

Description of a new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar

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SYNOPSIS. A new species of *Microgale* (shrew-tenrec) from primary forest in eastern Madagascar is described. Morphological comparisons are made with other members of the genus, in particular with those of the *Microgale cowani* and *M. gracilis* clusters, with which it shows greatest affinity.

INTRODUCTION

Eleven species of shrew-tenrecs belonging to the genus *Microgale* are currently accepted (MacPhee, 1987; Jenkins, 1988). The genus was believed to be much more diverse until the revision by MacPhee (1987) showed that over half of the named forms of *Microgale* were merely juveniles or morphological variants. Fortunately in the present case, adults of both sexes, a subadult and a juvenile were included in the small sample collected, so that adults could be distinguished with a good measure of confidence from those of other species and some observations were possible on the deciduous dentition. Distinctive cranial and dental features characterise the new species, which is further distinguished from most other species by its large size.

Brief comments are included on the other species of *Microgale* collected from the same locality.

MATERIALS AND METHODS

Small mammal trapping was carried out for two months by the Madagascar Environmental Research Group in primary forest of the Ambatovaky Forest Reserve (Barden, in prep.). A mixed collection of rodents and small tenrecs was collected, including the undescribed form. Preliminary identifications based on external features were made by members of the Research Group, who then brought the specimens to The Natural History Museum [BM(NH)] for formal identification, which in these mammals, requires the examination of a suite of craniodental characters in addition to external features. The preliminary identifications were recorded (Nicoll & Rathbun, 1990), some of which were found to be incorrect following detailed examination.

Measurements were taken with dial calipers and are given in millimetres. The dental nomenclature follows that of Mills (1966), Swindler (1976), Butler & Greenwood (1979) and MacPhee (1987). The following abbreviations are used in the text c.—circa, GCL—greatest cranial length, HB—head and body length.

Microgale dryas sp. nov.

HOLOTYPE. BM(NH)91.230, collector's number RAN 33610, adult female, in alcohol, skull extracted. Collected 20 February 1990 by Tanya Barden and Christopher Raxworthy, Madagascar Environmental Research Group from Site 1, Ambatovaky Special Reserve, [northeast] Madagascar, 16°51'S 49°08'E, in primary rainforest, between 600–750 metres altitude.

Paratypes: BM(NH) 91.227, collector's number RAN 33592, adult male; BM(NH)91.228, collector's number RAN 33593, juvenile female; BM(NH)91.229, collector's number RAN 33596 subadult male. All with the same collection data as the holotype but collected 14 February 1990.

RESULTS

Diagnosis

Intermediate in size between the smaller *M. thomasi* Major, 1896 and *M. gracilis* (Major, 1896), and the larger *M. dobsoni* Thomas, 1884 and *M. talazaci* Major, 1896. Braincase narrow relative to skull length. Upper second and third premolars (P³ and P⁴) with well defined anterior ectostyle, separated by a notch from the distinct posterior ectostyle and distostyle. Mid region of guard hairs of the dorsal pelage flattened and broadened in cross-section.

Description

Size large; external measurements follow with those of the holotype in brackets: head and body length 105.5–113.5 (105.5), mean 110.9, SD 3.16; tail length 68.0–70.5 (70.4), mean 69.5, SD 1.02; hindfoot length 18.1–18.7 (18.7), mean 18.5, SD 0.23; weight 38–40 grams (38), mean 39.25, SD 0.83. Tail greater than half as long as head and body length: 60–67% (67%), mean 62.8%, SD 2.68. Dorsal pelage dark reddish or greyish brown, with a grizzled appearance; bases of hairs grey, distal portion light brown or red brown, some with black tips; interspersed with long guard hairs which are grey at the base but black for most of their length; unlike any other member of the genus, these hairs are flattened and

broadened in cross-section in their mid portion, rounded in cross-section distally. Hairs of ventral pelage grey at the base with light grey tips; colour of dorsal pelage merges gradually with that of the venter. Forefeet grey brown dorsally, light ventrally; hindfeet grey brown above and below; tail uniformly grey. The claws of the forefoot are elongated; claws of the third digit of the hindfoot are 65.1–78.9% (65.1%), mean 71.28, SD 5.63 of the length of those of the forefoot.

The skull is long and gracile (see Figs 1–3); the rostrum is elongated but moderately robust; the interorbital region is narrow and slightly concave in dorsal view; the braincase is long and deep, yet narrow; the squamosal region is not inflated and the superior articular facet is angular and clearly visible in dorsal view; the sinus canal forms a markedly peaked curve (see Fig. 3). The mandible is long, moderately robust, the corpus is sinuous in profile, with a moderately deep and broad coronoid process; the angle between the dorsal articular facet and the coronoid process is shallow; the mental foramen lies below the anterior portion of P_3 .

The dentition is moderately robust and illustrated in Figures 4 to 7. Interproximal diastemata are present between all the upper incisors and canine, those on either side of the first upper premolar (P^2) are large. Posterior basal cusps (distostyles) are well defined on all three upper incisors, that on the first incisor (I^1) is robust and more than half the height of the principal cusp; anterior accessory cusps are scarcely evident on the upper incisors; the upper canine lacks an anterior accessory cusp and mesiolingual cusp, while the distostyle is small, slender and approximately one quarter of the height of the principal cusp; the first upper premolar (P^2) is robust,

with well defined anterior and posterior basal cusps; the second upper premolar (P^3) has a slender paracone, the anterior ectostyle is well developed and separated by a notch from the posterior ectostyle and distostyle, the talon is moderately large and the lingual shelf well developed; the third upper premolar (P^4) is similar in structure to P^3 in buccal aspect but the paracone is more robust and the anterior ectostyle separated from the well defined posterior ectostyle and distostyle by an even more distinct notch, the talon is large with a small yet well defined cusp; the upper molars are similar to those of other members of the genus, but the talons of M^1 and M^2 are broad and deep, while that of M^3 is lingually extended. Small diastemata are present on either side of the third lower incisor (I_3), the lower canine (C) and the first lower premolar (P_2); a small anterior accessory cusp is present on the lower canine; the first lower premolar (P_2) is large, being only slightly smaller than the second lower premolar (P_3); the anterior and posterior accessory cusps of P_2 are well marked, the main cusp is 'anteroflexed' due to the short convex anterior slope and the longer, concave posterior slope; the paraconid is well developed on P_3 and the third lower premolar (P_4), and on the molars (M_1 to M_3); the anterior face of the protoconid of P_4 and all the molars is markedly convex.

Etymology

The name of this species is derived from the greek στυγς, dryad or wood nymph.

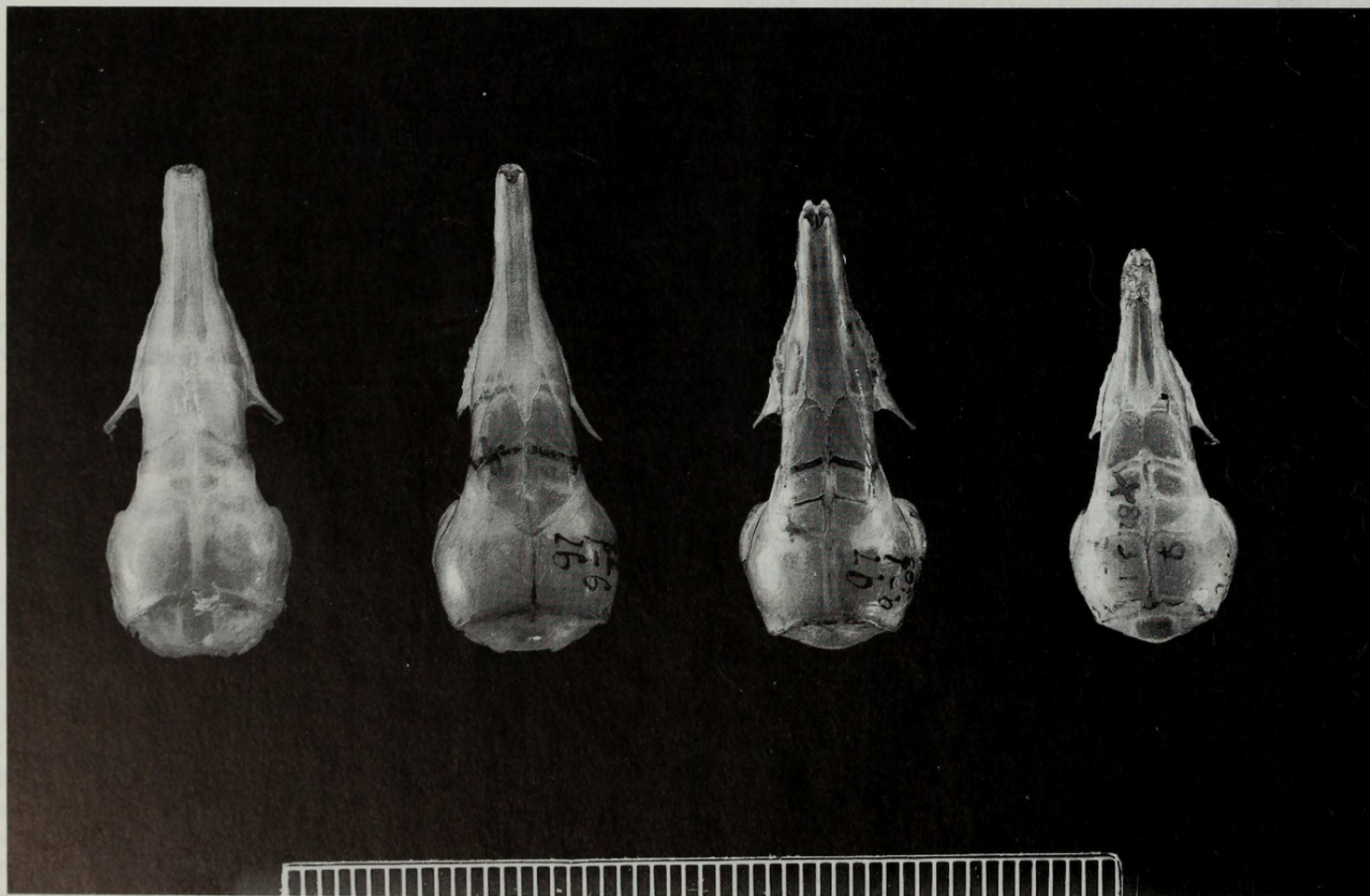


Fig. 1 Dorsal view of skulls, from left to right *Microgale dryas*, *M. gracilis*, *M. thomasi* and *M. cowani*. Scale 500 mm.



Fig. 2 Ventral view of skulls, from left to right *Microgale dryas*, *M. gracilis*, *M. thomasi* and *M. cowani*. Scale 500 mm.

Comparison with other species

Microgale dryas (HB 105–114, GCL 30–32) is intermediate in size between *Microgale thomasi* (HB < 98, GCL c.27) and *M. gracilis* (HB c.93, GCL c.29), and *M. dobsoni* (HB < 103, GCL > 29) and *M. talazaci* (HB > 115, GCL > 34). It is considerably larger than the other known species of *Microgale* (HB < 83, GCL < 25), see MacPhee (1987, table 2). It is readily distinguished from *M. talazaci* and *M. dobsoni* in which I_2 is larger than the lower canine, while, as in the other species of *Microgale*, I_2 is smaller or subequal to the lower canine.

M. dryas is distinguished from all other species by the dorsal pelage, in which the guard hairs are flattened and broadened in their mid region. On cranial and dental characters it is clearly associated with the *cowani* cluster [see MacPhee (1987), p.9], which includes *M. cowani* Thomas, 1882, *M. parvula* Grandidier, 1934, *M. pulla* Jenkins, 1988 and *M. thomasi*, and the *gracilis* cluster (*M. gracilis*).

All members of the *cowani* and *gracilis* clusters have gracile skulls with a long, narrow rostrum and diastemata between the anterior teeth. The skull of *M. dryas* is larger than any of the other members of the *cowani* or *gracilis* clusters and is intermediate in elongation of the rostrum between *M. thomasi* and *M. gracilis*. *M. gracilis* shows the greatest degree of attenuation of the rostrum, which is slender, with very long diastemata between the anterior teeth, in *M. dryas* the diastemata are moderately long (especially between the upper canine and P_2) and the rostrum is narrow (in these dimensions the new species resembles *M. cowani*) but in *M.*

thomasi the diastemata are small and the rostrum is relatively broader and shorter (see Table 1). The interorbital region of *M. dryas* is narrow and slightly concave in dorsal view, in contrast to other members of the *cowani* and *gracilis* clusters in which the interorbital region increases in size from the anterior to the posterior region. The braincase of *M. dryas* is narrower relative to skull length than any of the other members of the genus; it is slightly narrower but deeper than that of *M. gracilis*, yet markedly narrower but deeper than that of *M. thomasi* (see Table 1). The squamosal region dorsal to the bulla is scarcely inflated in *M. dryas*, slightly inflated in *M. gracilis*, inflated in *M. cowani* and markedly inflated in *M. thomasi*; the sinus canal follows a shallow curve in *M. cowani*, *M. thomasi* and *M. gracilis* but forms a peaked curve in *M. dryas*. The corpus of the mandible of *M. dryas* is sinuous as in *M. cowani* and *M. gracilis*, unlike the straighter profile of *M. thomasi*; the mandible is shallower at the coronoid process in *M. dryas*, *M. cowani* and *M. gracilis*, than in *M. thomasi*.

Although only slightly larger than *M. gracilis* and with similarly elongated claws on the manus, *M. dryas* differs markedly from it in the cranial features given above and the following dental features. The toothrow length in *M. gracilis* is not markedly shorter than that of *M. dryas*, due to the much longer diastemata between the anterior teeth of *M. gracilis*, than those of *M. dryas*. The teeth of *M. gracilis* are smaller in all dimensions than those of *M. dryas* (buccal length x crown height of P_2 1.08 in *M. gracilis* but 1.64–1.85 in *M. dryas*). The most marked dental difference between the



Fig. 3 Lateral view of skulls, top row left *Microgale cowani*, right *M. gracilis*, bottom row left *M. thomasi*, right *M. dryas*. Scale 500 mm.

M. dryas and *M. gracilis* is in the size of the talon of the molariform maxillary teeth; this is large in *M. dryas* but in *M. gracilis* is effectively absent and more reduced than in any other species.

Microgale dryas and *M. thomasi* differ in the following dental features. The distostyle of I^1 is more robust and greater than 50% of the height of the principal cusp in *M. dryas*, while it is more slender and less than 50% of the height of the principal cusp in *M. thomasi*. A mesiolingual accessory cusp is present on I^3 in *M. thomasi* but absent in *M. dryas*. A mesiolingual cusp is present and the distostyle is larger, more robust and approximately one third of the height of the principal cusp in *M. thomasi*, while in *M. dryas* the mesiolingual cusp is absent or reduced to a ridge and the distostyle is small, slender and approximately one quarter the height of the principal cusp. In *M. dryas* the anterior ectostyle of P^3 is well defined and separated from the distostyle, and the talon is large, unlike the condition in *M. thomasi* in which the anterior ectostyle is not separated and the talon is small. The posterior ectostyle and distostyle of P^4 are moderately well defined and separated from the anterior ectostyle by a notch, the talon is large with a well defined cusp in *M. dryas* but in *M. thomasi* there is no posterior ectostyle, the distostyle is barely evident and merges with the anterior ectostyle, and while the talon is moderately large it lacks a well defined cusp. A posterior ectostyle is present on M^1 and the talon is large and unicuspid or bicuspid in *M. dryas* but in *M. thomasi* there is no posterior ectostyle and the talon is medium sized

and unicuspid. In all the molariform teeth the talon of *M. dryas* is larger than that of *M. thomasi*. There are fewer differences in the mandibular teeth of the two species. The incisors are similar but there are no diastemata between the incisors of *M. thomasi*, while in *M. dryas* a diastema is present between I_3 and the canine of all specimens and between I_2 and I_3 of three of the four specimens. An anterior accessory cusp is present on the canine in *M. dryas* but not in *M. thomasi*. Although P_2 is similar in both species, there is a slight difference in shape, in *M. dryas* the tooth is anteroflexed and tends to be caniniform, while in *M. thomasi* it is not anteroflexed and more molariform in appearance. P_2 and P^2 in both species are larger relative to the rest of the toothrow than in any other species (see Table 1). The molariform teeth (P_4 to M_3) are similar in the two species except that the anterior face of the paraconid of M_1 and M_2 is markedly convex in *M. dryas* but only slightly convex in *M. thomasi*.

DISCUSSION

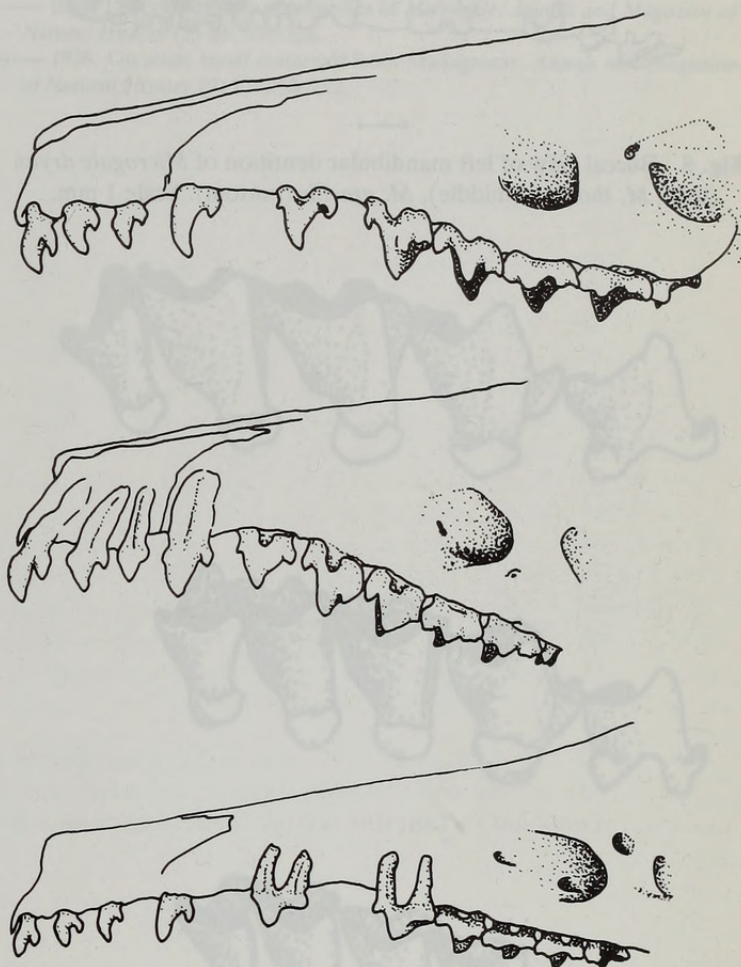
Microgale is a taxonomically complex genus containing many named forms, over half of which were shown to be juveniles or morphological variants (MacPhee, 1987). In his revision, MacPhee demonstrated the high morphological within-species variation found in the genus, and described and

Table 1 Comparing *M. dryas*, *M. thomasi* and *M. gracilis*

	<i>M. gracilis</i>	<i>M. thomasi</i>	<i>M. dryas</i>
Condylolincisive length mean	29.0	25.9, 26.8	30.4–31.0
SD			30.63
n			0.23
Upper tooththrow length mean	14.4	12.5, 13.1	15.2–15.6
SD			15.43
n			0.18
Length of anterior teeth (I ¹ —anterior of P ³) mean	8.4	6.6	7.5–8.0
SD			7.78
n			0.18
Breadth of rostrum (P ² –P ²) mean	2.5	3.5, 3.6	3.5–3.6
SD			3.55
n			0.05
Ratio of length of anterior teeth (I ¹ –P ³) to upper tooththrow length mean	0.58	0.50, 0.53	0.49–0.52
SD			0.50
n			1.13
Ratio of breadth of rostrum (P ² –P ²) to upper tooththrow length mean	0.17	0.27, 0.28	0.22–0.24
SD			0.23
n			0.47
Braincase breadth mean	11.3	11.4, 11.5	11.2–11.6
SD			11.4
n			0.14
Braincase height mean	7.2	7.5, 7.6	7.9–8.2
SD			8.05
n			0.11
Ratio of braincase breadth to condylolincisive length mean	0.39	0.43, 0.44	0.37–0.38
SD			0.37
n			0.36
Ratio of braincase height to braincase breadth mean	0.64	0.66, 0.66	0.70–0.71
SD			0.71
n			0.36
Ratio of mandible height at coronoid process to mandible length mean	0.27	0.33, 0.36	0.26–0.30
SD			0.28
n			1.45
Buccal length x crown height of P ₂ mean	1.08	1.49	1.64–1.85
SD			1.74
n			0.08
Head and body length mean	c.93	91, 97	105.5–113.5
SD			110.88
n			3.16
			4

Tail length	73–81 ¹	62–70 ¹	68–71
mean	78.0	67.2	69.53
SD	3.46	4.91	1.02
n	4	3	4
Ratio of tail to head and body length	0.73–0.87 ¹	0.66–0.75 ¹	0.60–0.67
mean	0.83	0.69	0.63
SD			0.03
n	4	3	4

Note: ¹ data from MacPhee (1987)

**Fig. 4** Buccal view of left maxillary dentition of *Microgale dryas* (top), *M. thomasi* (middle), *M. gracilis* (bottom). Scale 1 mm.

illustrated the deciduous and adult dentitions of most species. Since the small sample of the new species contained a juvenile, subadult and two adults, it was possible to be confident that the specimens did indeed represent an undescribed species. MacPhee suggested the existence of growth curves, unusual in mammals, in which some subadults may exceed the average size of adults. This feature may be indicated by *M. dryas*, in which both the juvenile and subadult specimens are slightly larger than the adults in head and body length, although the small sample size precludes any meaningful comparison.

MacPhee divided the genus into six 'clusters' on the basis of dental traits and body proportions; he emphasised that this was a phenetic, not a phylogenetic arrangement. On the basis of the characters employed by MacPhee, *M. dryas* groups with the *cowani* and the *gracilis* clusters and is intermediate in many features between *M. thomasi* and *M. gracilis*. Since *M. thomasi*, *M. gracilis* and *M. dryas* are known from such small

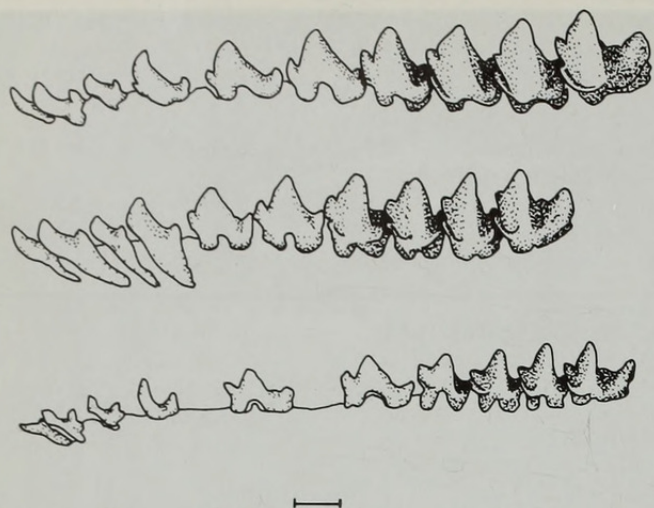


Fig. 5 Buccal view of left mandibular dentition of *Microgale dryas* (top), *M. thomasi* (middle), *M. gracilis* (bottom). Scale 1 mm.

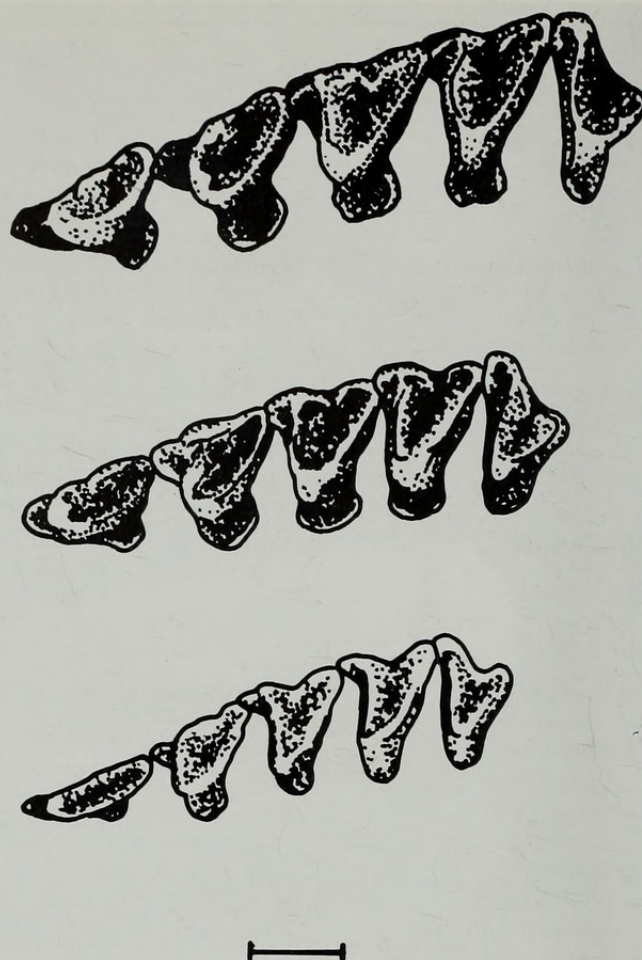


Fig. 7 Occlusal view of left P^3 to M^3 of *Microgale dryas* (top), *M. thomasi* (middle) and *M. gracilis* (bottom). Scale 1 mm.

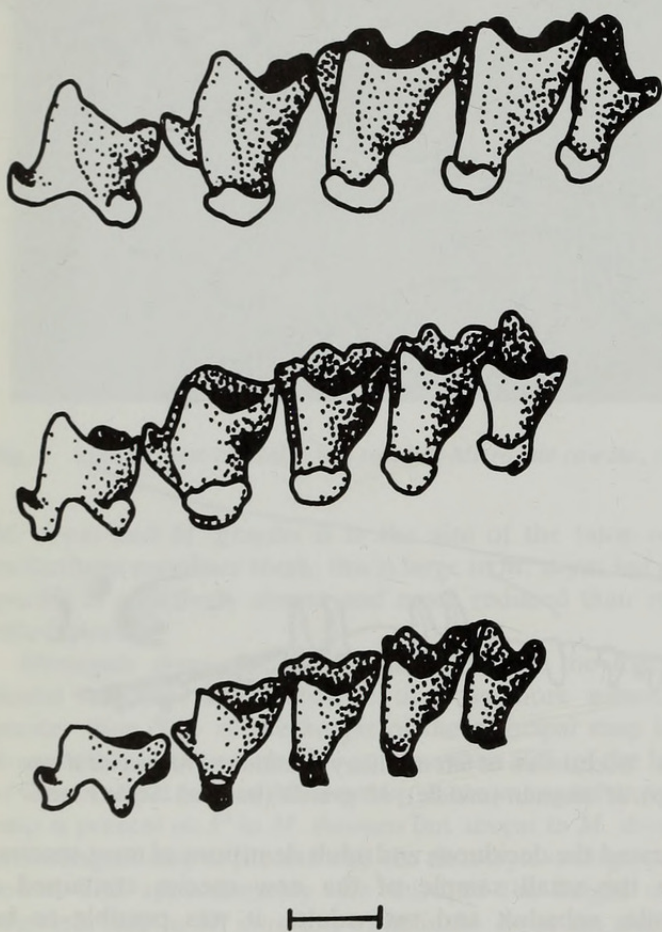


Fig. 6 Lingual view of left P^3 to M^3 of *Microgale dryas* (top), *M. thomasi* (middle) and *M. gracilis* (bottom). Scale 1 mm.

samples, it is impractical to speculate about possible relationships. Eisenberg & Gould (1970) divided *Microgale* into four behavioural classes on the basis of external morphology. However this classification was challenged by MacPhee (1987) because of redefinition of within-species variation and lack of field study data to support the theory. Specimens of three other species of *Microgale*: *M. cowani*, *M. principula* Thomas, 1926 and *M. talazaci* were collected from the same locality as *M. dryas*. This sympatric association of several different species is apparently common in *Microgale* (see MacPhee, 1987; Nicoll & Rathbun, 1990). Regrettably, some

of the species recorded for this locality by Nicoll & Rathbun were based on incorrect preliminary field identifications. Although found in the same habitat, it seems likely that these four species are occupying different ecological niches. Eisenberg & Gould (1970) hypothesised that *M. principula* was a climbing form on the basis of its long tail, which is naked on its distal dorsal surface, and long hindfeet. Although MacPhee (1987), pointed out that there was no evidence of the long tail being prehensile, and studies that might confirm such locomotor behaviour are lacking, these morphological differences do suggest adaptations to a specialised life-style. Studies were made on *M. talazaci* (Eisenberg & Gould, 1970), which show that it is scansorial and shows some burrowing behaviour; its much greater size suggests that it may take larger prey than the smaller species. Since there is no field data for *M. dryas*, no speculation about its ecology or behaviour is attempted here. A species of rice-tenrec, *Oryzorictes talpoides* and two species of rodent, *Eliurus minor* and *E. myoxinus* were also collected from the same locality. The specimens of *M. principula* from this locality represent a northern extension of the recorded range for this species (see MacPhee, 1987).

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INTRODUCTION

This paper forms part of a continuing investigation of the biology of deep-sea protobranch bivalves of the Atlantic (Allen & Hannell 1969; Allen & Sanders 1973, 1977; Sanders & Allen 1975, 1977, 1985). The present study includes an appraisal of the biology, systematics and ecology of ten species of the deep-sea Nuculidae.

From the time of Linnaeus taxonomists have had difficulty in classifying the Nuculidae (e.g. Hanley 1806; Adams 1856; Sowerby 1871; Seguenza 1877; Jeffreys 1881; Verrill 1884; Rees 1885; Dall 1886; Hedley 1907; Jeffreys 1931; Schenck 1934, 1939; Allen 1954; Jarvis 1972; Lubinsky 1972). The nuculids were originally regarded as members of the family Arcidae. The type species of the genus *Arcus*, and of the family Nuculidae, is *Arcus nuxia* Linnaeus. This is now generally accepted as equivalent to *Nucula nuxia* (Linn.). As with other protobranch groups (Allen 1978) taxonomy

difficulties arise because of the very great conservatism of shell and body form.

The Subfamily *Nuculinae* has a long fossil record possibly dating from the Ordovician. The apparent widespread prevalence of cladogenic events possibly results from an early adaptation to a swimming benthic environment that was persisted throughout much of the soft period. The morphology of this early adaptation appears to have still little room for selective pressure change. For example, Lubinsky & Smith (1972) in a comparative study of Silurian soft-bodied bivalve-bearing bivalve communities found that the supposed deep-sea-dwelling nuculid *Nucula* was in the non-compacted, watery sediments of both shallow and deep, even though separated by 400 million years. The Silurian counterpart of *Nucula* was a species of *Protocardia* which is similar in size and morphology to *Nucula* and probably had similar life style as an active deposit feeder, not near the sediment-water interface. Rhoads & Young (1982) found that intensive near-surface reworking of the



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