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A biochemical and morphological investigation of *Suncus dayi* (Dobson, 1888) and discussion of relationships in *Suncus* Hemprich & Ehrenberg, 1833, *Crocidura* Wagler, 1832, and *Sylvisorex* Thomas, 1904 (Insectivora: Soricidae)

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Abstract. A recent field expedition in South India yielded a series of seven specimens of *Suncus dayi* (Dobson, 1888), a poorly known crocidurine shrew collected in high-altitude wet evergreen forests in the Nilgiri Hills. The morphology (external, cranial, dental) of this species was investigated in a comparative study with a few taxa of the genera *Suncus* Hemprich & Ehrenberg, 1833 (e. g. *S. stoliczkanus* (Anderson, 1877), *S. fellowesgordoni* Phillips, 1932), *Sylvisorex* Thomas, 1904 (e. g. *S. morio* (Gray, 1862), *S. granti* Thomas, 1907 group) and *Crocidura* Wagler, 1832 (e. g. *C. attenuata* Milne-Edwards, 1872). A biochemical survey of isozyme variation at 32 genetic loci allowed the estimation of the genetic differentiation between *S. dayi* and four other white-toothed shrews: *Suncus murinus* (Linnaeus, 1766), *Crocidura olivieri* (Lesson, 1827), *C. fuliginosa* (Blyth, 1855) and *C. russula* (Hermann, 1780). In its cranial and dental morphology, *Suncus dayi* retains many plesiomorphic features common to some members of the African genus *Sylvisorex*, whereas other species of *Suncus* instead show many apomorphic states. The electrophoretic survey indicates that *S. dayi* shares derived characters with *Crocidura* and *Suncus*, not with *Sylvisorex*. In combination, these studies do not exclude the conclusion that the peculiar morphology of *Suncus dayi* could be the result of convergent evolution related to its possibly scansorial way of life.

Key words. *Suncus*, Insectivora, India, systematics.

Introduction

Suncus dayi (Dobson, 1888) is a poorly known species from southern India recorded from the holotype deposited in the Natural History Museum, London and one other specimen presumed to be in the collection of the Zoological Survey, Bombay (see Lindsay 1929). Few authors elaborated on its original short description or commented on its status (Blanford 1888; Ellerman & Morrison-Scott 1966) and a century elapsed from the initial discovery, before seven additional specimens were collected from the Nilgiri Hills in southern India by the Catzeflis-Boursot Expedition to India in October 1990. These specimens have enabled us to study variation within the species and to perform more extensive comparisons with other taxa.

Although *S. dayi* has always been associated with species currently assigned to the genus *Suncus*, it exhibits a suite of characters differing from those found in most other members of this genus, which suggest that its affinities lie elsewhere. Comparisons have therefore been made with other similar and closely related genera belonging to the subfamily Crocidurinae or white-toothed shrews, namely *Suncus*, *Crocidura* and *Sylvisorex*, and theories of possible relationships have been advanced, as reported below.

Besides the morphological examination, a comparative biochemical study of isozyme variation was undertaken in *Suncus dayi* and four other crocidurine shrews: *Suncus murinus*, *Crocidura russula*, *C. fuliginosa*, and *C. olivieri*. Electrophoresis of homologous proteins has proved an adequate and powerful approach for solving the systematics and evolutionary relationships of species and genera within the family Soricidae, as exemplified by recent studies of Catzeflis et al. (1985), George (1986) and Maddalena (1990b). The primary aim of the genetic survey was to decipher the probable relationships of *Suncus dayi* with regard to other white-toothed shrews, and to compare the new findings with those published for other Asian, African, and European members of the genus *Crocidura* sensu lato (Maddalena 1990b, Ruedi et al. 1990, 1993).

Material

Specimens used in the morphological analysis include the holotype of *Suncus dayi* BM (NH) 1867.11.14.7 adult of undetermined sex, skin and skull, Trichur, Cochin (10°31'N 77°13'E), and seven individuals from the Nilgiri Hills collected in October 1990 by P. Boursot, A. Orth and F. Catzeflis:

V-543 undetermined sex: Ootacamund: wet evergreen forest, 2150 m, 11°24'N 76°42'E;
V-557 juvenile male, V-562 subadult male, V-563 juvenile female,
V-567 juvenile female: Avallanchi: wet evergreen primary forest, 2100 m, 11°23'N 76°36'E;
V-572 subadult male, V-576 juvenile female: Kotagiri: wet evergreen primary and secondary forest, 1500 m, 11°26'N 76°53'E.

The following comparative material of other taxa in The Natural History Museum collections was examined:

13 specimens of *Suncus stoliczkanus* (Anderson, 1877) from Pakistan and India;
6 specimens of *Suncus etruscus* (Savi, 1822) from India;
3 specimens of *Suncus fellowesgordoni* Phillips, 1932 from Sri Lanka;
28 specimens of *Suncus murinus* (Linnaeus, 1766) from the Nilgiri Hills, India;
7 specimens of *Suncus lixus* (Thomas, 1898) from southern Africa;
7 specimens of *Sylvisorex johnstoni* (Dobson, 1888) from East and West Africa;
17 specimens of *Sylvisorex granti* Thomas, 1907 from East and West Africa;
11 specimens of *Sylvisorex megalura* (Jentink, 1888) from East and West Africa;
9 specimens of *Sylvisorex morio* (Gray, 1862) from Cameroon, West Africa;
20 specimens of *Crocidura attenuata* Milne-Edwards, 1872 from Assam, North East India;
20 specimens of *Crocidura fuliginosa dracula* Thomas, 1912 from North Vietnam.

The material used in the electrophoretic study included frozen tissue samples of seven *Suncus dayi* (V-543, V-557, V-562, V-563, V-567, V-572 and V-576) from Nilgiri Hills; eight *Suncus murinus* (V-546 to V-551, V-554 and V-555) from Mudumalai, Tamil Nadu, South India; three *Crocidura olivieri* (Lesson, 1827) from Central Africa (Maddalena 1990a, b); five *Crocidura russula* (Hermann, 1780) from Switzerland (Maddalena 1990a); and three *Crocidura fuliginosa* (Blyth, 1855) from Malaysia (Ruedi et al. 1990). Voucher specimens of all these animals are deposited in the collections of Lausanne (IZEA) and/or London (BM[NH]).

Methods

Morphological analysis

Measurements in millimetres were taken using dial calipers or a microscope measuring stage. The dental nomenclature follows that of Heim de Balsac & Lamotte (1957), Swindler (1976) and Butler & Greenwood (1979).

In their bench-mark work on African *Sylvisorex*, *Suncus* and *Crocidura*, Heim de Balsac & Lamotte (1957) determined which external and cranial characters were primitive for this group and which were derived. Butler & Greenwood (1979) and Butler et al. (1989) similarly assessed the mandibular characters of fossil and Recent African Soricidae. One of us (PJ) has provided additional characters from the maxillary dentition and external features. Using the studies of these authors as a framework for the current analysis, primitive (plesiomorph) and derived (apomorph) characters have been scored for Asian and African members of the genera *Suncus* and *Sylvisorex*, with the objective of obtaining a relative ranking of *S. dayi*.

Electrophoretic study
Tissue samples (kidney, liver, heart) were frozen in liquid nitrogen immediately after autopsy in the field, and maintained at –70 °C at Lausanne until processing. Electrophoresis of homologous proteins was done as described in Ruedi et al. (1993) for studying the variation at the following 32 presumptive nuclear loci: (abbreviations as in Ruedi et al. 1993): Ada, Adh, Ak-1 & -2, Alb, Ck-1 & -2, Est-1, Got-1 & -2, Gpd, G-6-pd, Hk-1, Idh-1 & -2, Lap, Ldh-1 & -2, Mdh-1 & -2, ME, Mpi, Pa, Prot-x, 6-Pgd, Pgi, Pgm, Sod-1, -2 & -3, and Xdh-1 & -2. Alleles were designated by their mobility relative to the most common allele found in *C. olivieri* (Maddalena 1990b). Individual genotypes were transformed into allelic frequences by the BIOSYS-1 program (release 1.7; Swofford & Selander 1981) in order to compute Rogers (1972) and Nei (1978) genetic distances between pairs of compared taxa. The Rogers (1972) distances, which are additive, were treated by the Neighbor-Joining (Saitou & Nei 1987) and distance Wagner procedures (in BIOSYS-1) in order to yield dendrograms built without the hypothesis of rate-equality of biochemical changes among lineages.

Abbreviations used
BM(NH): The Natural History Museum, London, British Isles (formerly British Museum [Natural History]); IZEA: Institut de Zoologie et Ecologie Animale, University of Lausanne, Switzerland; ISEM: Institut des Sciences de l'Evolution de Montpellier, France.

c: circa; CBL: condylo-basal length; HB: head and body length; HF: hind foot length; m: metre; n: number; p: page; pers. comm.: personal communication; SD: standard deviation; TL: tail length.

Abbreviations for dental nomenclature are given in the text.

Results

Morphological analysis

Diagnosis and description: *Suncus dayi* is a dark brown, medium sized shrew (HB 70—78, CBL 18.9—20.2), with a long slender tail (TL 83—88), clothed in short hairs but lacking long bristle hairs. The hindfeet are elongated (15.5—16.5; ratio of HF to CBL 79.1—84.7), with elongated cheiridia.

The cranium has a relatively short rostrum, with a broad interorbital region and the braincase is rounded and domed (see Figs 1—2 and Table 1). The fourth upper unicuspid (Un^4) is slightly smaller than the second (Un^2); the cingula on the upper unicuspids are broad and distally flared. The third upper molar (M^3) is long relative to the upper toothrow. The first lower incisor (I$_1$) has two marked denticulations. The last lower molar (M$_3$) has a distinct talonid basin and entoconid with a very short entoconid ridge.

Comparison with other taxa: *Crocidura* is characterised by the possession of three upper unicuspid teeth, so clearly *S. dayi* does not conform in this diagnostic character; *S. dayi* also lacks the bristle hairs on the tail characteristic of *Suncus* and of most species of *Crocidura*. *Crocidura* apparently has a restricted distribution in India; only the very small *Crocidura horsfieldii* (Tomes, 1856) has been recorded from southern India (HB < 75, CBL < 18.0). Brief comparisons were therefore made

Table 1: Characters of *Suncus dayi* and *Suncus fellowesgordoni* relative to *Sylvisorex* and *Suncus*. P: plesiomorphic character state; I: character of intermediate expression; A: apomorphic character state.

Character	Plesiomorphic state	*Sylvisorex*	*Suncus dayi*	*Suncus fellowesgordoni*	*Suncus*	Apomorphic state
Tail: vibrissae	absent	P	P	A	A	present
hairs	very short	P	I	A	A	long
thickening	absent	P	P	P	A	present
Hindfeet:	longer & broader	P	P	A	A	shorter, narrower
cheiridia	widely spaced	P	P	A	A	adpressed
Braincase	convex or elevated	P	P	A	A	flattened
ratio of braincase height to upper toothrow length		>58 %	58–60 %	51.7 %	<54 % [*S. lixus* 51–56 %]	
Interorbital region	broad	P/I	P	P	A [*S. etruscus* P]	narrow
ratio of interorbital breadth to maxillary breadth		>75 % [*S. johnstoni* 71 %]	76–88 %	77.5 %	<71 % [*S. etruscus* 76–84 %]	
I1: anterior cusp	short, stout, proodont	P	P	A	A	tall, slender, opisthodont
talon	well developed	P	P	P	A	reduced
Fourth unicuspid	present	P	P	P	P	absent
	less reduced in size	P	P	P	A	more reduced
buccal and lingual cingula	broad, well developed	P	P	P	A [*S. etruscus* I, *S. lixus* P]	narrow
P^4: talon	long, well developed	P	P	P	A	short, reduced
protocone	well developed	P [*S. johnstoni* A]	P	P	P [*S. etruscus* A]	reduced
hypocone	well developed	P [*S. johnstoni* A]	I	A	A	reduced
parastyle	well developed	P [*S. johnstoni* A]	I	P	A [*S. murinus* I, *S. etruscus* P]	reduced
M^3:	long, well developed	P	P	I	A [*S. murinus* I]	short, reduced
Ratio of M^3 length to upper toothrow length		>7.5 %	7.8–8.5 %	7.6, 7.8 %	<7.4 % [*S. murinus* 6.6–8.1 %]	

Table 1: continued

Character	Plesiomorphic state	*Sylvisorex*	*Suncus dayi*	*Suncus fellowesgordoni*	*Suncus*	Apomorphic state
Mandible: ratio of condyle width to height	less than 80 %	A >80 %	P 57−65 %	P 76.3 %	A >82 %	greater
ratio of horizontal ramus depth to M_1-M_3 length	less than 36 %	P <36 %	P 29−33 %	P 30.3 %	A >36 %	greater [*S. etruscus* 29−35 %]
I_1: elevations on posterior ridge	two	P	P	P	A	none
anterolingual ridge	low, parallel to ventral border, long	P	P	P	A [*S. lixus* P]	higher, divergent short
posterolingual cingulum	present	P	A	[P]	A	absent
ratio of I_1 length to M_1-M_3 length	75 % or less	I <86 %	I 76−81 %	I 72, 78 %	A >82 %	greater, up to 100 % or more
ratio of I_1 height to M_1-M_3 length	20 % or less	P, I <24 % [*S. granti* 17−20 %]	P 18−20 %	I 18, 21 %	I, A >20 % [*S. lixus* 17−23 %]	greater, up to 28−29 % or more
I_2: protostylid	present	P, A	A	A	A	absent
P_4: protostylid	present	P, A	A	A	A	absent
overlap of I_2	c 0.25 length of I_2	P, A	P	P	A [*S. lixus* P]	greater
M_1: ratio of breadth to length	67 % or less	I	A	A	A	greater, up to 80 %
M_1, M_2: post-entoconid ledge	wide	P, I	I	I	A	narrow
lingual cingulum	complete	P, A	P	P	P, A	confined to anterior or absent
M_3: talonid	well-developed, resembling M_2	P, I, A	P	I	I, A	simplified

between *S. dayi* and the slightly larger *Crocidura attenuata* found in Assam, north east India and in Southeast Asia (Assam specimens HB 70—87, CBL 19.7—21.6), and also with *Crocidura fuliginosa* from Southeast Asia, which is considerably larger (Vietnam specimens HB>85, CBL>22.2). The latter was the only Asian species available for the electrophoretic analysis, therefore it was also included in the morphological study, but because it is readily distinguished from *Suncus dayi* by its much greater size, comparisons given below were restricted to the more comparably sized *C. attenuata.*

Crocidura attenuata differs externally from *Suncus dayi* in its grey brown pelage colour and shorter, bristle haired tail (ratio of TL to HB 70—95). The skull has a longer, shallower rostrum and the braincase is shallower, less rounded with slightly more angular superior articular facets. The mandible has a deeper, straighter horizontal ramus, while the ramal fossa is smaller and broader. The most obvious dental differences are the absence of the fourth upper unicuspid, and the shape of the first upper incisor, with its elongated anterior cusp (see Fig. 2).

Suncus dayi is compared here with other species of *Suncus* which occur in India: *S. murinus*, *S. stoliczkanus* and *S. etruscus*. *Suncus dayi* is considerably larger than *S. etruscus* (HB<55, CBL<14.0), and considerably smaller than *S. murinus* (HB>100, CBL>23.5). Confusion with *S. murinus* and *S. etruscus* is therefore unlikely and no further reference is made to these two species.

Suncus dayi (HB 70—78, CBL 18.9—20.2) is similar in size to *S. stoliczkanus* (HB 68—85, CBL 18.6—22.2); however the external appearance of *S. dayi* and *S. stoliczkanus* is otherwise quite different: *S. dayi* is dark brown dorsally and ventrally, the tail is uniformly dark brown, longer than head and body (TL 83—88; ratio of TL to HB 109.9—123.5), clothed with short hairs but lacking the long bristle hairs which are characteristic of *Suncus* and most species of *Crocidura;* the hindfeet are elongated (15.5—16.5, ratio of HF to CBL 79.1—84.7), the cheiridia are widely spaced and elongated. In contrast, *Suncus stoliczkanus* ranges in colour from pale grey to grey brown dorsally, paler ventrally; the tail is pale grey to grey brown, shorter than head and body (TL 44—55; ratio of TL to HB 60.8—76.8), with long bristle hairs; the hind feet are medium sized (10.5—15.0; ratio of HF to CBL 56.5—75.2), and the cheridia are adpressed and rounded.

Suncus dayi is similar in many features to members of the African genus *Sylvisorex*, and it is compared here with the slightly smaller *Sylvisorex morio*, with additional comments on other species of *Sylvisorex* where *S. morio* is atypical. In the following external features, *S. dayi* shows a closer resemblance to members of the genus *Sylvisorex* than to those of *Suncus*. The tail is long, slender and, as in *Sylvisorex*, lacks the long bristle hairs which are characteristic of *Suncus* and most species of *Crocidura;* instead the tail has short hairs, which are longer and more numerous than those of *S. morio* (some Indomalayan species of *Crocidura-C. elongata* Miller & Hollister, 1921; *C. miya* Phillips, 1929 and *C. paradoxura* Dobson, 1887 — also have a long slender tail with few or no long bristle hairs). The cheiridia on the hindfeet of *S. dayi* and *S. morio* are elongated, unlike the rounded cheiridia of *S. stoliczkanus.*

In craniodental morphology and proportions, *S. dayi* is also more similar to *Sylvisorex* than to *Suncus* (see Figs 1—6, and Tables 1—2). The skull of *S. dayi* is more similar to that of *S. morio* in general shape; the rostrum of both species is

Fig. 1: Dorsal view of cranium from left to right of *Sylvisorex morio* (BM [NH] 88.81), *Suncus dayi* (V-576), *Suncus fellowesgordoni* (BM [NH] 32.6.11.1), *Suncus stoliczkanus* (BM [NH] 79.586) and *Crocidura attenuata* (BM [NH] 27.3.7.2).

Fig. 2: Lateral view of cranium from left to right of above *Sylvisorex morio* (BM [NH] 88.81) and *Suncus dayi* (V-576), below *Suncus fellowesgordoni* (BM [NH] 32.6.11.1), *Suncus stoliczkanus* (BM [NH] 79.586) and *Crocidura attenuata* (BM [NH] 27.3.7.2).

relatively short, while that of *S. stoliczkanus* is slightly elongated and parallel-sided; the angle between the rostral portion of the maxilla carrying the unicuspid teeth and the premolar and molar portion of the maxilla is much more acute in *S. stoliczkanus*

Table 2: Selected measurements in specimens of *Suncus stoliczkanus*, *Suncus dayi*, *Sylvisorex morio* and *Crocidura attenuata*. Range, mean ± standard deviation, sample size.

	Suncus stoliczkanus	*Suncus dayi*	*Sylvisorex morio*	*Crocidura attenuata*
Condylobasal length	18.6–22.2 19.78±1.03 11	18.9–20.2 19.66±0.40 7	17.1–18.8 17.91±0.50 9	19.7–21.6 20.20±0.52 10
Upper toothrow length	8.1–10.3 9.07±0.65 11	8.5–8.8 8.66±0.13 7	7.8–8.4 8.07±0.21 9	8.0–9.8 8.90±0.47 21
Maxillary breadth at level of M^2	5.2–6.9 5.98±0.40 11	5.6–6.0 5.83±0.16 7	5.1–5.4 5.29±0.10 9	5.5–6.5 6.00±0.23 21
Interorbital breadth	3.8–4.3 3.98±0.14 10	4.3–4.7 4.47±0.13 7	4.1–4.6 4.31±0.13 9	4.1–4.7 4.37±0.15 14
Braincase breadth	8.3–9.8 8.73±0.41 10	8.9–9.6 9.34±0.22 7	8.6–9.4 8.97±0.23 9	8.7–9.8 9.08±0.32 11
Braincase height	3.9–5.0 4.30±0.32 10	5.0–5.3 5.12±0.12 6	4.8–5.2 5.01±0.15 8	4.4–5.3 4.89±0.25 10
Braincase length	7.9–9.0 8.36±0.30 10	7.8–8.5 8.09±0.21 7	6.9–7.4 7.20±0.17 8	8.0–8.9 8.26±0.25 10
Interorbital breadth: maxillary breadth	59.4–71.4 66.33±0.28 10	72.9–88.0 78.10±4.40 7	75.9–86.8 81.40±3.12 9	68.9–77.6 72.69±2.24 14
Length of M^3: upper toothrow length	6.0–7.0 6.48±0.28 10	7.6–8.5 8.07±0.35 7	8.2–9.6 8.96±0.41 9	7.1–8.0 7.56±0.25 18
Braincase breadth: condylobasal length	42.0–45.3 43.90±1.12 10	46.1–48.0 47.51±0.37 7	47.0–52.6 50.08±1.53 9	42.0–47.6 44.81±1.42 10
Braincase height: condylobasal length	19.8–23.2 21.65±1.00 10	25.1–27.0 25.82±0.58 6	26.9–28.9 28.06±0.59 8	21.9–25.5 24.22±1.04 9
Braincase length: braincase breadth	91.8–100.0 95.72±2.33 10	83.9–89.9 86.57±2.40 7	76.7–83.1 80.12±2.07 8	87.9–96.6 90.95±3.00 10

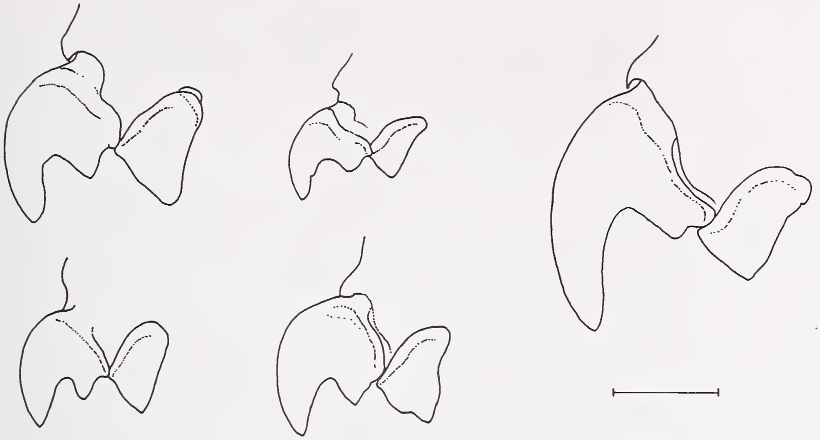

Fig. 3: Buccal view of left upper Incisor and Un^1 from left to right of above *Suncus dayi* (V-576) and *Suncus fellowesgordoni* (BM [NH] 32.6.11.1), middle *Sylvisorex granti* (BM [NH] 11.4.7.12) and *Sylvisorex morio* (BM [NH] 88.86), right *Suncus stoliczkanus* (BM [NH] 79.586). Scale 1 mm.

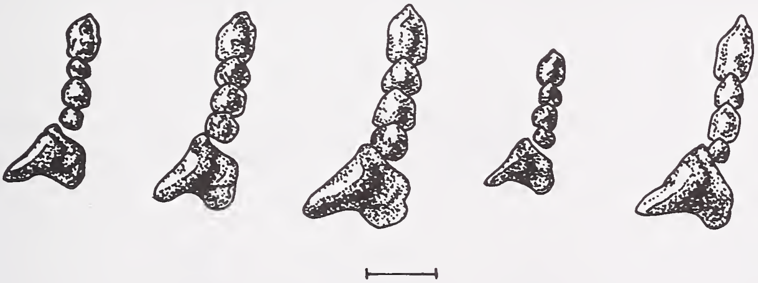

Fig. 4: Occlusal view of right Un^1—Un^4 and P^4 from left to right of *Sylvisorex granti* (BM [NH] 11.4.7.12), *Sylvisorex morio* (BM [NH] 88.86), *Suncus dayi* (V-576), *Suncus fellowesgordoni* (BM [NH] 32.6.11.1) and *Suncus stoliczkanus* (BM [NH] 30.2.11.138). Scale 1 mm.

than in *S. dayi* or *S. morio.* The interorbital region of *S. stoliczkanus* is relatively narrower and increases only slightly from anterior to posterior, whereas the posterior portion of the interorbital region is much broader than the anterior in *S. dayi* and *S. morio.* Both *S. dayi* and *S. morio* have rounded, domed braincases, while that of *S. stoliczkanus* is shallow, flat and laterally angular. The braincase is short relative to condylobasal length in *S. morio*, moderate in *S. dayi* but long in *S. stoliczkanus.* The parieto-occipital suture is prominently ridged in *S. stoliczkanus*, scarcely evident in *S. dayi* and practically absent in *S. morio.* The shape of the first upper incisor (I^1) is more similar in *S. dayi* and *S. morio* than in *S. stoliczkanus.* In *S. dayi* and

S. morio this tooth is more proodont, the anterior cusp is moderately stout, and less than twice the height of the posterior cusp, while in *S. stoliczkanus* I^1 is opisthodont, the anterior cusp is slender and elongated and more than twice the height of the posterior cusp. The cingula on the upper unicuspid teeth of *S. dayi* are broad and distally flared as in *S. morio* but unlike those of *S. stoliczkanus*, which further differs in the position of the fourth upper unicuspid (Un^4), which is partially obscured by the protocone of the premolar (P^3) in distal view. In *S. dayi* the lingual cingula of Un^1 , Un^3 and Un^4 and the buccal cingulum of Un^2 are broader than those of *S. morio*. In *S. dayi* and *S. morio*, P^3 has a prominent hypocone and well-developed talon, unlike *S. stoliczkanus* in which the hypocone is low and the talon reduced in size. The third upper molar (M^3) of *S. dayi* and *S. morio* is longer relative to the upper toothrow than that of *S. stoliczkanus*. The first lower incisor (I_1) of *S. dayi* has two marked denticulations and the anterolingual ridge is complete and parallel with the ventral border as in *S. morio* but unlike *S. stoliczkanus* which shows no denticulation and the anterolingual ridge is incomplete and divergent. A protostylid is present on the lower premolar (P_4) of *S. morio* and *S. granti*, but absent in most other species of *Sylvisorex* as well as in *S. dayi* and *S. stoliczkanus*. The talonid of the last lower molar (M_3) differs in all three species; in *S. morio* the talonid basin, entoconid and entoconid ridge are well developed; in *S. dayi*, the talonid basin and entoconid are distinct but the entoconid ridge is very short, while in *S. stoliczkanus* the talonid basin is distinct, the entoconid ridge low but the entoconid less distinct. The development of the talonid of M_3 is variable within *Sylvisorex* but is usually reduced in *Suncus*.

Historical perspective and morphological relationships: In his original description, Dobson (1888) placed the new species in *Pachyura* Sélys-Longchamps, 1839, which at that time was considered to be a subgenus of *Crocidura* but was later recognised as a distinct genus under the senior synonym of *Suncus*. An illustration of the lateral view of the anterior maxillary toothrow was given by Dobson (1890, Plate 28, Fig. 6). The few subsequent authors (Blanford 1888; Lindsay 1929; Ellerman & Morrison-Scott 1966) who examined this litte known and poorly represented species, only commented on the unusually large fourth upper unicuspid. Ellerman & Morrison-Scott considered that it was probably a member of the *Suncus stoliczkanus* group.

In the course of collaborative work with R. Hutterer, Bonn (pers. comm. 1988), several of the taxa of Asian *Suncus* were examined, including the holotype of *S. dayi* and three specimens of *S. fellowesgordoni*, another poorly known taxon generally regarded as a subspecies of the widespread species *Suncus etruscus* (see Ellerman & Morrison-Scott 1966; Eisenberg & McKay 1970; Corbet & Hill 1992). These two taxa (*S. dayi*, *S. fellowesgordoni*) showed some similarities in several characters not generally found in other species of *Suncus* (see Table 1). Many of these characters are regarded as primitive, following the views of Heim de Balsac & Lamotte (1957), Butler & Greenwood (1979), and Butler et al. (1989). Butler (1978: p. 62) stated that some species of *Suncus* in Asia, such as *S. fellowesgordoni* from Sri Lanka, have primitive characters like *Sylvisorex*, such as a narrow mandibular condyle and a basined talonid on M_3, and they cast doubt on whether the two genera should be

Fig. 5: Lingual view of right 1_1 and I_2 from left to right of above *Sylvisorex granti* (BM [NH] 71.1828) and *Sylvisorex morio* (BM [NH] 88.86), middle *Suncus dayi* (V-576) and *Suncus fellowesgordoni* (BM [NH] 32.6.11.1), below *Suncus stoliczkanus* (BM [NH] 79.586). Scale 1 mm.

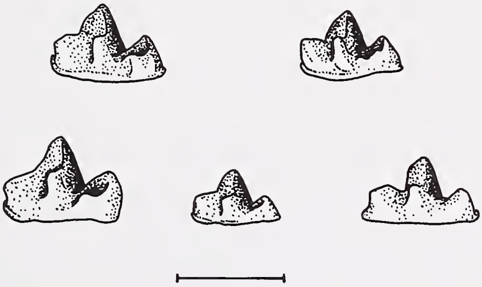

Fig. 6: Lingual view of right M_3 from left to right of above *Sylvisorex morio* (BM [NH] 88.86) and *Syvisorex granti* (BM [NH] 11.4.7.12), below *Suncus dayi* (V-576), *Suncus fellowesgordoni* (BM [NH] 32.6.11.1) and *Suncus stoliczkanus* (BM [NH] 79.586). Scale 1 mm.

separated. Butler et al. (1989: p. 402) repeated this view that *Suncus* includes some primitive forms such as *S. fellowesgordoni*; they noted that most species of *Suncus* are from the Indomalayan Region and suggested that this genus may have arisen from a *Sylvisorex*-like form in Asia, which subsequently extended its range into Africa.

Table 1 shows that *Sylvisorex* is plesiomorphic in the majority of its character states, while the majority of the characters of *Suncus* are apomorphic. Although not shown here, *Crocidura attenuata* and *C. fuliginosa* also show more apomorphic than plesiomorphic characters; it is hoped to discuss the relationships of these species of *Crocidura* and *Suncus* in a separate paper.

Examination of *S. fellowesgordoni* confirms the above observations that many of its characters are plesiomorphic (see Table 1) and common to *S. dayi* and *Sylvisorex*, but also shows 10 shared derived features (synapomorphies) with *Suncus* and 3 with the *Sylvisorex granti* group. Comparison of *S. dayi* reveals an even larger suite of plesiomorphic characters in common with *Sylvisorex*, and a few synapomorphic features with *Suncus* (4), *S. fellowesgordoni* (3) and 2 with the *Sylvisorex granti* group.

Electrophoretic study

Among the 32 assayed presumptive loci, 19 did evidence some intra- and/or interspecific polymorphism, whereas 13 showed no electrophoretic variation (Ak-1, Ck-1 & -2, Got-2, Gpd, Hk-1, Ldh-1, Mdh-1 & -2, Prot-x, Sod-3, and Xdh-1 & -2). Table 3 indicates the observed allelic frequences at all polymorphic loci. An intra-specific polymorphism for *Suncus dayi* does exist at the two most variable loci (Ada and Est-1), but only two heterozygotes were observed, namely alleles 65 and 87 at locus Ada for specimens V-543 and V-563.

The genetic distances (based on all 32 loci) were computed by using the indices of Rogers (1972) and of Nei (1978) (Table 4), which indicate a clearcut biochemical (genetical) differentiation between all samples (minimum value of ca. 0.28 for Nei's distance and 0.26 for Rogers' distance). Interestingly, *Suncus murinus* is roughly equally divergent from *S. dayi* as from *C. fuliginosa*, and these are the smallest distances in the matrix of Table 4. According to both kinds of genetic distances, *S. dayi* is however slightly more related to *Suncus murinus* than to any other crocidurine shrew so far tested. These relationships are tentatively represented on the dendrograms derived from two clustering methods which do not depend upon the hypothesis of rate-uniformity (Neighbor-Joining and Wagner) neither of which take into account the standard-deviation of branch lengths estimates. Both tree-reconstruction methods indicate strong differences in rates of biochemical change, with for example *C. russula* having accumulated more changes than the other taxa. Moreover, as illustrated by Figure 7, the two branching patterns conflict with regard to the position of the two species of *Suncus* relative to the Eurasian *Crocidura*. This is not astonishing, as a casual inspection of the half matrices of Table 4 indicates that there is no strong genetic discontinuity between these crocidurine shrews, as all taxa appear to split off at about the same genetic level of differentiation (at a genetic distance of ca. 0.3). Thus, the branching patterns derived from both clustering procedures suggest the paraphyly of the genus *Suncus* and/or of the genus *Crocidura*.

Ecology

Suncus dayi has recently been collected from tropical evergreen forest (with *Rattus satarae* Hinton, 1918, *Rattus rattus* [Linnaeus, 1758], *Mus famulus* Bonhote, 1898 and *Suncus murinus*) in the Nilgiri Hills at 1500—2150 m and is also recorded in the

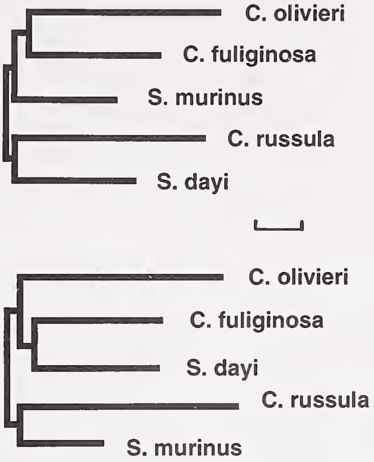

Fig. 7: Phenograms derived from the Neighbor-Joining (above) and Wagner (below) procedures on Rogers (1972) genetic distances. Both networks were arbitrarily rooted at midpoint of longest path. The branch lengths are a good approximation of the observed distances (of Table 4), as indicated by the values of the percent standard deviation (2.87 % and 6.16 %) and of the cophenetic correlation (0.984 and 0.968) for the Neighbor-Joining and Wagner trees, respectively. The bar (scale) is 0.05 units of genetic distance.

literature from the Palni Hills (Lindsay 1927). There is doubt about the collection locality of the holotype, as Dobson (1888) stated that the exact locality was unknown but gave the habitat as the Madras Presidency, India. Blanford (1888: 240) surmised that this specimen was probably obtained from the Palni or Travancore Hills in the Madras Presidency; subsequently Blanford (1891: 602) explained that the specimen had been brought to the donor, Dr. F. Day, from Trichur, Cochin. All of these localities are in southern India; the vegetation consists of tropical, high altitude evergreen rain forests. Both Nilgiri and Palni are hill forests, isolated from each other by the surrounding lower lying country which consists of a mixture of secondary forests (most of which are cultivated by man) and cleared, cultivated land (mainly tea and potatoes) and scrub.

Heim de Balsac & Lamotte (1957) stated that *Sylvisorex* and *Suncus* ecologically differ in Africa, *Suncus* occurring in semi-arid savanna, while *Sylvisorex* inhabits wetter forests (although one species, *S. megalura* — which has clear scansorial adaptations [Vogel 1974, Hutterer 1985] —, has been recorded in grassland).

The combination of features such as a long tail, elongated feet with elongated, well-spaced cheiridia, were interpreted as adaptations to a scansorial way of life (Hutterer 1985) and are characteristic of *Sylvisorex megalura*, *Suncus mertensi* Kock, 1974 and of some Indomalayan *Crocidura* such as *C. miya*, *C. paradoxura* and *C. elongata*. The implication is that *S. dayi* is also scansorial and therefore probably occupies a different ecological niche to the sympatric pigmy, *S. etruscus*, and the

Table 3: Allelic frequences observed at 19 polymorphic loci among five studied species. N: sample size..

Locus/Allele		*Suncus dayi* N=7	*Suncus murinus* N=8	*Crocidura olivieri* N=3	*Crocidura fuliginosa* N=3	*Crocidura russula* N=5
Ada:	211		.375			
	173		.625			
	138				.167	
	119				.833	
	100			.833		.375
	83	.714				.625
	75			.167		
	64	.286				
Adh:	.100		1.000	1.000	1.000	1.000
	73	1.000				
Ak-2:	125					1.000
	100		1.000	1.000	1.000	
	70	1.000				
Alb:	103	.071				
	100		1.000	1.000		
	96	.929				
	94				1.000	
	91					1.000
Est-1:	135	.857	1.000			1.000
	112	.143				
	100			1.000		
	82				1.000	
Got-1:	200				1.000	
	100	1.000	1.000	1.000		1.000
G-6-pd:	123				1.000	
	112	1.000	1.000	.500		1.000
	100			.500		
Idh-1:	150	1.000	1.000		1.000	1.000
	100			1.000		
Idh-2:	120		1.000			
	100	1.000		1.000	1.000	
	75					1.000
Lap:	100			1.000		
	96	1.000	1.000		1.000	1.000
Ldh-2:	110	1.000	1.000		1.000	1.000
	100			1.000		
Mod:	100			1.000		
	85	1.000				
	74		.313		1.000	
	70					1.000
	26		.687			

Table 3: continued

Locus/Allele		*Suncus dayi* N=7	*Suncus murinus* N=8	*Crocidura olivieri* N=3	*Crocidura fuliginosa* N=3	*Crocidura russula* N=5
Mpi:	132		1.000			
	100	1.000		.500	1.000	.500
	70			.500		.500
Pa:	100			1.000		
	80	1.000	1.000		1.000	1.000
6-Pgd:	140					1.000
	100	1.000	1.000	1.000	1.000	
Pgi:	200					1.000
	100	1.000	1.000	1.000	1.000	
Pgm:	150		.063		.278	
	117		.938		.722	
	100			1.000		1.000
	78	1.000				
Sod-1:	115		.625			
	100	1.000	.375	1.000	1.000	
	84					1.000
Sod-2:	100	1.000	1.000	1.000	1.000	
	30					1.000

giant, *S. murinus*, species. Regrettably there are no detailed observations to support these hypotheses.

Discussion

Species currently assigned to the genus *Sylvisorex* are confined to Africa. There is some controversy over the number of species recognised as belonging to the genus *Suncus*, which is found in Asia, Africa and Europe. Following Hutterer (1993) only four species are endemic to Africa, whereas nine occur in Asia and a tenth — *S. murinus* — is Asian in origin and believed to be a recent introduction to Africa (Heim de Balsac & Lamotte 1957, Hutterer & Tranier 1990). The area of greatest species diversity is generally accepted as the most probable site of origin of the group which, in the case of *Suncus*, is likely to be Asia.

Morphological results

Heim de Balsac & Lamotte (1957) suggested that *Sylvisorex* is ancestral to *Suncus*, the former possessing a greater number of primitive, and the latter a greater number of derived characters. These authors briefly alluded to the resemblance noted by Ellerman et al. (1953) between the African *S. lixus* and the Asian *S. stoliczkanus*. It was Butler (1978), Butler & Greenwood (1979) and Butler et al. (1989) who produced

Table 4: Genetic distances measured between five species of Crocidurinae. Below diagonal: Rogers (1972) genetic distance; above diagonal: Nei (1978) unbiased genetic distance. *S.*: *Suncus*; *C.*: *Crocidura*.

	Suncus dayi	*Suncus murinus*	*Crocidura olivieri*	*Crocidura fuliginosa*	*Crocidura russula*
S. dayi	000	.281	.432	.303	.400
S. murinus	.261	000	.377	.277	.378
C. olivieri	.366	.332	000	.407	.572
C. fuliginosa	.269	.262	.347	000	.517
C. russula	.342	.323	.439	.412	000

evidence of the possible derivation of African species of *Suncus* from *Sylvisorex* and furthermore, suggested that if this did not occur in Africa it might have done so from a *Sylvisorex*-like ancestral form in Asia which subsequently extended its range into Africa. They suggested that the fossil species of *Suncus* may have entered Africa rather late and that the main source of the immigrants was the Indomalayan region. They also demonstrated that *Suncus lixus* is dissimilar to the other African species of *Suncus*; it shares derived characters with two species of *Sylvisorex*, the fossil *S. olduvaiensis* Butler & Greenwood, 1979 and the Recent *S. johnstoni* (Dobson, 1888b) and could have been derived from a related species of *Sylvisorex* and, if it did not originate from *Sylvisorex* in Africa, it must be presumed to be an immigrant from Asia. Butler et al. (1989) cited the primitive characters, reminiscent of *Sylvisorex* found in some species of Asian *Suncus*, such as *S. fellowesgordoni*. It is therefore interesting to note that their view is further supported by another Asian species, *S. dayi* which shows an even higher proportion of primitive characters, so much so that it groups more readily with species of *Sylvisorex* than with those of *Suncus*. Butler et al. (1989) observed that *Sylvisorex* is definable only by primitive characters. These authors noted that *Suncus* was much more advanced than *Sylvisorex* and could feasibly be related to the *Sylvisorex granti* group (defined by these authors to include the species *granti*, *megalura*, *howelli* Jenkins, 1984, *johnstoni* and *olduvaiensis*). Table 1 shows that *S. dayi* has many primitive (plesiomorphic) features in common with *Sylvisorex*, but fewer with *Suncus*, which exhibits many more derived (apomorphic) character states. The results show that *Suncus dayi* is synapomorphic in only four characters, whereas *S. fellowesgordoni* is synapomorphic with *Suncus* in ten characters. This suggests that *S. fellowesgordoni* has a closer relationship with other species of the genus *Suncus* than does *S. dayi*. *Suncus dayi*, however, retains many plesiomorphic features common to *Sylvisorex*, shows few synapomorphies with either *Sylvisorex* or *Suncus*, and exhibits such a close resemblance to *Sylvisorex* that it could feasibly be reassigned to this genus. However, as shown in the next section discussing electrophoretic data, the lack of shared derived alleles between *S. dayi* (this paper) and *Sylvisorex* (Maddalena et al. 1990a, b) is a strong argument for preferring the conservative decision to continue to assign *S. dayi* to the genus *Suncus*.

Based on the interpretation of characters listed in Table 1, the problem remains as to whether *S. dayi* is a relict species, differing only in a few apomorphic features from the *Sylvisorex*-like ancestral form of *Suncus*, as postulated by Butler et al. (1989); or one of convergent evolution due to adaptation to a similar ecological niche, as suggested by Hutterer (1985) who pointed out that convergent evolution may have occurred several times in scansorial shrews.

Additional experiments with genetic markers (DNA sequencing, protein electrophoresis) are needed to understand the relationships of Asian and African white-toothed shrews of the genera *Suncus*, *Sylvisorex* and *Crocidura*. Furthermore, our comparative morphological analysis should be extended to include Indomalayan scansorial species of *Crocidura* such as *C. miya* from Sri Lanka, *C. paradoxura* from Sumatra and *C. elongata* from Sulawesi in order to test for morphological convergence.

Electrophoretic results

The endemic South Indian *Suncus dayi* appears to be genetically well differentiated from the sympatric species *Suncus murinus* (Fig. 7). However, *S. murinus* is almost as divergent from *S. dayi* as from the Indomalayan *C. fuliginosa* (Nei's distances of ca. 0.28: Table 4). This observation, as well as the conflicting topologies derived from the two phenetic reconstructions, suggest that all taxa analysed here might have diverged from each other at about the same time. Table 4 also reveals that the genetic distances measured in inter-generic comparisons are quite low by crocidurine standards: for example, Maddalena (1990b) has measured an average Nei's distance of 0.72 (SD 0.12, range 0.50—0.92) between *Suncus etruscus* and 20 species of African and European *Crocidura*. When Indomalayan representatives of *Suncus* and *Crocidura* are compared (Figure 11), the apparent paraphyletic placement of *Crocidura* is reminiscent of the finding of Maddalena (1990b), and this is in agreement with some traditional morphological studies (Heim de Balsac & Lamotte 1957, Butler et al. 1989). As *Sylvisorex* could not be included in this electrophoretic study, its genetic relationship with *S. dayi* cannot be directly assessed. Nevertheless, as Maddalena (1990a, b) used the same standard (*Crocidura olivieri*) for naming the different alleles, some comparison is possible for a subset of loci. In the cladogram proposed by Maddalena (1990b: 301), *Sylvisorex megalura* and *S. lunaris* (which were considered as an outgroup relative to *Crocidura*) shared two synapomorphic alleles: Ldh-2^{170} and Mdh-2^{84}. Neither of these alleles has been found among our Asian samples, thus suggesting no direct link between *S. dayi* and these two species of *Sylvisorex*. On the contrary, allele Idh-1^{150} in Maddalena (1990a, b) is shared by most other crocidurine shrews, and it is also observed in *S. murinus*, *S. dayi* and *C. fuliginosa*. Several synapomorphies (AK-1^{100}, Est-1^{110}, Ldh-2^{100}, Mdh-2^{100}, and Pgi^{100}) link our Asian samples with most species of *Crocidura* analysed by Maddalena (1990a, b), and not with *Sylvisorex*. These few genetic comparisons all indicate that *Suncus dayi* (and, by extension, the other Asian taxa analysed here) is not closely related to the African *Sylvisorex*, but instead shares several derived genetic characters with other shrews of the genera *Crocidura* and *Suncus*. The genetic affinities of *Suncus dayi* within a cluster containing *Suncus murinus* as well as some species of *Crocidura* indicate polyphyly for one or both genera. In conclusion, the genetic results, although still preliminary, do not support a close relationship between *S. dayi* and *Sylvisorex*, but rather suggest parallelism for the cranial similarities and convergence for the external scansorial adaptation.

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Zusammenfassung

Biochemische und morphologische Untersuchungen von *Suncus dayi* (Dobson, 1888) und die Diskussion der Verwandtschaft von *Suncus*, *Crocidura* und *Sylvisorex* (Insectivora: Soricidae). — Während einer Feldexpedition in den immergrünen Bergregenwald von Südindien konnten im Nilgiri Gebirge 7 Exemplare von *Suncus dayi* (Dobson, 1888), einer wenig bekannten Weißzahn-Spitzmaus, erbeutet werden. Die äußere Morphologie sowie Schädel- und Zahnmerkmale dieser Spezies wurden in einer vergleichenden Studie mit wenigen Arten der Gattungen *Suncus* (z. B. *S. stoliczkanus*, *S. fellowesgordoni*), *Sylvisorex* (z. B. *S. morio*, *S. granti* Gruppe) und *Crocidura* (z. B. *C. attenuata*) betrachtet. Eine biochemische Untersuchung der Isoenzymvariation an 32 Genloci erlaubt die Abschätzung der genetischen Differenzierung zwischen *S. dayi* und vier weiteren Weißzahn-Spitzmäusen: *Suncus murinus*, *Crocidura olivieri*, *C. fuliginosa* und *C. russula*. In der Schädel- und Zahnmorphologie teilt *Suncus dayi* viele plesiomorphe Merkmale mit einigen Vertretern der afrikanischen Gattung *Sylvisorex*, wohingegen andere Arten der Gattung *Suncus* in diesen Merkmalen apomorphe Muster aufweisen. Eine elektrophoretische Untersuchung zeigt Übereinstimmung in abgeleiteten Merkmalen zwischen *Crocidura* und *Suncus*, aber nicht zwischen *Sylvisorex* und *Suncus*. Insgesamt kann diese Studie nicht ausschließen, daß die eigentümliche Merkmalsverteilung bei *Suncus dayi* ein Ergebnis konvergenter Entwicklung in Verbindung mit kletternder Lebensweise ist.

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