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POSTCRANIAL MORPHOLOGY AND SPRINGING ADAPTATIONS IN PEDETIDAE FROM ARRISDRIFT, MIDDLE MIOCENE (NAMIBIA).

by

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ABSTRACT

Arrisdrift, an early Middle Miocene site in the Proto-Orange river deposits of Namibia, was excavated in the mid 1970s by Corvinus and since 1993 by the Namibia Palaeontology Expedition. These excavations resulted in the discovery of several postcranial elements of springhares. Generally, these appear to have been smaller than those of modern *Pedetes capensis* or *P. surdaster*, but more robust that those of the extant taxa. The Arrisdrift pedetid was larger than the lower Miocene Namibian species, *Parapedetes namaquensis*; must smaller and less robust than the lower Miocene East African species, *Megapedetes pentadactylus*; but larger than *Pedetes laetoliensis* from the Pliocene site of Laetoli (Tanzania). The limb proportions, morphology of the proximal femur, distal tibia, astragalus and the calcaneum suggest that the pedetid from Arrisdrift was saltatorial, but to a lesser degree than modern springhares. It exhibits features probably related to locomotor behaviour which are different from *Parapedetes*, *Megapedetes* and *Pedetes* suggest that they may represent a different genus in accordance with results of research on the cranio-dental remains (Mein & Senut, in prep.)

KEYWORDS: Pedetidae, Middle Miocene, Namibia, post-cranial anatomy, Arrisdrift.

INTRODUCTION

The earliest representatives of the family Pedetidae have been found in the early Miocene of East Africa in Kenya (Songhor, Rusinga) and in Uganda (Napak) with *Megapedetes pentadactylus* (MacInnes 1957; MacInnes *in* Bishop 1962; Lavocat 1973) and a smaller species is known at Kalodirr and Meswa Bridge in Kenya (Winkler 1992). *Parapedetes namaquensis* was described by Stromer in 1926 from the early Miocene of the South West African Sperrgebiet. Pedetids are known from the Middle Miocene of East Africa in Kenya at Fort Ternan (Denys & Jaeger 1992) and Muruyur and Maboko (Winkler 1992), from North Africa in Morocco at Beni Mellal (Lavocat 1961) and in Tunisia (Batik & Fejfar 1990) where the genus *Megapedetes* occurs. Pedetids are also known from the Middle Miocene of the Aegean area at Chios in Greece and Bayraktepe 1 in Turkey whence *Megapedetes aegaeus* has been described (Tobien 1968; Sen 1977). The living genus occurs in the Plio-Pleistocene of Tanzania at Laetoli (Dietrich 1942; Davies 1987), Olduvai Gorge Bed I (Leakey 1965) and at several sites in South Africa at Florisbad (Dreyer & Lyle 1931) and Taung (Broom 1930, 1934). They have also been recorded in the Pleistocene of Zimbabwe in breccias identified near Bulawayo (de Graaff 1981; Zeally 1916). More recently, field work by the Namibia Palaeontology Expedition in the Miocene aeolianites at Rooilepel and late Miocene deposits at Berg Aukas and Harasib 3a in Northern Namibia (Pickford *et al.* 1994; Mein *et al.* in press) led to the discovery of other pedetids which are still under study.

Miocene Pedetidae have been known in Nambia since 1926 when Stromer published the first remains, *Parapedetes namaquensis*, from the early Miocene site, Elizabethfeld. More recently work was done in the Proto-Orange deposits at Arrisdrift in the mid 1970's which resulted in the discovery of a very rich Middle Miocene fauna (Anonymous 1976; Hendey 1978; Corvinus & Hendey 1978) including new specimens of Pedetidae which have never been published. Since 1993, excavations by the Namibia Palaeontology Expedition at the invitation of NAMDEB (previously, CDM Pty Ltd) at Arrisdrift (Pickford *et al.* 1996), have led to the recovery of several new specimens including adult hindlimb elements which are described here. Another paper on the systematics of early Miocene Pedetidae is in preparation with Dr. P. Mein.

GEOLOGICAL SETTING

The site of Arrisdrift is located in the lower part of the Orange River in a fossil loop of the river which cut into Proterozoic rocks of the Gariep Group. The fluviatile deposits, which accumulated in a palaeo-channel of the river, consist of 1m thickness of indurated conglomerates, clays silts and sands which have yielded a very rich fauna (Hendey 1978; Pickford 1995; Pickford *et al.* 1996), the age of which is estimated to be 17.5 Ma.

MATERIAL

AD 215'95 :	right femur
AD 216'95 :	distal end of right tibia
AD 540'94 :	right calcaneum
AD 279'95 :	right metatarsal V
PQ AD 2018 :	Left calcaneum
PQ AD 845 :	fragmentary right calcaneum
PQ SAD 64 :	distal left metatarsal III
PQ AD 220 :	distal metatarsal IV
PQ AD 302 :	pedal proximal phalanx
PQ AD 427 :	pedal proximal phalanx

PQ AD specimens come form an assemblage which was housed up to 1995 at the South African Museum in Cape Town (Palaeontology Quaternary, Arrisdrift) and now at the Geological Survey of Namibia Museum in Windhoek (Namibia).

The specimens labelled AD come from collections made at Arrisdrift since 1993 by the Namibia Palaeontology Expedition and are housed at the Geological Surveyu of Namibia Museum in Windhoek (Namibia.)

DESCRIPTIONS

Femur (AD 215' 95) (Figures 1, 2)

The right femur was broken at the midsharft level and was naturally reconsolidated by a thin calcitic layer. The bone is smaller but more robust than that of the modern *Pedetes capensis*, but both species exhibit a straight shaft in anterior view. On its medial border, the rounded *caput femoris* exhibits a depression for the insertion of the *ligamentum teres*. This resembles the morphology seen in *Megapedetes* whereas in modern *Pedetes* the depression is almost absent. The *caput femoris* faces more anteriorly and slightly more proximally than that of the *Pedetes capensis*. The *trochanter major*, albeit strongly projected proximally above the *caput femoris*, is not as salient as in modern Pedetidae from Southern Africa and is not splayed out as in *Pedetes*. In this regard, it recalls the morphology seen in *Megapedetes*. Moreover, it is slightly more massive and less bowed forward as is the case in extant species. Its median part is thicker than that of the modern species. In posterior view, the *trochanter major* is rectangular in shape being elongated

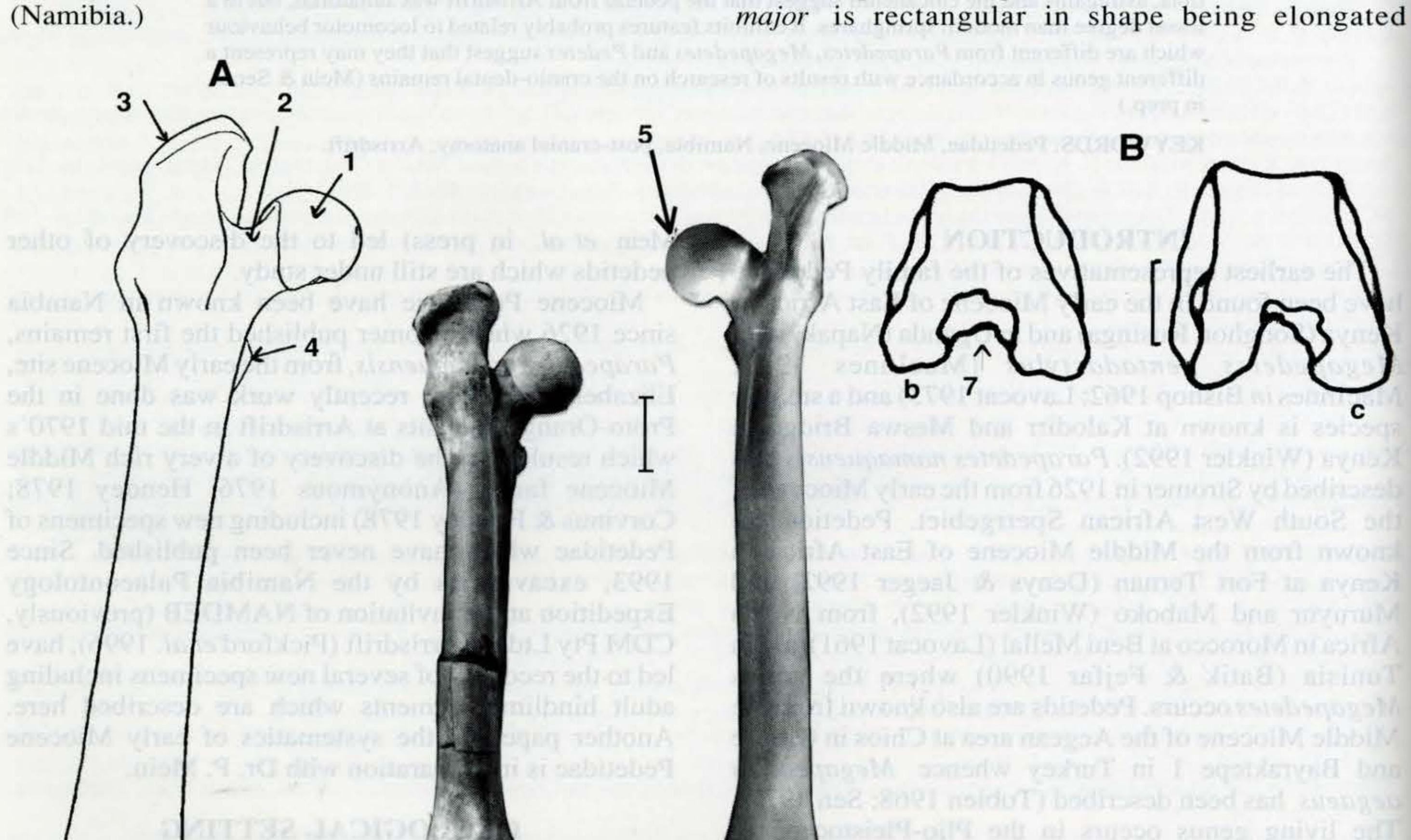

Figure 1: Comparisons of femora Pedetidae (A: anterior view and B: distal view) a: *Megapedetes pentadactylus* (right) (from MacInnes, 1957), b: AD 215'95 from Arrisdrift (right), c: modern *Pedetes* (left) (Bar = 1cm) 1. *caput femoris*, 2. *collum femoris*, 3. *Trochanter major*, 4. *trochanter minor*, 5. insertion for *ligamentum teres*, 6. *trochlea femoris*, 7. *incisura intercondyloidea*, 8. *fossa intertrochanterica*. (Bar = 1cm)

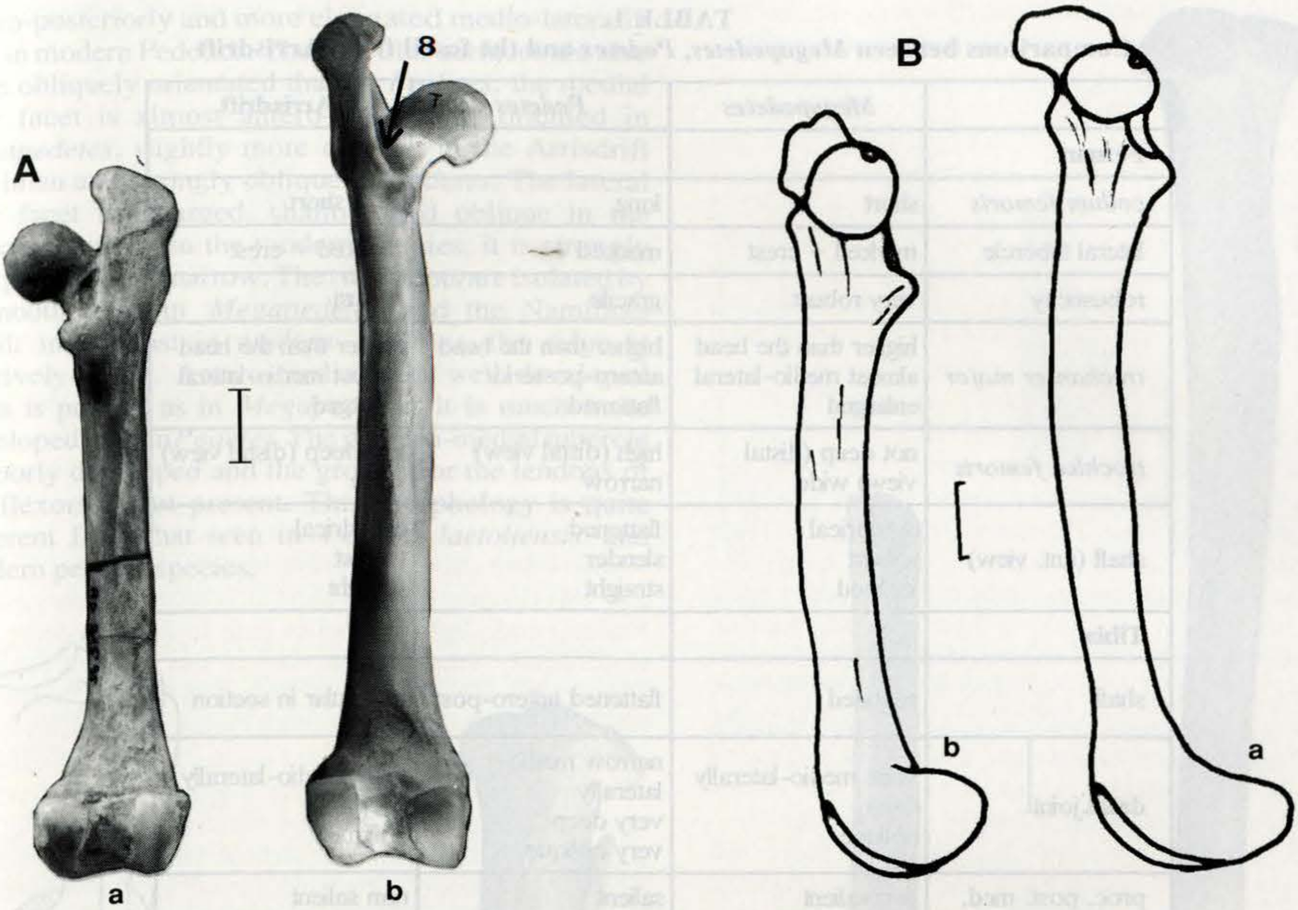

Figure 2: Comparisons of femora of Pedetidae (A: posterior view and B: medial view). a: AD 215'95 from Arrisdrift (right), b: modern *Pedetes* (left) (Bar = 1cm)

proximo-distally. In anterior view, three crests initiate from the *trochanter major*: a clear lateral one, a massive median one which ends in a thick tuberosity and a weak medial one. The *trochanger major* is enlarged at this level instead of being flattened with a very salient tubercle as in the modern genus. In proximal view, the *trochanter major* exhibits a blade-like shape in the modern species. In the Miocene fossils, there is an enlargement of the area related to the salience of the proximal tubercle. The *trochanger minor* is a very tubercle on the postero-medial border. The *trochanter minor* is set about 13 mm below the level of the middle of the head (it is 12 mm below it in modern *Pedetes* and 18 mm in *Megabedetes pentadactylus*). If we calculate the ratio of the distance between the *trochanter minor* and the *caput femoris* to the total length of the femur, we find the following values: 13.65 for the Arrisdrift specimen, 13.84 for *Megapedetes* and 10.85 for the modern spinghare. It seems that the distance between the *trochanger minor* and the middle of the femoral head is greater in *Megapedetes* and the Namibian fossil than in modern Pedetidae. This is due to the fact that the *caput femoris* faces more proximally in the fossil species than in the modern ones. The *trochanter minor* gives insertion to the ligament of the *m.ilio-psoas* which acts as a flexor of the hip joint and as an outward rotator of the thigh. This feature is probably related to the adaptation for bipedal springing. The *collum femoris* is rather thick and the proximal part of the shaft is slightly antero-posteriorly flattened, whereas it is slightly medio-laterally flattened in the modern animal. The deep *fossa intertrochanterica* is proximo-distally elongated. Along the diaphysis two crests run downwards for the insertion of the stabiliser muscles of the hip. They are slightly less visible on the fossil specimen, but this can be variable in modern animals. Distally and anteriorly, the *trochlea femoris* is high, narrow and shallow and the *incisura intercondyloidea* is proportionally wider and shorter than it is in *Pedetes capensis*. The lateral border of the *trochlea femoris* is salient and higher than the medial one, but this area is slightly abraded in the fossil and the degree of salience cannot be accurately estimated. However, it does not seem to have been salient as in modern pedetids. Posteriorly and distally, the *condylus medialis* is narrower and placed slightly higher than the *condylus lateralis*. Proximally to the condyles, two facets for the sesamoids are visible and the origins of the heads of the *m. gastrocnemius* are clearly marked. Laterally, the condyles are less antero-posteriorly elongated and less flattened than in *Pedetes capensis*. This would suggest a reduced flexion-extension at the knee joint in the fossils in which the articular surface is more compact. As a whole, compared with *Pedetes laetoliensis*, the fossil from Arrisdrift is longer and stouter. Moreover, the fossils

TABLE 1.
Comparisons between *Megapedetes, Pedetes* and the fossil from Arrisdrift

	Megapedetes	*Pedetes*	**Arrisdrift**
Femur			
collum femoris	short	long	very short
lateral tubercle	marked + crest	marked	marked + crest
robusticity	very robust	gracile	robust
trochanter major	higher than the head almost medio-lateral enlarged	higher than the head antero-posterior flattened	higher than the head almost medio-lateral enlarged
trochlea femoris	not deep (distal view) wide	high (distal view) narrow	not deep (distal view) wide
shaft (ant. view)	cylindrical robust inclined	flattened slender straight	cylindrical robust straight
Tibia			
shaft	rounded	flattened antero-post.	triangular in section
distal joint	wide medio-laterally deep oblique	narrow medio-laterally very deep very oblique	wide medio-laterally deep oblique
proc. post. med.	non salient	salient	non salient
Calcaneum			
shaft	long	elongated	long
lateral talar facet	salient	non salient	salient
anterior part	elongated	very elongated	elongated
cuboid facet	wide	elongated-triangular	wide and short
Metatarsals			
Metatarsa V	very robust cylindrical shaft stright shaft	gracile flattened shaft strongly inclined shaft	robust cylindrical shaft inclined shaft

from Laetoli are closer to modern *Pedetes* (Davies 1987). The morphology and the robusticity of the Namibian fossilo clearly recalls *Megapedetes* from the lower Miocene site of Songhor in Kenya (MacInnes 1957). The latter is larger and more massive than the Namibian fossil. The tubercle on the *trochanter major* is more developed. On a flat substrate, the shaft of *Megapedetes* leans about 5° from the perpendicular, whereas the femoral shafts of *Pedetes* and the Arrisdrift fossil are straight. It is also less curved in the Miocene fossils than it is in the Pliocene and modern species.

Tibia (AD 216'95) (Figures 3,4)

This right distal tibia (maximum measurable length : 73.1 mm) which is broken roughly at the midshaft level would have been about the same size as that of the modern *Pedetes capensis.* It shows, as in the extant species, an elongation of the shaft which indicates saltatorial activities. It is impossible to confirm whether the fibula was fused to the tibia as is the case in modern pedetids, as the specimen is broken just at the level where the fusion should occur distally. The tibial shaft is straight in anterior view and anteriorly concave in lateral view as in the *Megapedetes*, but is different from *Pedetes* which is slightly concave. The anterior tibial crest is distinct on the distal shaft, but smooth in the Miocene fossils, whereas it is not expressed in the distal tibia of modern Pedetidae. The shaft section is triangular at the midshaft (where the bone is broken) and strongly compressed medio-laterally. The postero-medial and postero-lateral crests are rounded and the base of the anterior crest for the insertion of the *m. gracilis* and *semiendinosus* is barely visible. The *processus posterior medialis* is clearly expressed but not bordered by two crests as is the case in modern pedetids. The articulation for the astragalus is shorter antero-posteriorly and more elongated medio-laterally than in modern Pedetids. The articular surfaces are also more obliquely orientated than in *Pedetes*: the medial talar facet is almost antero-posteriorly oriented in *Megapedetes*, slightly more oblique in the Arrisdrift specimen and strongly oblique in *Pedetes*. The lateral talar facet is enlarged, shallow and oblique in the Miocene fossils; in the modern species, it is strongly oblique, deep and narrow. The two facets are isolated by a smooth ridge in *Megapedetes* and the Namibian fossil; in contrast in modern *Pedetes*, the ridge is relatively sharp. Antero-medially, a well developed fossa is present as in *Megapedetes*; it is much more developed than in *Pedetes*. The postero-medial tubercle is poorly developed and the groove for the tendons of the flexors is not present. This morphology is quite different from that seen in *Pedetes laetoliensis* and modern pedetid species.

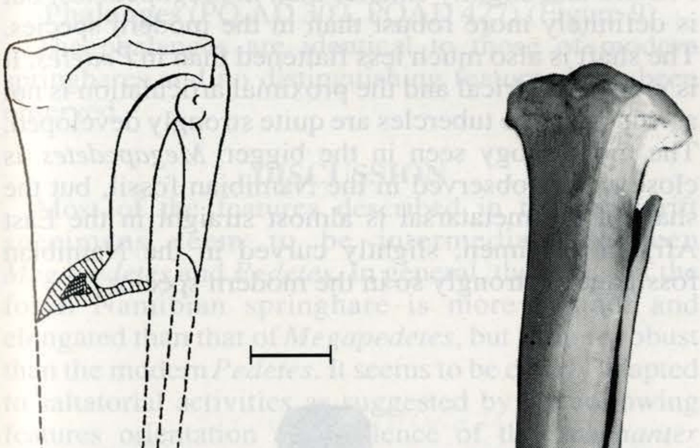

Figure 3: Comparisons of tibiae of Pedetidae (anterior view) (Bar = 1cm) a: *Megapedetes pentadactylus* (left) (from MacInnes, 1957), b: AD 216'95 from Arrisdrift (right), c: modern *Pedetes* (left) 1. talar joint, 2. *malleolus*.

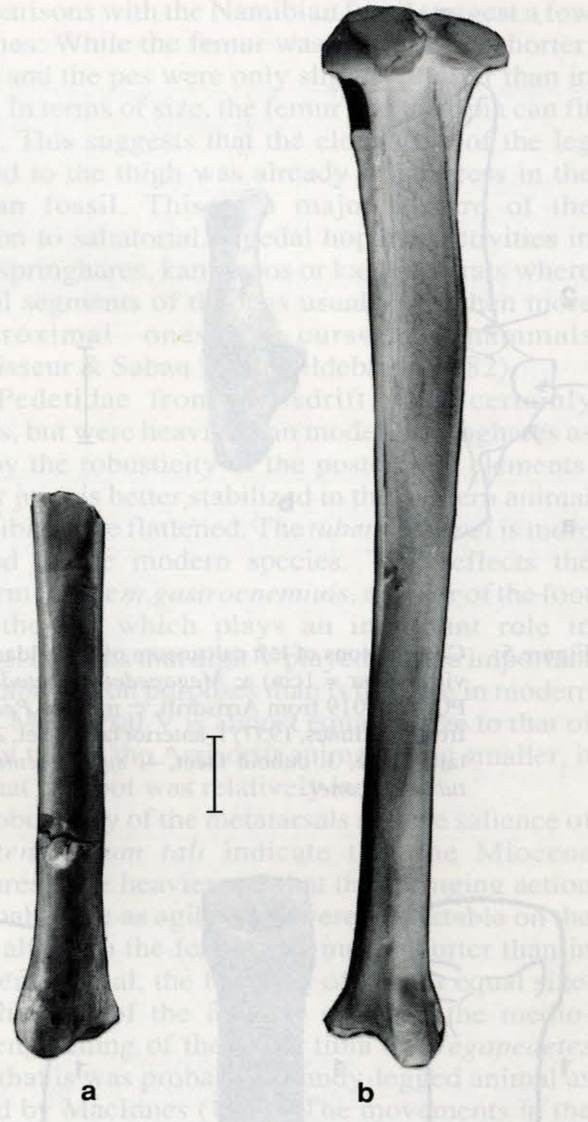

Figure 4: Comparisons of tibiae of Pedetidae (posterior view) (Bar = 1cm) a: AD 216'95 from Arrisdrift (right), b: modern pedetes (left).

Calcaneum (540'94, PQ AD 2018, PQ AD 845) (Figure 5)

The calcaneum is shorter and wider in the Arrisdrift fossils than in modern pedetids, and in this respect is closer to *Megapedetes*. In particular, the *sustentaculum tali* is medially salient and the anterior calcaneal facet more developed, whereas it is poorly offset and scarcely visible in modern pedetids. The posterior calcaneal facet is more medio-laterally elongated in the modern than in the Arrisdrift specimen and *Parapedetes namaquensis* (Stromer 1926). The anterior part of the calcaneum is clearly more elongated in *Pedetes* than in the fossils. The cuboid facet is slightly wider than in modern animals and the *tuber calcanei* are almost the same size. The morphology seen in the Arrisdrift fossil resembles *Megapedetes* from East Africa. The proportions of the *tuber calcanei* indicate that the talar joint was not as elongated as in the genus *Pedetes* where it reflects a longer lever for the *m. gastrocnemius*.

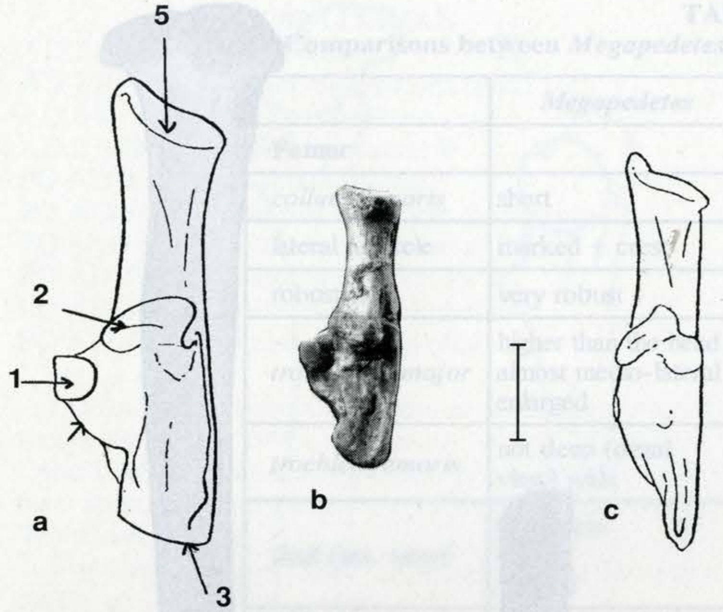

Figure 5: Comparisons of left calcaneum of Pedetidae (superior view) (Bar = 1cm) a: *Megapedetes pentadactylus*, b: PQ AD 2019 from Arrisdrift, c: modern *Pedetes*, (a, c from MacInnes, 1957) 1. anterior talar facet, 2. posterior talar facet, 3. cuboid facet, 4. *sustentaculum tali*, 5. *tuber calcanei*.

Metatarsals (AD 279'96, PQ AD 64, PQ AD 220) (Figures 6, 7, 8)

The metatarsal bones are isolated and it is not known whether they belong to the same individual In the distal metatarsal III (PQ Ad 64) (figure 6), the shaft seems to be rather straight and more cylindrical than in the modern animal. The distal articular surface exhibits a strong median keel on the posterior face and a depression on the anterior face. Medially and laterally, a deep hollow can be seen on the shaft. This general morphology is very similar to that of *Megapedetes*. Moreover, the size of the Namibian fossil is close to that of the modern animal and slightly smaller than *Megapedetes*.

The distal metatarsal IV (PQ AD 220) (Figure 7) exhibits roughly the same features as metatarsal III, but is generally smaller and more slender.

The most striking feature in the Metatarsal V (AD 279'96) (Figure 8) is its size. It is almost as large as in *Pedetes* and slightly smaller than in *Megapedetes*, but is definitely more robust than in the modern species. The shaft is also much less flattened than in *Pedetes*. It is more cylindrical and the proximal articulation is not as wide, but the tubercles are quite strongly developed. The morphology seen in the bigger *Megapedetes* is close to that observed in the Namibian fossil, but the shaft of the metatarsal is almost straight in the East African specimen, slightly curved in the Namibian fossil and is strongly so in the modern species.

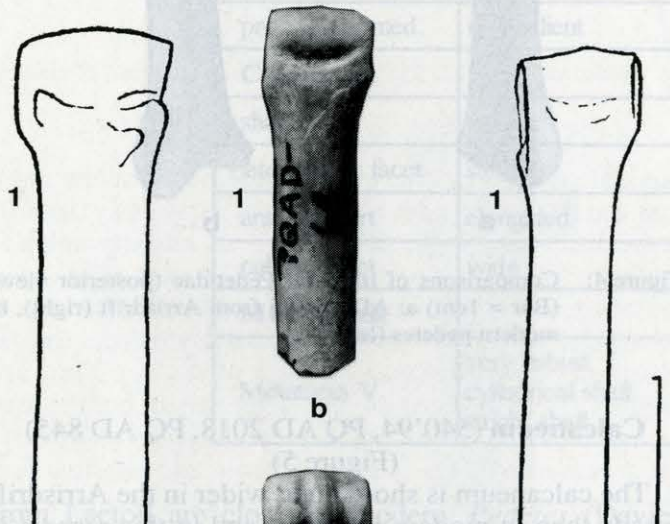

Figure 6: Comparisons of left Metatarsal III of Pedetidae (1: anterior view; 2: posterior view) (Bar = 1cm) a: *Megapedetes pentadactylus*, b: PQ AD 64 from Arrisdrift, c: modern *Pedetes*, (a, c from MacInnes, 1957).

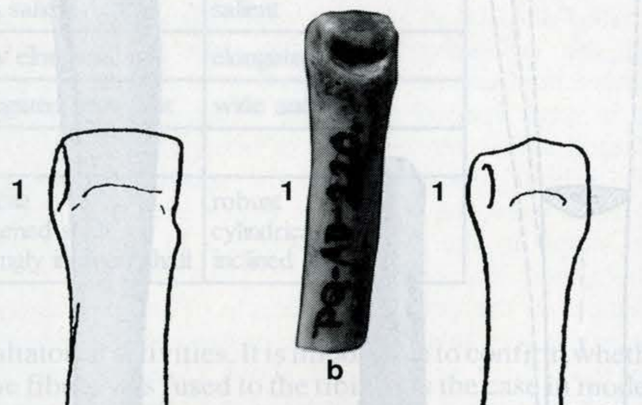

Figure 7: Comparisons of left Metatarsal IV of Pedetidae (1: anterior view; 2: posterior view) (Bar = 1cm) a: *Megapedetes pentadactylus*, b: PQ AD 220 from Arrisdrift, c: modern *Pedetes*, (a, c from MacInnes, 1957).

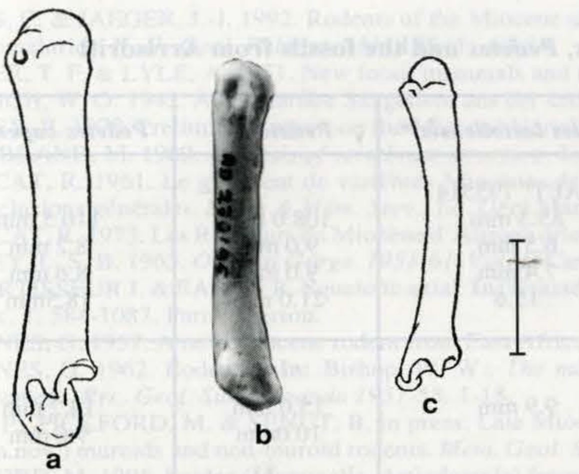

Figure 8: Comparisons of left Metatarsal V of Pedetidae (anterior view) (Bar = 1cm) a: *Megapedetes pentadactylus*, (left), b: AD 279'96 from Arrisdrift (right), c: modern *Pedetes* (left)(a, c from MacInnes, 1957).

Phalanges (PQ AD 302, PQAD 427) (Figure 9)

The phalanges are identical to those of modern springhares and no distinguishing features have been observed.

DISCUSSION

Most of the features described in the Arrisdrift specimens seem to be intermediate between *Megapedetes* and *Pedetes*. In general, the femur of the fossil Namibian springhare is more slender and elongated than that of *Megapedetes*, but is more robust than the modern *Pedetes*. It seems to be clearly adapted to saltatorial activities as suggested by the following features orientation and salience of the *trochanter major*, salience and position of the *trochanter minor*, robusticity of the lateral tubercle on the proximal femur, morphology of the patellar surface of the femur, depressed surfaces on the tibia for the articulation with the talus (which suggest stabilisation of the talar joint) and elongation of the anterior part of the talus. Most of

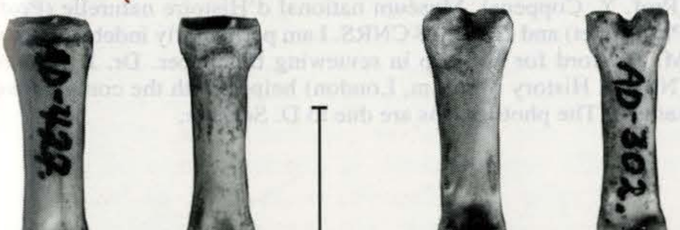

Figure 9: Phalanges of Pedetidae from Arrisdrift (1: anterior view; 2: posterior view) (Bar = 1cm) a: PQ AD 427, b: Pq AD 302.

these features reflect strong flexion at the hip and at the knee joint. However, comparisons with modern *Pedetes* suggest that the springing adaptation was slightly different, especially in the orientation of the articular surfaces and their better stabilisation in modern pedetids.

Comparisons with the Namibian fossil suggest a few similarities. While the femur was appreciably shorter, the tibia and the pes were only slightly shorter than in *Pedetes*. In terms of size, the femur and the tibia can fit together. This suggests that the elongation of the leg compared to the thigh was already in progress in the Namibian fossil. This is a major feature of the adaptation to saltatorial, bipedal hopping activities in modern springhares, kangaroos or kangaroo rats where the distal segments of the legs usually lengthen more than proximal ones in cursorial mammals (Lessertisseur & Saban 1967; Hildebrand 1982).

The Pedetidae from Arrisdrift were certainly springers, but were heavier than modern springhares as shown by the robusticity of the postcranial elements. The talar joint is better stabilized in the modern animal and the tibia more flattened. The *tuber calcanei* is more elongated in the modern species. This reflects the longer arm for the *m. gastrocnemiuis*, a flexor of the foot and of the leg which plays an important role in springing. It seems that digit V played a more important role in stabilization purposes than is the case in modern animals. Metatarsal V is almost equal in size to that of the extant taxon: the Arrisdrift animal being smaller, it shows that the foot was relatively larger.

The robusticity of the metatarsals and the salience of the *sustentaculum tali* indicate that the Miocene springhares were heavier and that the springing action was probably not as agile. they were very stable on the ground: although the femur was much shorter than in the modern animal, the foot was of almost equal size. The inclination of the femoral shaft, or the medio-lateral lengthening of the distal tibia in *Megapedetes* suggest that is was probably a bandy-legged animal as proposed by MacInnes (1957). The movements in the Namibian fossil would be more antero-posterior, the femoral shaft being straightened as in modern pedetids.

The differences observed with modern *Pedetes* are also found in the Pliocene species, *Pedetes laetoliensis*, which is very similar to *Pedetes surdaster* and *P. capensis*. This is also an argument supporting the suggestion that the Arrisdrift springhare was not as saltatorial as the modern ones are. The peculiarity of the features exhibited and their similarity with the Miocene East African Pedetidae suggests that the Arrisdrift specimens do not belong to the genus *Pedetes*, but are closer to *Megapedetes*. However, dental differences would suggest that the material belongs to a different genus (Mein & Senut in prep.)

In the light of the new discoveries of pedetids at Arrisdrift, we cannot conclude that the fossil from Arrisdrift was ancestral to modern pedetids. As a matter of fact, new discoveries made in the early Miocene of Namibia and South Africa would suggest that another pedetid smaller in size but closer to modern pedetids was inhabiting these areas. There is also important undescribed material from East Africa. The history of the Pedetidae seems then to be more complex than previously thought.

TABLE 2.
Comparative measurements between *Megapedetes, Pedetes* and the fossils from Arrisdrift

	Arrisdrift	*Megapedetes*	*Pedetes laetoliensis* *	*Pedetes*[$]	*Pedetes capensis*
Femur	AD 215'95		LAET' 795514		
Total length	95.2 mm	130.0mm[1]	85.3 mm	108.0 mm	110.5 mm
Ant.-post width	7.5 mm	11.0 mm	6.5 mm	9.0 mm	8.2 mm
Med. lat. width	8.2 mm	12.0 mm	7.4 mm	9.0 mm	8.6 mm
Bicond. width	18.3 mm	27. mm	15.6	21.0 mm	18.5mm
Tibia	AD 540'94				
Med.-lat. width	11.8 mm	18.1 mm	9.9 mm	15.0 mm	14.2 mm
Ant.-post. width	9.6 mm	13.2 mm		10.0mm	9.6 mm

[1] our measurment differs from MacInnes who measured 134.0 mm; this is probably due to the fact that the *trochanter major* is incomplete. This measurement can be only estimated on the right femur of the holotype.

	Arrisdrift			*Megapedetes*	*Pedetes laetoliensis* *	*Pedetes*[$]	*Pedetes capensis*
Calcaneum	AD 540'94	PQ AD 2018	PQ AD 845	LAET' 795514			
Total length	30.0 mm	29.5 mm		42.0 mm	29.4 mm	39.0 mm	37.4 mm
Total breadth	10.2 mm	10.0 mm	10.7 mm	15.6 mm	7.3 mm	9.5 mm	10.0 mm
L. tub. calci	15.1 mm	13.0 mm		23.7 mm	12.5 mm	18.0 mm	16.0 mm
Metatarsal V	AD 279'96						
Total length	30.7 mm			37.0 mm	25.8 mm	28.0 mm	30.6 mm

* measurements after Davies, (1987); [$] measurements after MacInnes, (1957).

CONCLUSION

Most of the features exhibited by the Arrisdrift fossils are close to those observed in *Megapedetes* and suggest a less agile springer than modern and Pliocene *Pedetes*. This is confirmed by the smaller size of the Namibian species, combined with a greater robusticity, by the less stabilized-talar joint and the longer metatarsals despite the fact that the anterior part of the calcaneum is not elongated. *Magapedetges* appears to exhibit less derived saltatorial adaptations than the Arrisdrift animal which seems to be less derived than the extant taxon. The postcranial differences suggest that the Namibian fossil belongs to a different taxon from *Pedetes* and that postcranial features can be useful in the systematics of pedetids.

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