origins of both heads of m. gastrocnemius. The latter muscle is one of the principal extensors of the ankle and its large size is, therefore, considered to be related to the needs of ricochetal locomotion. M. extensor digitorum longus is, as its name implies, an extensor of the toes but in addition it may act as a flexor of the ankle. Its large size may possibly be due to the need for a powerful mechanism for holding the toes rigid when they act as the last segment of the "lever" propelling the animal in leaping.

The antero-lateral and posterior surfaces of the upper tibia are deeply concave allowing the presence of large muscles. Those posterior to the tibia assist in extending the foot which is an important action in jumping: the antero-lateral muscles are largely flexors of the foot.

In the pes digit 3 is dominant in the pedetines and this type of pes, with a single digit dominant, is common in

ricochetal mammals. Parapedetes has a paraxonic pes with digits 3 and 4 equally dominant. The pes in Megapedetes is considered to be the most primitive pes of any known pedetid as it has all five digits present and is mesaxonic: both the hallux and digit 5 are a little reduced while the other three digits are of more equal size although digit 3 is slightly the largest. The pes in Pedetes can be easily derived from that of Megapedetes by suppression of the hallux but this would not affect the functioning of the pes.

Parapedetes has a different design of pes to the pedetines (see Chap. 7 for the taxonomic implications). Digit 3 and 4 are of equal size; digit 2 is slightly smaller; digit 5 is very reduced: there may have been a hallux present as well. A paraxonic design of the pes appears to be unusual in ricochetal mammals: in most of these the principal longitudinal axis of the foot runs down one of the metatarsals rather than between two of them. In the macropodid marsupials the axis runs down the greatly enlarged Mt.IV (Saunders et al., 1969) while in the dipodid rodents it runs down the cannon bone which is formed by the fusion of Mts.II, III and IV (Walker, 1975). Zapus and related forms have a somewhat paraxonic hind-foot with digits 3 and 4 of about equal length (Pocock, 1922), rather as in Parapedetes; however these two digits are held close together in the zapodids which does not appear to have been the case in Parapedetes.

Elongation of the hind-limb in saltatorial mammals is to increase leverage (Young, 1962) and thus make leaping more efficient but there seems no reason why this, acting in

isolation, should favour a design in which the principal axis of the foot runs along a metatarsal rather than between two. A possible explanation for the paraxonic form of the hind-foot in Pa. namaquensis is that it is an adaptation for locomotion on a soft substrate, spreading the weight of the animal over a greater area than is the case in the pedetines.