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Middle Pleistocene *Crocidura* (Mammalia, Insectivora) from Oulad Hamida I, Morocco, and their phylogenetic relationships

Denis Geraads

Laboratoire de Paléontologie des Vertébrés, Université Paris VI, 4 pl. Jussieu 75252 Paris Cedex 05, France and
URA 49 CNRS, Musée de l'Homme, pl. du Trocadéro, 75116 Paris

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ABSTRACT

The Middle Pleistocene site of the 'Grotte des Rhinocéros', and related fissure fillings of the Oulad Hamida 1 (= Thomas III) Quarry, Casablanca, Morocco, have yielded abundant remains of two species of *Crocidura*. The most common one, *C. darelbeidae* n.sp., is probably the sister-species of *C.viaria/C.bolivari*, although more primitive by most of its characters. A second species shares several derived characters with the Recent *C.tarfayaensis*, and could be its ancestor. The fossil species from Oulad Hamida I are less different from each other than their Recent counterparts, suggesting relatively late (Pliocene?) diversification of the Moroccan *Crocidura*.

INTRODUCTION

The co-operation programme between the 'Institut National des Sciences de l'Archéologie et du Patrimoine' (dir. J. Benslimane) and the 'Mission Paléontologique et Préhistorique Française au Maroc' (dir. J.-P. Raynal) led to the discovery of several new archaeological and/or palaeontological localities associated with ancient shorelines of the Moroccan coast, mainly around Casablanca. One of these, the Rhino cave ('Grotte des Rhinocéros', GDR) was discovered in the Oulad Hamida I Quarry (OH1; Raynal et al., in press), formerly called Thomas III Quarry. This cave, opened by quarry works, most probably belongs to the same system of fillings as the locality that I (Geraads, 1980) called 'fissures dans le Tensiftien de Thomas III', hereunder called 'ThIII-fiss' (1979 collections) or 'OH90' (1990 collections) (Raynal et al., in press; Geraads, in press). These fillings are different, however, from the site known as 'grotte de Thomas III' where the first Hominid of this quarry was found (Ennouchi, 1972). The OH1/GDR cave is,

from the biochronology of the Rodents (Geraads, in press) slightly older than the Rodent site of Thomas I (Jaeger, 1975; Tong, 1989), itself probably (but only 'probably') identical with the Hominid-site of Thomas I (Ennouchi, 1969; Sausse, 1975).

The GDR and OH90/ThIII-fiss fillings are extremely rich in microfauna. Rodents are described elsewhere (Geraads, in press); Chiroptera and Insectivora other than shrews are extremely rare (Raynal et al., in press). Shrews are represented by several tens of mandibles, some maxillary fragments and snouts, and hundreds of isolated teeth. This is certainly one of the largest collections of fossil *Crocidura* from Africa. In the Maghreb, the only important published collection is that from the middle Pleistocene of Irhoud Derbala Virage, from where Rzebik-Kowalska (1988) described a new species, *C.marocana*, as well as *C.* cf *russula* and *C.* cf *viaria*.

All diagnostic specimens from OH1 (GDR, OH90) belong to two species of *Crocidura*, different by size, and all specimens are here assigned to these two species, although the occurence of a third species (of *Crocidura* or of an other Soricid) among the scrappy material cannot be ruled out (specific distinction of similar-sized species may be difficult, even on Recent complete material: Aulagnier & Hermas, 1989).

SYSTEMATIC DESCRIPTIONS

genus *Crocidura* WAGLER, 1832

Crocidura darelbeidae n.sp.

Crocidura sp A *in* Geraads, 1980
Crocidura sp B *in* Geraads, 1980

The two 'species' (from ThIII-fiss) mentioned in my 1980 paper are now believed to belong to the same species. The second species described below was not represented in the ThIII-fiss material.

Holotype: skull, from OH90. The rear part of the neurocranium and some molars are missing.

Paratype: complete mandible, OH90.

Derivatio nominis: from Dar el Beida, Arabic name for Casablanca.

Diagnosis: A *Crocidura* slightly smaller than *C.bolivari*. Crown bases of upper I and of P4/ little angled on unicuspid row. Upper I relatively small, with strong labial cingulum. Unicuspids, P4/ and upper molars labio-lingually narrow. Parastyle of P4/ *russula*-like, with high cingulum. Mesostyle of M1/-M2/ fused, simple, extended into labial crest. Pre-orbital bar narrow. Coronoid apophysis very high. Lower border of coronoid fossa level with upper border of condyle. Condyle small. Upper border of I/1 almost straight. Lingual groove long and poorly divergent from lower border. Lower unicuspids moderately crowded, with accessory cuspids reduced. Lower molars with reduced lingual cingulum. Talonid of M/3 simple.

C. darelbeidae is the largest and by far the most common species of shrew at OH1. In the following description, it has been compared with similar-sized spe-

cies from North-West Africa: *C.viaria* (incl. *C.sericea*) from Senegal (several specimens from the Muséum National d'Histoire Naturelle, Paris) and *C.bolivari* from Morocco (a part of the collection from Massa described by Aulagnier & Hermas, 1989, kindly lent by the former author).

The holotype of *C.darelbeidae* n.sp. (fig. 1) is the only specimen with an almost complete upper tooth row, although much worn. In contrast to *C.viaria*, the angle between the base of the crown of I1/ and that of U1/ is obtuse, and the same difference can be observed between the line of the unicuspids and P4/; thus, the alveolar line of the antemolariform teeth forms a less compressed Z (fig. 1–2); some specimens of *C.bolivari*, especially the old ones, are more like *C.darelbeidae*. The upper incisor (fig. 3) is shorter (between the posterior end and the anterior crown-root junction) than the first unicuspid. These teeth are of the same size in *C.bolivari*, and the incisor is larger in *C.viaria*. The labial cingulum is very strong in the posterior part of the tooth, much more so than in the Recent species, forming a protruding shelf on all specimens. The talon is low: its height is much less than one-half the total height of the tooth, contrary to the *C.* cf *viaria* from Irhoud Derbala Virage (Rzebik-Kowalska, 1988b; 77). The dimensions are:

	N	min.	max.	mean
L	25	1.43	1.71	1.58
H (little worn)	11	2.08	2.44	2.20
H of talon	13	0.70	0.98	0.84

The unicuspids are rarely preserved; they are less elongated than in *C.viaria*/*C.bolivari*; the average length/width ratio of U1/ is 1.60 (N = 5; in the Recent

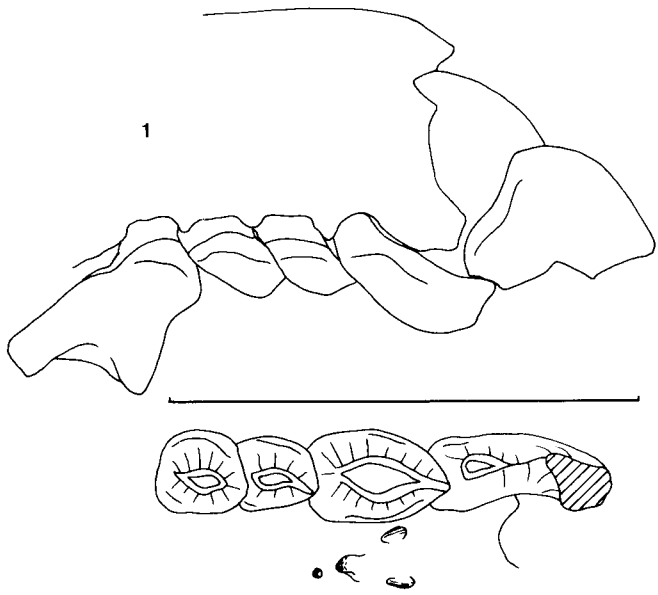

Fig. 1. *Crocidura darelbeidae* n.sp., holotype, OH90, upper anterior teeth in labial and occlusal views. Scale = 5 mm.

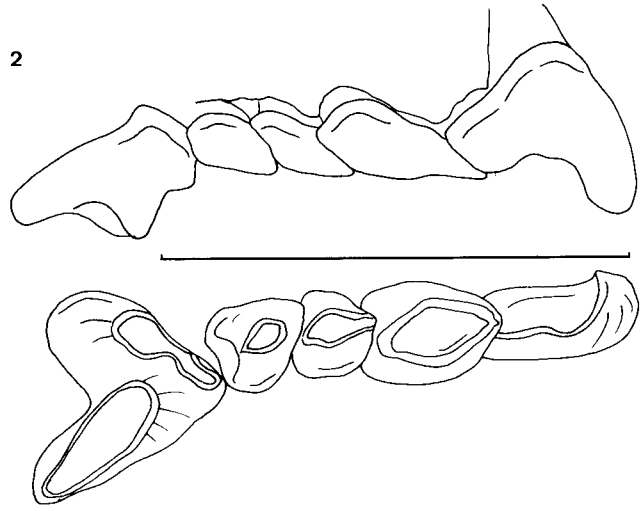

Fig. 2. *Crocidura darelbeidae* n.sp., GDR-EF13, upper anterior teeth in labial and occlusal views. Scale = 5 mm.

species = 1.87, N = 10); that of U2/ is 1.28 (N = 3; in the Recent species = 1.46, N = 8); that of U3/ is 1.17 (N = 10; in the Recent species = 1.33, N = 10). U1/ is much larger than U2/ and U3, which are approximately of the same size (table 1).

The parastyle of P4 (fig. 4) is the most diagnostic area of this tooth. It is well separated from the main cusp, labially protruding in occlusal view, and always large, although variably so. Its height is not much inferior to the length of U3/, and its development may cause expansion of the antero-labial corner of P4/, making the alveolar line of the crown sinuous in labial view. The labial cingulum at the base of the parastyle is very high, whereas it is more restricted to the base in *C.viaria*. The lingual cingulum usually reaches the antero-lingual corner of the

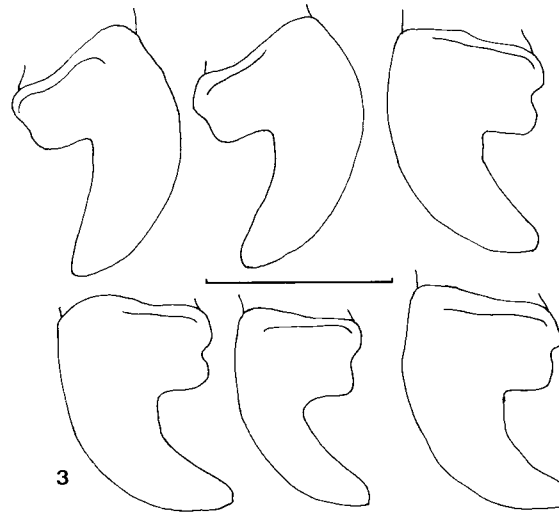

Fig. 3. *Crocidura darelbeiae* n.sp., upper incisors. Scale = 2 mm.

Table 1. Dimensions of the upper teeth of *C.darelbeidae*. Specimens with unicuspids. Length of M1/-M2/ labial, not including posterior cingulum; width between parastyle and protocone. Width of P4/id., not including lingual cingulum.

	U1		U2		U3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
1*:	1.71	1.01	1.07	0.82	0.98	0.88	2.44	1.37	1.89	2.13	1.49	2.35	0.70	1.43
2*	1.56	1.01	1.04	0.79	1.04	0.85	2.35	1.31	1.89	1.92				
3*	1.80	1.19			1.10	0.90	2.23	1.43	1.83	2.10				
4*	1.71	1.01			1.04	0.85	2.13	1.37						
5*	1.77	1.07	1.13	0.91	1.01	0.95	2.32	1.68						

*: 1=Type, OH90; 2–5=other specimens, from GDR-EF13

tooth but, at the base of the protocone, it is never very thick. In a few cases, the protocone is shifted labially, making the outline of this corner more obtuse. The outline of the internal talon is never as square as on the *C.* cf *varia* from Irhoud Derbala Virage (Rzebik-Kowalska, 1988, fig. 6A). The dimensions of P4/ are:

	N	min.	max.	mean
Maximum length	40	2.08	2.47	2.27
Anterior width (not incl. ling. cingulum)	40	1.22	1.68	1.40

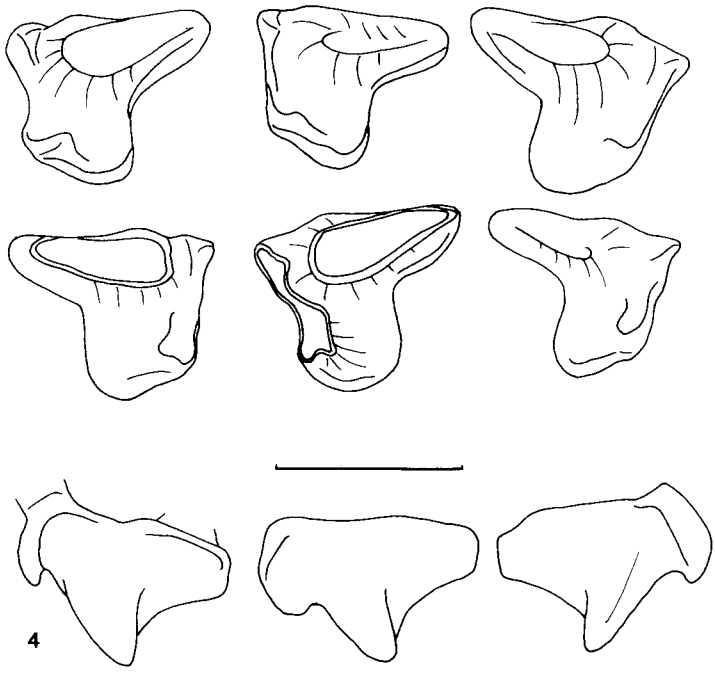

Fig. 4. *Crocidura darelbeidae* n.sp., GDR-EF13, variation of P4/ outline, in occlusal and labial views. Scale = 5 mm.

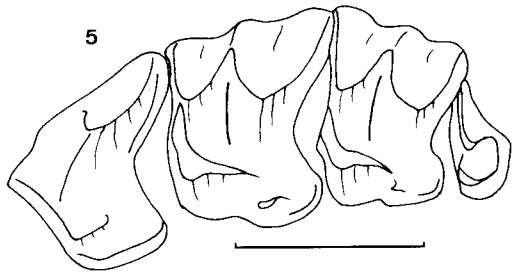

Fig. 5. *Crocidura darelbeidae* n.sp., GDR-EF13, P4/-M3/, occlusal view, scale = 2 mm.

The molars (fig. 5) are less transversely elongated than those of *C.viaria* and *C.bolivari* (fig. 6). The hypocone is always well developed (more so, on the average, than in *C. viaria*), but the talon area of M2/ is perhaps more reduced relatively to M1/, than in *C.viaria*. The main characteristic of all molars is the fusion, complete on M1/ and almost complete on M2/, of the arms of the external crescents to form a closed, simple, mesostyle, which extends into a postero-labial crest. *C.bolivari* is more similar to the fossil than *C.viaria*, in which the arms of the paracone and metacone remain separated. The last upper molar is slightly more reduced than in the Recent species.

The pre-orbital bar (between orbit and pre-orbital foramen) is narrower than in *C.viaria/bolivari*. Its average minimum length is 0.96 mm (mini. = 0.76, max. = 1.22); in the Recent species its length ranges from 1.22 to 1.55 mm.

Characters analysed in the lower jaw are those noted by Butler & al. (1989), whose abbreviations are used below.

The most noticeable feature of the lower jaw is the small size of the condyle (fig. 7–8). Its internal part is reduced and bent downwards; it is more transversal in the Recent species. The small size of the condyle increases the height/breadth ratio (COH/ARL) of this area, but *C.viaria* and *C.bolivari* both have high coronoid apophyses.

The upper border of I/1 is almost straight. The lingual groove is always long (fig. 10). Its foremost part is low, running close and parallel to the ventral side of the tooth, then it diverges gently and almost reaches the posterior notch, but it is still rather low (= ventral) at this level; thus, it differs from *C.viaria* and *C.bolivari*, where the groove is shorter and higher (= more dorsal) at its posterior end. On the labial side, the rear part of the crown is at the level of the main cusp of P/4. The postero-lingual crest of I/2 is short and incomplete. P/4 overlaps about 1/4 of I/2; it has a straight or slightly convex anterior border and a weak metaconid. Its 'downgrowth' is moderate, and the mental foramen is posterior to it. The molars have a variable lingual cingulum, but it is usually reduced, and never complete, in contrast to *C.viaria* and *C.bolivari*. The talonid of M/1 and M/2 is postero-lingually closed (fig. 9); that of M/3 is simple, with no trace of entoconid.

Using the system of measurements of Butler & al. (1989), I have performed a principal component analysis on 2 complete mandibles of *C.darelbeidae*, the average measurements of the same species, 9 mandibles of *C.bolivari* from Massa,

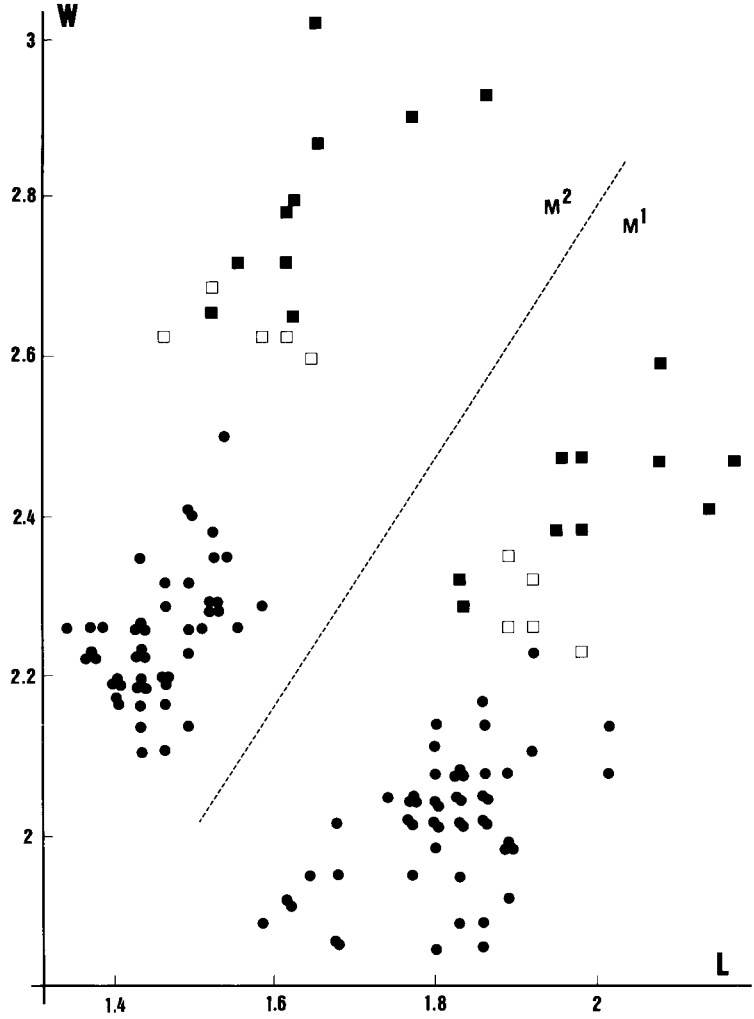

Fig. 6. Plot of M1/ and M2/ anterior width (between parastyle and protocone) vs labial length (excluding posterior cingulum) in *C.darelbeidae* n.sp. (black dots), *C.viaria* from Senegal (black squares) and *C.bolivari* from Massa (open squares).

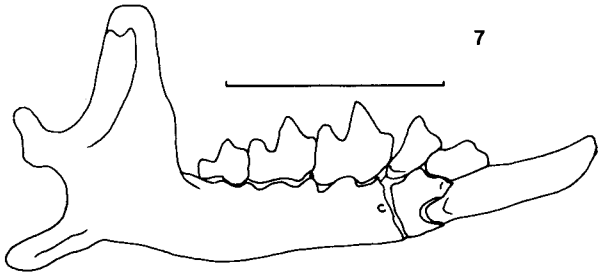

Fig. 7. *Crocidura darelbeidae* n.sp., paratype, OH90, right mandible, labial view. Scale = 5 mm.

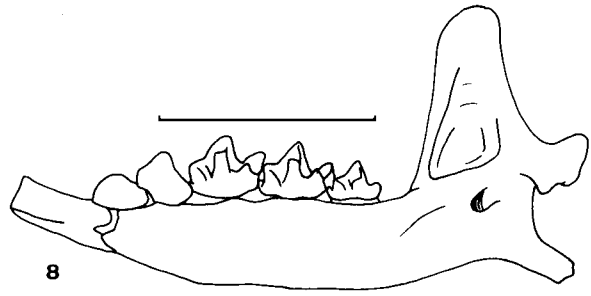

Fig. 8. *Crocidura darelbeidae* n.sp., OH90, another right mandible, lingual view. Scale = 5 mm.

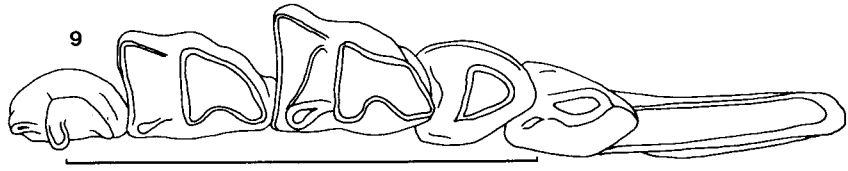

Fig. 9. *Crocidura darelbeidae* n.sp., OH90, composite left tooth-row in occlusal view (M/3 and I-M/2 from two different specimens). Scale = 5 mm.

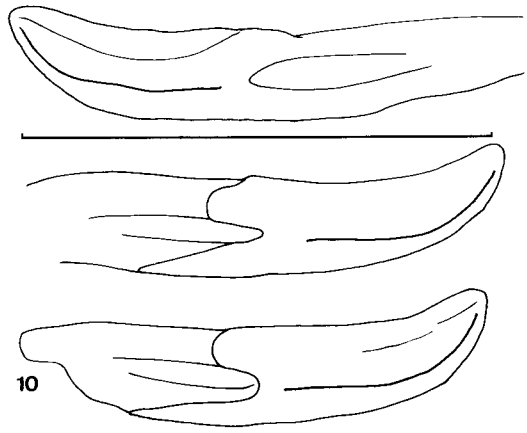

Fig. 10. *Crocidura darelbeidae* n.sp., OH90, 3 incisors in lingual view, to show the low long groove. Scale = 5 mm.

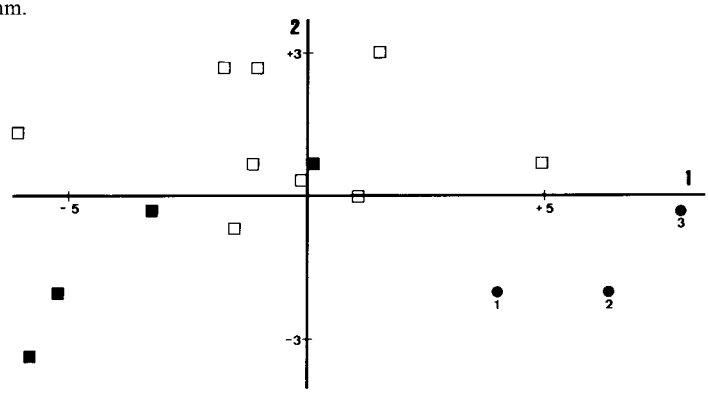

Fig. 11. Plane 1-2 of the principal component analysis of metric characters of the lower jaw of *C.darelbeidae* n.sp., *C.bolivari* and *C.viaria*. Open squares: *C.bolivari*, Massa; black squares: *C.viaria*, Senegal; black dots: *C.darelbeidae* (1, 2: two mandibles; 3: average of several specimens, cf table 2)

and 4 *C.viaria* from Senegal. Projection of plane 1–2 is shown on fig. 11: *C.darelbeidae* is well separated from *C.viaria* and *C.bolivari.*

Crocidura sp, cf *C.tarfayaensis* VESMANIS & VESMANIS, 1979

This species is much less common than *C.darelbeidae*, the upper teeth being especially rare, but there are several lower tooth rows and more or less complete mandibles, the dimensions of which are indicated in table 2.

Of the upper teeth, only two fragments of maxillae are preserved (fig. 12), one with I, U1/ and U3/, the other with P4/ and M2/. A single isolated M1/ has also been retrieved. Their dimensions are:

I		U1/		U3/		P4/		M1/		M2/	
H	L	L	W	L	W	L	W	L	W	L	W
1.24	1.25	1.28	0.82	0.64	0.58	1.68	0.85	1.40	1.60	1.19	1.65

The incisor is smaller but otherwise not much different from that of *C.darelbeidae*. It is about as long as U1/. The most noticeable feature of the unicuspids is the very small size of U3/. The size discrepancy between U1/ and U3/ is much smaller in *C.marocana* from Irhoud Derbala Virage (Rzebik-Kowalska, 1988); among similar-sized species from Morocco, only *C.tarfayaensis* and *C.whitakeri* show the same small U3/.

P4/ is also similar to that of *C.tarfayaensis*, with its protocone strongly shifted labially.

The lower teeth are somewhat less derived than those of *C.darelbeidae*. The incisor is almost straight, and not curved upwards as in some of the mandibles from Massa. The lingual groove is long and gently divergent, as in *C.tarfayaensis*; P/4 overlaps about 1/4 of I/2. The accessory cusps are reduced, but the postero-lingual crest of I/2 is less reduced, on the average, than in the larger species. The postentoconid ledge is also broader. All teeth from P/4 to M/2 are clearly less high than in *C.tarfayaensis*. As in the latter species, and as in *C.darelbeidae*, the coronoid apophysis is high and narrow.

The Recent species *C.tarfayaensis* and *C.whitakeri* are very difficult to distinguish on purely dental grounds, in spite of careful attempts by Hutterer (1986) and

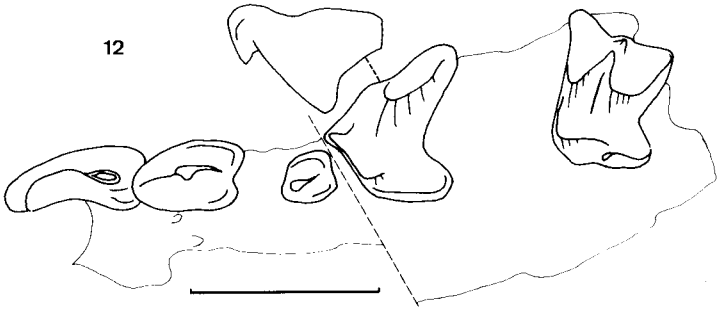

Fig. 12. *Crocidura* cf *tarfayaensis*, GDR-EF13, composite maxilla (I, U1/, U3/ and P4/, M2/), Scale = 2 mm.

Table 2. Mandibular dimensions of the two species of Crocidura from OH1. Abbreviations are those used by Butler & al. (1989).

		Crocidura darelbeidae		*C.* cf *tarfayaensis*	
		N	mean (min.-max.)	N	mean (min.-max.)
1	IB	14	4.02 (3.61–4.64)	8	3.00 (2.84–3.17)
2	IL	8	3.04 (2.90–3.29)	4	2.16 (2.07–2.26)
3	IH	11	1.04 (0.98–1.13)	8	0.78 (0.76–0.82)
4	IW	16	0.75 (0.64–0.82)	6	0.55 (0.43–0.66)
5	I2L	7	1.40 (1.34–1.43)	3	0.98 (0.91–1.04)
6	I2W	7	0.97 (0.93–1.05)	5	0.68 (0.66–0.70)
7	PL	10	1.38 (1.31–1.46)	4	1.00 (0.91–1.04)
8	PW	18	1.10 (0.98–1.24)	5	0.77 (0.75–0.79)
9	PDG	12	0.60 (0.49–0.70)	4	0.50 (0.34–0.58)
10	I2P	7	2.41 (2.29–2.50)	4	1.72 (1.68–1.77)
11	M	21	4.48 (4.19–4.71)	11	3.53 (3.39–3.66)
12	M1L	12	1.64 (1.46–1.74)	8	1.22 (1.16–1.28)
13	M1W	22	1.34 (1.22–1.49)	9	0.95 (0.91–1.04)
14	M1T	12	1.09 (0.95–1.19)	8	0.82 (0.76–0.88)
15	M2L	14	1.56 (1.46–1.68)	7	1.17 (1.10–1.25)
16	M2W	20	1.19 (1.10–1.28)	9	0.87 (0.82–0.91)
17	M2T	14	1.03 (0.98–1.10)	7	0.82 (0.76–0.97)
18	M3W	12	0.78 (0.70–0.82)	10	0.62 (0.58–0.64)
19	M3T	8	0.95 (0.91–1.04)	4	0.72 (0.70–0.73)
20	R	20	2.00 (1.77–2.23)	18	1.32 (1.01–1.52)
21	CH	18	1.61 (1.46–1.77)	5	1.28 (1.13–1.37)
22	CW	16	1.47 (1.40–1.59)	5	1.23 (1.13–1.31)
23	COH	21	5.72 (5.42–6.26)	5	4.06 (3.68–4.39)
24	ARL	17	4.77 (4.26–5.10)	5	3.69 (3.61–3.74)
25	F	24	1.70 (1.52–1.95)	9	1.22 (1.07–1.34)
26	AMF	27	1.52 (1.34–1.77)	9	1.24 (1.13–1.34)
27	SCL	26	2.78 (2.44–2.96)	7	2.06 (1.86–2.20)
28	PCH	23	2.86 (2.59–3.20)	8	2.10 (1.98–2.17)
29	AL	5	2.93 (2.59–2.99)	0	2.15*
30	AW	6	0.72 (0.64–0.79)	1	0.43

* Estimated value

Aulagnier and Hermas (1989). It is therefore hard to tell which one stays closer to the smaller species from GDR.

RELATIONSHIPS

The number of Recent species of *Crocidura* in Morocco is probably only 5 (Hutterer, 1986) but in the whole of Africa it reaches almost 100, and the deciphering of their phylogenetic relationships is a huge task. A phenetic classification implies the use of multivariate methods, and Butler & al. (1989) used principal component analysis on mandibular data to distinguish several groups of African species. Using again the same system of measurements, I have added

Fig. 13. *C.* cf *tarfayaensis*, OH90, left mandible in occlusal and lingual views. Scale = 2 mm.

C.darelbeidae and *C.* cf *tarfayaensis*, plus the Recent species *C.bolivari* and *C.tarfayaensis*, to their 20 supplementary OTU, and performed a principal component analysis upon them.

The first axis, which accounts for 93.5% of the variance, reflects overall size. *C.darelbeidae* is grouped with members of the *hirta* and *turba* groups, while *C.* cf *tarfayaensis* is intermediate between the *C.fuscomurina* and the *C.fumosa*/*C.russula* groups. On the second axis, which discriminates mainly the species with long unicuspids (negative values) from species with thick incisors and unicuspids (positive values), both species from GDR score close to 0 or low positive values, like most species of the *hirta* and *fuscomurina* groups, while all species of the *turba* and *fumosa* groups have negative values (fig. 14 and Butler & al., 1989, fig. 5). The third axis, which accounts for only 1% of the variance, separates species with wide molars from those with large posterior part of the mandible, and both species from GDR clearly belong to the former set.

Thus, the phenetic analysis prompts me to classify *C.darelbeidae*, without much hesitation, as an outlier of the *hirta* group. *C.* cf *tarfayaensis* plots close to the Recent *C.tarfayaensis*, but is less eccentric, which most probably means less derived. It may perhaps best be classified among the *fuscomurina* group.

Using the most discriminant metric characters, and the non-metric ones, I have also performed a parsimonious cladistic analysis (using the programm HENNIG86 of S. Farris) on 81 OTU, the outgroup being either the *Sylvisorex lunaris* group, which stands apart according to Butler & al. (1989), or an hypothetical taxon with all non-metric characters at the supposedly primitive state (0 in the system of Butler & al., 1989). The height of the coronoid process, being the measurement best correlated with the first axis of the principal component analysis on metric characters, was used as an estimate of size and all measurements expressed as a fraction of it (X/COH). The values for each character were then coded according to their distance (in standard deviations) from the average. For non-metric characters, the decimal scores given by Butler & al. (1989) have been converted into integers.

Three analyses were performed: on all characters, metric only, and non-metric only. The results are all unsatisfactory, since consistency indexes are low (11, 14

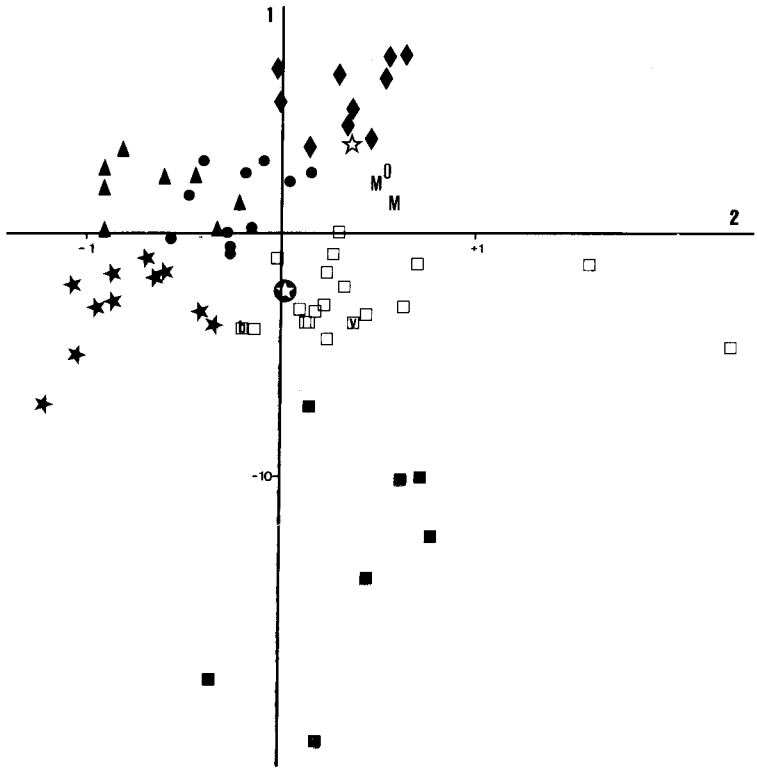

Fig. 14. Plane 1-2 of the principal component analysis on metric characters of the lower jaw. Open star: average of *C.* cf *tarfayaensis*; letters: *C.tarfayaensis* (O: average of 6 mandibles from Massa, M: two mandibles from southern Morocco); star in black circle: average of *C.darelbeidae* n.sp.; square 'b': average of *C.bolivari*, Massa. Other species from data of Butler & al. (1989), *Suncus* and *Sylvisorex* omitted; open squares: *C.hirta* group ('v': *C.viaria*); black squares: *C. flavescens* group; black stars: *C.turba* group; dots: *C.russula* group; triangles: *C.fumosa* group; diamonds: *C.fuscomurina* group.

and 10 respectively), even for such relatively large matrices (84 × 35, 84 × 17 and 83 × 18). With such a high degree of homoplasy, changes in the trees do not much increase their lengths, and detailed analysis of the most parsimonious trees would not be very meaningful. A large monophyletic group containing most, if not all, species of the *C.hirta* group can be recognized. It also includes *C.darelbeidae* and *C.* cf *tarfayaensis* (as sister-species, except in the metric analysis) and various species from other groups. The results are always so ambiguous, however, that the proposal of a phylogenetic tree would be misleading.

The failure of parsimonious cladistic analysis to provide satisfactory (unambiguous) results and the fact that *C.viaria* and *C.bolivari*, which are known to be genetically very similar (Vogel & al., 1988) are well separated on the second axis of the principal component analysis show that neither method is able to establish the precise relationships of the fossil species.

Occurrence of two similar-sized species of the *hirta* group, *C.darelbeidae* and *C.bolivari*, in the same area, strongly suggests that they are closely related. *C.darelbeidae* has mostly primitive states in comparison with the Recent species, but also a few more derived ones (strong cingulum on upper I, mesostyle extended

into long crest, reduced cingulum on lower molars): both species could have originated in Atlantic Morocco with subsequent spreading southwards or, rather, they could be sister-species (their separation dating perhaps back to the Pliocene), the subsequent extinction of *C.darelbeidae* allowing northwards spreading of *C.viaria*/ *C.bolivari* into Morocco, as Aulagnier (1992) thinks.

C. cf *tarfayaensis*, on the other hand, has only primitive characters in comparison with *C.tarfayaensis*, with which it shares the high and narrow coronoid apophysis, the very small U3/ and the labially displaced protocone of P4/. It can reasonably be taken as its direct ancestor.

Among an extended *hirta*-group, both species from GDR retain several primitive characters. Thus, they occupy a basal position, and a few derived features (such as the reduced cingulum on the molars) suffice to make them appear as closely related. This may be an artefact, but both fossil species are certainly less different than their modern counterparts. This suggests relatively late divergence of Moroccan *Crocidura*.

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