Paludicola 12(4):247-258 March 2020


# SIWALIK FOSSIL SORICIDAE: A CALIBRATION POINT FOR THE MOLECULAR PHYLOGENY OF *SUNCUS*

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ABSTRACT

The Miocene small mammal fossil record of South Asia includes previously undocumented shrews as a minor element. Nonetheless, fossil Soricidae, especially in the Siwalik deposits of the Potwar Plateau, Pakistan, offer early records of the Subfamily Crocidurinae, particularly a new species of the crocidurine *Suncus*. In addition to elucidating shrew diversity in the Miocene of South Asia, Siwalik fossils provide dated first occurrences that can be integrated with time-trees and evolutionary scenarios based on molecular data of living shrews. The Siwaliks record the establishment of Asiatic Crocidurinae by 14 Ma, and the oldest known member of the extant genus *Suncus* at 10.5 Ma. Older deposits in Pakistan indicate the presence of other shrew stem taxa in the early Miocene of South Asia.

## INTRODUCTION

Extant crown group shrews (Family Soricidae) comprise some 350 species in three subfamilies distributed in tropical and temperate climates across the globe, but absent from Australia and Antarctica (Hutterer, 2005). The fossil record indicates an emergence of crown Soricidae in the early Miocene around 20 Ma (Reumer, 1987, 1995). Despite a few notable exceptions, the fossil record of shrews is woefully inadequate and often based on isolated teeth, which in many characters are confoundingly subtle across the family. Consequently, taxonomic and nomenclatural issues based on morphology have presented complications in sorting phylogeny and biogeography among living as well as fossil species.

Nevertheless, molecular phylogenetic analyses of shrews by Dubey et al. (2007, 2008), employing nuclear and mitochondrial genetic markers from 189 samples of soricids, including members of all three extant subfamilies (Soricinae, Crocidurinae, and Myosoricinae) and all six tribes of the Soricinae (Soricini, Anourosoricini, Neomyini, Notiosoricini, Blarinini, and Blarinellini), provided a clear, well-resolved, and strongly supported phylogeny. Their chronology is constrained through molecular clock methods and three dates from the fossil record. Using their phylogeny and chronology, Dubey et al. (2007, 2008) constructed hypotheses of historical biogeography and distribution patterns among soricids.

Our focus in this paper is on the meager remains of fossil shrews, primarily Subfamily Crocidurinae, from Siwalik Group deposits of the Potwar Plateau in Pakistan. The samples were recovered from localities ranging in age from 14 to less than 2 Ma (Figure 1). Field work in Pakistan and laboratory studies at Harvard University and several other institutions have continued for five decades. Extensive screen-washing efforts in the Potwar Plateau during the 1970s, 1980s, and 1990s (Badgley et al., 2004, 2005) recovered over 11,000 small mammal specimens, mostly rodents and mostly isolated teeth. These illustrate species-rich middle and late Miocene paleocommunities comprising ten families of rodents and lagomorphs. Only 104 of the 11,000 specimens are shrews (<1% of the total overall), constituting a small, if persistent, element of Siwalik paleocommunities through time. Most Siwalik shrews represent small indeterminate crocidurines, cf. *Crocidura* sp., which we briefly discuss below. Forty late Miocene teeth represent shrews of larger body size that cluster as a new species of the genus *Suncus*. The studies by Dubey et al. (2007, 2008), and their hypotheses consistent with their cladograms, allow us to

evaluate and consider the significance of the fossil record of shrews in Pakistan.

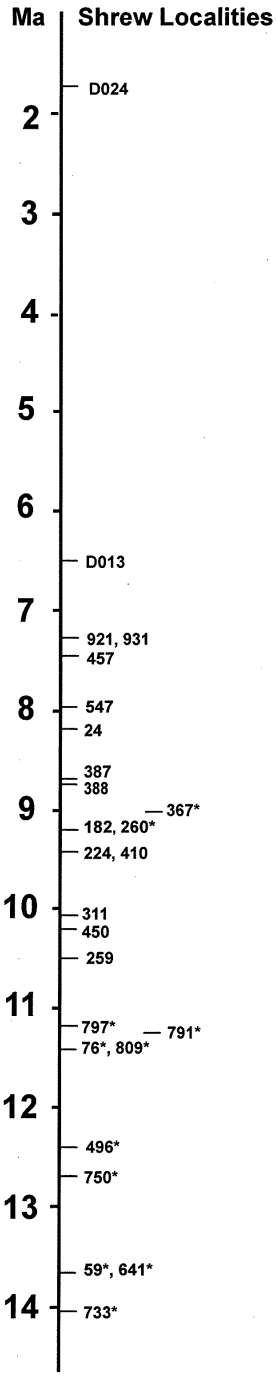


FIGURE 1. Biostratigraphic distribution of Potwar Plateau shrew localities with time scale derived from our paleomagnetic correlations (see Barry et al. 2002). The stratigraphic relationship of localities is shown, with a timeline in millions of years given on the left and localities positioned on the right. Locality numbers have 'Y' prefixes, except for the two youngest sites with 'D' from the Dartmouth-Peshawar field project. Here all localities have yielded shrews. Those with an asterisk (generally older sites) produced only small cf. *Crocidura* sp. The oldest site with *Suncus* is Y259 at 10.5 Ma.

Roberts (1977) recognized five species of extant shrews in Pakistan: *Sorex minutus* (at high elevation), *Suncus murinus*, *Suncus stoliczkanus*, *Suncus etruscus*, *Crocidura russula*, and *Crocidura pergrisea*. He noted that *S. stoliczkanus* and *C. pergrisea* may not be separable. Of particular interest here is the modern species *Suncus murinus* because it is an unusually large, characteristically Asian, species. One of the issues highlighted by Dubey et al. (2007) is the alleged distribution of *Suncus* in Africa, Europe, and Asia, and its systematic clustering with disparate groups of shrews in those regions. The trees of Dubey et al. (2007, 2008) show that African species of *Suncus* belong in a clade with *Sylvisorex*, true *Suncus* (type species *S. murinus*) is Asian, and *Suncus etruscus* plots as basal to the Eurasian crocidurine radiation.

Our specific purpose here is to elucidate the role of shrews in the development of the Siwalik fauna through time, in which *Suncus* appears to become a characteristic species. We are grateful to offer this contribution in honor of our friend James G. Honey. The coauthors of this paper were originally students with Jim at the University of Arizona, under the tutelage of Everett Harold Lindsay, or have continued that tradition subsequently in the following academic generation. Jim was interested in all fossils and in the rocks in which they are found. We had many long conversations with him in the field and in the lab. He was expert at finding fossils, including screen-washing for minute specimens. We acknowledge our friendship with Jim, and we recognize that friendship among student peers is a great boon to science.

**Methods and Terminology**—We compared isolated dental elements of fossil shrews with specimens stored in collections of the Museum of Comparative Zoology (MCZ), Harvard University, and at the Shuler Museum of Paleontology, Southern Methodist University. Specimens were studied by microscope observation (with a calibrated ocular for measurement) and, uncoated, by SEM (Zeiss Gemini Supra 55VP). Measurements follow the methods of Reumer (1984); for small teeth and fragments we measured maximum observed lengths and widths.

Upper teeth are designated by capital letters and lower teeth by lower-case letters (M1, m1), all measured in millimeters (mm). Most localities have a Y-prefix (for the locality system that started at Yale University). Specimens are registered in the YGSP (Yale-Geological Survey of Pakistan) database. The D-prefix signifies localities discovered under the Dartmouth-Peshawar project (as maintained in the YGSP catalog at Harvard University). A Z-prefix is used for early Miocene localities and some of the specimens from the Zinda Pir area in western Pakistan (see Lindsay et al. 2005).

## SYSTEMATIC PALEONTOLOGY

Order Soricomorpha Gregory, 1910

Family Soricidae Fischer de Waldheim, 1817

Soricid Indet.

**Referred Specimens—**Seven early Miocene teeth and fragments from the Zinda Pir region, western Pakistan, local stratigraphy and dating in Flynn et al. (2013). From locality Z113, 22.5 Ma, Z 773 (broken M2, transverse width 1.45 mm) and Z 774 (upper incisor 1.25 mm long), from Z150, 22.2 Ma, Z 2193, M1 fragment, buccal length 1.20 mm; from Z124, 18.8 Ma, Z 597 (M2 fragment, buccal length 1.25 mm) and Z 598 (broken M1, length x width, 1.35 x 1.65 mm); from Z122, 18.7 Ma, YGSP 36685 (P4 fragment, buccal length 1.45 mm), and YGSP 36686 (broken M1, length x width, 1.1 x 1.55).

**Discussion—**These few specimens, seven compared to 653 rodents from the same localities, were retrieved from early Miocene terrestrial deposits of the Zinda Pir Dome, 250 km southwest of the Potwar Plateau (Lindsay et al., 2005). They are from four early Miocene localities (22.5 to 18.7 Ma ion age). Subfamily attribution for these small shrews cannot be determined without diagnostic jaw and dental material. The upper incisor (Figure 2A) of yellow hue is simple, with a blunt talon. The P4 fragment of similar color includes the buccal blade and a distinct parastyle. Upper molar fragments Z 597 and 2193 are also yellowish but preserve a narrow zone of iron pigmentation on the lingual side of the metacone and paracone. In contrast, the larger Z 598 is beige in color and shows no iron pigmentation. Z 598 is corroded and possibly represents an early white-tooth shrew (Crocidurinae) at 18.8 Ma. Upper molars Z 773 and YGSP 36686 are brown.

These seven specimens appear to indicate at least two shrews in western Pakistan, one ac possible crocidurine and one that differs principally in its iron staining from small white-toothed shrews. As a feature of the dentition, iron staining is widespread in Soricinae, and occurs in extinct Crocidosoricinae (Hugueney et al., 2012). The Zinda Pir sites show that two kinds of shrew were present 250 km southwest of and well before the Potwar Plateau. Both differ from the crocidurine lineages described below for younger Potwar Miocene Siwalik localities in northern Pakistan.

Subfamily Crocidurinae Milne-Edwards, 1868

*Crocidura* Wagler, 1832

cf. *Crocidura* sp.

**Referred Specimens—**Isolated dental specimens from middle and late Miocene Siwalik deposits of the Potwar Plateau represent a small shrew with unpigmented teeth not distinguishable at the genus level from extant *Crocidura* (see Figure 2). Older horizons between Y773 and Y311 (14 - 10 Ma) in the Chinji and Nagri Formations produced only 23 specimens. The shrew is better represented in the Dhok Pathan Formation with 34 specimens from localities Y224 to D13 (9.4 - 6.5 Ma).

Older Siwalik material includes left m1 YGSP 36182 from Y733, left m2 36216 from Y59, upper incisor 36279 from Y641, dentary fragment 48057 from Y750. From Y496, right m1 YGSP 27329 and P4 fragment 40504. From Y76, dentary with m1-3 YGSP 40587 and broken M1 40598. From Y809, upper incisor YGSP 53958 and left m1 53961. From Y791, M2 YGSP 34945 and upper incisor 53264. From Y797, jaw fragment YGSP 33086, right m1 YGSP 36183 and upper incisor 36184. From Y259 three lower molars YGSP 40561, 40562, 49196. From Y450, m1 YGSP 40581 and M2 40583. From Y311, jaw fragment with m1-2, YGSP 21876, right m2 54200 and broken P4 54199.

From the Dhok Pathan Formation three lower molars: Y224 (YGSP 40588) and Y260 (YGSP 19493, 19494). From Y182, four dentate mandible fragments YGSP 40514-40517, one edentulous jaw YGSP 40519, lower molars 40520-40523, partial M1 YGSP 40524, M1 40525, and upper incisors YGSP 40526, 40527. From Y367, three dentate mandible fragments and one lower molar, YGSP 40552-0555. From Y388, P4 fragment YGSP 40536 and M1 fragment 40537. From Y387, four lower molars 40542-40545, P4 fragment YGSP 40546 and broken M1 40547. From Y24, dentary with m1-2 YGSP 40579. From Y547, dentary fragment, maxillary fragment with M1-2, isolated M2 (YGSP 40571-40573). From Y931, trigonid YGSP 54339. From D013, left m2 YGSP 40568.

**Notes and Discussion—**The upper incisor (Length: YGSP 40526, 1.4 mm; 40527, 1.3 mm) has a short talon (Figure 2B), stronger than that on the smaller Z 774 specimen. P4 (buccal lengths of 40546, 40536 are 1.40 and 1.45 mm) has a protruding parastyle, high paracone, and straight posterior buccal blade. M1 (length x width of YGSP 40525 = 1.25 x 1.55 mm) has a narrow, sloping hypoconal shelf with small hypocone; its parastyle is small and the metastyle is indistinct. This tooth and M2 YGSP 34945 (Figure 2C, 1.30 x 1.85 mm) both show the paracone connected to the anterior arm of the protocone; the posterior arm of the protocone is directed to the hypoconal shelf, bypassing the lingual side of the metacone. YGSP 40572 (Figure 2D) shows that M1 (1.3 x 1.8 mm) is slightly larger than M2 (1.1 x 1.7 mm).

YGSP 40515 from Y182 (Figure 2E-G) preserves a small p4 (0.75 x 0.80 mm) followed by m1 and m2 (1.30 x 0.95; 1.20 x 0.85). The p4 has a very short talonid with posterior notch into which the following molar is seated. Its high principle cusp is accompanied by small cuspules, the counterparts of a “paraconid” and

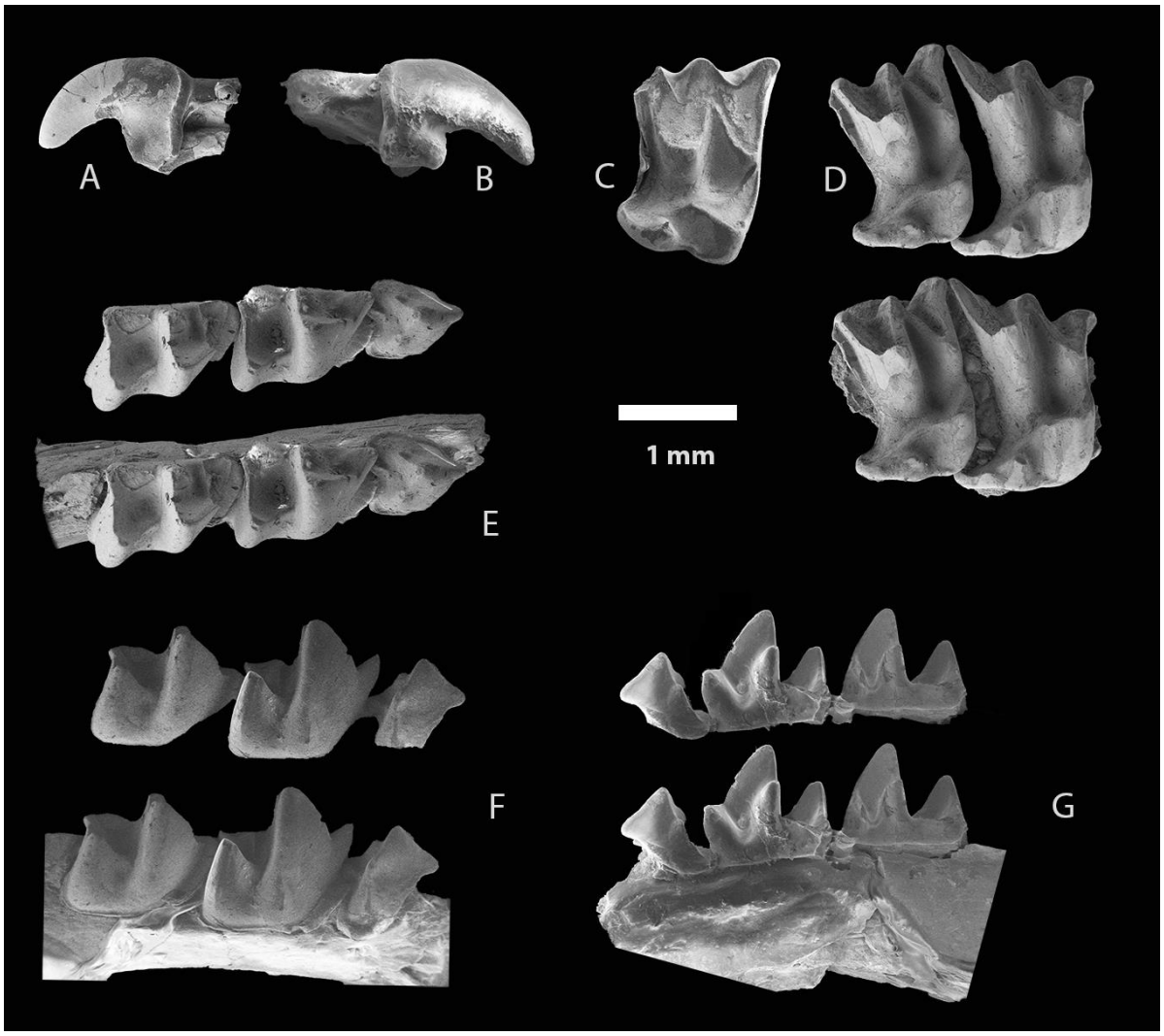


FIGURE 2. Scanning electron microscope images of dental remains of small Miocene shrews. A: Indeterminate Soricidae Z 774, left upper incisor from locality Z113, 22.5 Ma, Chitarwata Formation of western Pakistan. B-G: cf. *Crocidura* sp. from the Nagri and Dhok Pathan Formations of the Potwar Plateau. B, right upper incisor YGSP 40527; C, right M2 YGSP 34945; D, YGSP 40572 right M1-M2 in maxilla fragment (below), bone removed above; E-G YGSP 40515 right dentary with p4m1m2, in occlusal, buccal, and lingual views (bone removed above in each pair). Bar scale = 1mm.

"metaconid". Lower molars have short entoconid crests that terminate posterior to the metaconid, and small, indistinct hypoconulids posterior to the entoconid. There is an anterior cingulum; m1 is larger and its talonid broader than m2. The very small m3 has a 3-cusped trigonid and its talonid is reduced to a heel. Molar row length for YGSP 40587 = 3.6 mm. Length of tooth row for YGSP 40515, including p4 and m3 alveolus = 3.8 mm.

The collection appears to represent a small crocidurine in the middle Miocene of South Asia. Its record begins in the Chinji Formation at 14 Ma. On the Potwar Plateau older rocks of the Kamlial Formation lack any indication of shrews. Potwar cf. *Crocidura* sp., distinguished from other shrew groups in lacking pigment, was a long-duration taxon during the early diversification of Subfamily Crocidurinae (Dubey et al., 2007, 2008). The small sample does not indicate size change through time, and no other features support genus or species level subdivision. Conceivably these specimens represent a single species level clade spanning 7.5 m.y., i.e., throughout the stratigraphic range of localities Y773 to D013 (14 to 6.5 Ma, Figure 1).

The middle to late Miocene interval for Potwar cf. *Crocidura* sp. informs biogeographic hypotheses and suggests a significant phase of evolution for the subfamily in South Asia. The material represents a stem

member of the subfamily, not necessarily a species of *Crocidura*. The 14 Ma appearance of cf. *Crocidura* sp. appears to be an immigration event but point of origin is unknown. As presently understood, these fossils are the oldest evidence of the subfamily yet known.

*Suncus* Ehrenberg, 1832
*Suncus honeyi* sp. nov.

**Holotype—**YGSP 40539 (Figure 3A), isolated right M2.

**Type Locality—**Y388, late Miocene site in the lower part of the Dhok Pathan Formation near Malhuwala Village in the Khaur anticline of the Potwar Plateau, Pakistan. Y388 is dated paleomagnetically at 8.75 Ma.

**Etymology—**Species named for our colleague and friend, fossil hunter James Gilbert Honey.

**Referred Specimens—**Holotype plus 39 isolated specimens from 12 localities of the upper part of the Nagri Formation through the Dhok Pathan Formation of the Siwaliks exposed on the Potwar Plateau (Table 1), with paleomagnetic age constraints of 10.5 to 6.5 Ma (Figure 1). From Y259, left m1 YGSP 40560. From Y450, left Incisor YGSP 40582. From Y311, left M1 YGSP 40556 and right Incisors 40557 and 54201. From Y410, right and left Incisors YGSP 40590, 40591. From Y224, left M2 40589. From Y182, right m2, left m1, right m1, left M1, right Incisor, YGSP 40528-40532. From Y388, right p4, right m1, and left P4 in maxilla, YGSP 40533-40535; three left M2, YGSP 40539-40541. From Y387, right m1, left M1, left M1, left M2, YGSP 40548-40551. From Y24, right m1 YGSP 40580, right lower incisor YGSP 40597. From Y457, left incisor in dentary fragment, YGSP 40593. From Y921, left m3 and right M1, YGSP 54277 and 54278. From Y931, four right Incisors YGSP 54334-54337, left M2 YGSP 54338, left m1 YGSP 39459, Antemolar 1 YGSP 39463, and right p4 YGSP 39464. From D013, right p4, YGSP 40564; right m1 and left m2 YGSP 40565, 40566. (Also, from D013, right M1 YGSP 40567 noted below as cf. *Suncus murinus*.)

**Diagnosis—**A large white-tooth crocidurine shrew of the genus *Suncus* based on size, non-fissident upper incisor, low-cusped (nonsectorial) antemolar and p4, upper molars with acute W-shaped ectoloph, m2 nearly equal to m1 in size, and proximal end of lower incicor ending anteriorly (below p4). It is a species of *Suncus* with average size of molars less than that of extant *Suncus murinus*, which is widespread in southern Asia, about the size of modern *Suncus montanus* (e.g., MCZ 27548, which is restricted to Sri Lanka [Meegaskumbura and Schneider, 2008]). Some specimens from younger localities approach smaller *S. murinus* in size (average observed maximum M1 width of nine extant *S. murinus* from the MCZ collection at Harvard University is 2.3 mm). Table 2 gives dimensions for measurable fossils. On the hypoconal flange, the hypocone is distinct, sometimes a doubled cuspule; P4 with a distinct parastyle, a straight posterior blade showing wear, and an abbreviated hypoconal flange; lower first and second molars close in size (m2 almost as large as m1), with very short entoconid crest and reduced hypoconulid; postero-buccal heel of the lower incisor terminates well anterior to p4. Only known Miocene member of the genus.

TABLE 1. Large shrew teeth with locality/specimen number, age estimate, and dental locus.
Localities have "Y" prefix except for two indicated here with "D" prefix.

| Loc/Specimen Number | Age (Ma) | Tooth Position |
|---|---|---|
| *Suncus honeyi* | | |
| 259/40560 | 10.5 | Left m1 |
| 450/40582 | 10.2 | Left U. Incisor |
| 311/40556 | 10.1 | Left M1 |
| 311/40557 | 10.1 | Right U. Incisor |
| 311/54201 | 10.1 | Right U. Incisor |
| 410/40590 | 9.4 | Right U. Incisor |
| 410/40591 | 9.4 | Left U. Incisor |
| 224/40589 | 9.4 | Left M2 |
| 182/40528 | 9.24 | Right m2 |
| 182/40529 | 9.24 | Left m1 |
| 182/40530 | 9.24 | Right m1 |
| 182/40531 | 9.24 | Left M1 |
| 182/40532 | 9.24 | Right U. Incisor |
| 388/40533 | 8.75 | Right p4 |
| 388/40534 | 8.75 | Right m1 |
| 388/40535 | 8.75 | Left P4 |
| 388/40539 | 8.75 | Left M2 |
| 388/40540 | 8.75 | Left M2 |
| 388/40541 | 8.75 | Left M2 |
| 387/40548 | 8.7 | Right m1 |
| 387/40549 | 8.7 | Left M1 |
| 387/40550 | 8.7 | Left M1 |
| 387/40551 | 8.7 | Left M2 |
| Y24/40580 | 8.2 | Right m1 |
| Y24/40597 | 8.2 | Right lower incisor |
| 457/40593 | 7.4 | L dentary + incisor |
| 921/54277 | 7.3 | Left m3 |
| 921/54278 | 7.3 | Right M1 |
| 931/54334 | 7.3 | Right U. Incisor |
| 931/54335 | 7.3 | Right U. Incisor |
| 931/54336 | 7.3 | Right U. Incisor |
| 931/54337 | 7.3 | Right U. Incisor |
| 931/54338 | 7.3 | Left M2 |
| 931/39459 | 7.3 | Left m1 |
| 931/39463 | 7.3 | First Antemolar |
| 931/39464 | 7.3 | Left p4 |
| D13/40564 | 6.5 | Right p4 |
| D13/40565 | 6.5 | Right m1 |
| D13/40566 | 6.5 | Left m2 |
| | | |
| Other Species | | |
| D13/40567 cf. *S. murinus* | 6.5 | Right M1 |
| D24/40576 *Suncus* sp. | 1.8 | Right M1 |
| 388/40538 Beremendiini | 8.75 | Right M1 |
| 547/40574 Beremendiini | 8.0 | Left M2 |

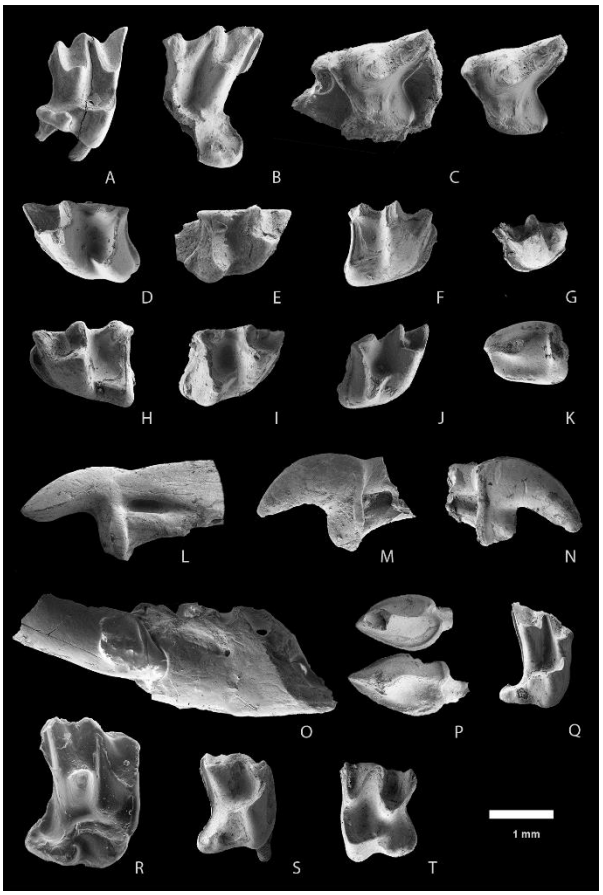


FIGURE 3. Dental remains of large shrews from the Potwar Plateau, Pakistan. *Suncus honeyi*: A. left M2 YGSP 40539 from Y388, B. right M1 40539 from Y387, C. left P4 40535 from Y388 in maxilla fragment (left) and removed (right), D. left m1 40566 from D013, E. right m1 40534 from Y388, F. right m2 40548 from Y387 G. left m3 54277 from Y921, H. left m1 39459 from Y931, I. right m1 40530 from Y182, J. right m2 40528 from Y182, K. A1 39463 from Y931, L. right upper incisor 54334 from Y931 (medial view), M. left upper incisor 40582 from Y450, N. right upper incisor 54201 from Y311 (M, N: lateral view), O. lower incisor in left dentary fragment 40593 from Y457, P. above: left p4 39464 from Y931, below: right p4 40564 from D013. *Suncus* or *Crocidura* sp.: Q. right M1 40576 from D024. Cf. *Suncus murinus*: R. right M1 40567 from D013. Beremendiini, gen. indet.: S. broken right M1 40538 from Y388. T. left M2 40574 from Y547 (beremendiin or *S. honeyi*). Bar scale = 1 mm.

**Description—**As in all crocidurines (white-toothed shrews), *Suncus honeyi* lacks iron pigmentation in the dentition. Also, upper molars show the characteristic (of the subfamily) tight W-shaped ectoloph, wide transversely, narrow anteroposteriorly, with acute reentrants. No M3 was recovered. In both M1 and M2 (Figure 3A, B) the metacone towers over the paracone. Four small roots are apparent. The parastyle is small and the metastyle is poorly developed. M1 with short preparacrista but wide posteriorly with lingually expansive hypoconal flange; M2 is wide anteriorly with long preparacrista and buccally retracted hypoconal flange. In upper molars the protocone joins the paracone, but the posterior arm of the protocone is lingual to the metacone and runs longitudinally to the hypoconal flange and the buccal side of the hypocone cusp. A narrow posterior cingulum continues buccally from the flange.

P4 is represented by a single specimen in a maxilla fragment (Figure 3C). The prominent paracone has a long, high posterior buccal blade showing wear. The small parastyle is an independent conical cusp. There is no distinct protocone, just a thickened fold of enamel; an abbreviated flange (without hypocone) slopes posteriorly from it. Anterior to P4, modern *Suncus* shows four antemolars. The first one termed A1 (Reumer, 1984) is large, nearly half the size of M2 (A2-4 are quite small). One fossil tooth, YGSP 39463 (Figure 3K) represents A1. A low cingulum surrounds a single, low anterior cusp with worn central anterior ridge. The posterior margin of A1 is invaginated slightly.

Several specimens, some quite reduced by heavy dental wear (advanced age), represent the upper incisor. It is anchored by two fused roots. The pointed apex is unsplit (not fissident); the talon is low as in modern *Suncus*, not a prominent cusp. The buccal cingulum of the incisor undulates slightly.

Lower molars have a high trigonid with prominent protoconid, large metaconid, and low paraconid. The V-shaped hypoconid of molar talonids extends buccally beyond the protoconid, the entoconid is a sharp lingual cusp with short, low entoconid crest. A small, low hypoconulid projects posteriorly and becomes indistinct with wear. The cristid obliqua intersects the trigonid below the protoconid. A cingulum encloses all but the lingual sides of m1-3. First and second lower molars (Figure 3D-J) are similar: the paracristid of m1 extends slightly more anteriorly and its talonid is somewhat longer than in m2, so the tooth length is greater than that of m2; the talonid of m1 is slightly broader than that of m2. The third molar (Figure 3G) is diminutive and its reduced talonid is primarily a lingually displaced small hypocone with a low ridge running from it to the middle of the trigonid.

Modern *Suncus* has a small a1 crowded between the incisor and p4. None are preserved but YGSP 40593 has an a1 alveolus (Figure 3O). There are two p4 (Figure 3P). That tooth has a single posteriorly projecting root and overhangs the preceding a1. The tooth is trenchant but not high-cusped, with a single laterally compressed cusp bearing a steep anterior ridge and sloping posterior ridge. The cusp is slightly lingually placed and there is a strong buccal cingulum and weaker lingual cingulum. However, as is characteristic of crocidurines the buccal cingulum is uninflated, not overhanging the lateral side of the dentary. The p4 is invaginated slightly posteriorly, which as Reumer (1987) notes is typical for

crocidurines. The p4 from younger locality D013 is larger than the p4 from Y931.

The lower incisor is represented by YGSP 40597 and YGSP 40593 in a jaw fragment (Figure 3O). The dentary of the latter includes alveoli for a1, p4, and the anterior root of m1. The mental foramen is below the posterior portion of p4. The simple incisor lacks accessory cusps (acuspulate), is robust and has a supero-internal longitudinal fold. A cingulum is present externally. The posterior rounded external extent of the incisor does not reach far distally as in some shrews, less than in *Crocidura*, and that alveolus ends below the anterior portion of a1.

**Discussion—**This large white-toothed shrew is represented mainly by isolated teeth that show characteristic features of extant *Suncus*. Our concept of *Suncus* is in the restricted sense of Jenkins et al. (1998) and supported by the molecular phylogeny of Dubey et a. (2007, 2008), who show that the genus is an Asian radiation; African species are distinct from Asian *Suncus* at the genus level. Premolar and incisor morphology of Siwalik specimens are consistent with *Suncus*. Molar features, including relative sizes and morphology of the upper molar ectoloph are also characteristic. The large size of Siwalik fossils indicates a late Miocene record in Asia of the genus *Suncus*. Today, *Suncus murinus* is present in the Potwar Plateau area (Roberts, 1977).

We classify this fossil species as a member of the white tooth shrew Subfamily Crocidurinae. It shows no red pigment in the dentition, thus ruling out most Soricinae (particularly Soricini, Blarinellini, Neomyini, Beremendiini). Although we lack fossil jaw articulation material to test attribution, incisor, premolar, and molar features support assignment to Crocidurinae. Other Old World genera lacking red pigment are *Anourosorex* and *Myosorex*. *Anourosorex* has a very different crushing dentition – crushing function extending onto the talon of the incisor, a huge m1 dominating the lower tooth row, and p4 with a buccal cingulum expanded laterally. *Myosorex*, basal to crocidurines (Meegaskumbura et al., 2014) has a large incisor talon, trenchant and high-cusped upper antemolar with cingulum, sectorial p4, and cuspulate lower incisor.

Among crocidurines, *Suncus honeyi* is distinguished by its large size, and by biogeography. Today crocidurines are diverse in Africa: the small *Sylvisorex* has a low incisor talon, small antemolar with high cusp, tall cusp on p4, cuspulate incisor, and m1 appreciably larger than m2. Larger *Scutisorex* has an extended talon, long antemolar row and long lower incisor, and p4 with a reduced trigonid. In Asia the minute Piebald Shrew *Diplomesodon* has a trenchant first upper antemolar, reduced parastyle on P4, and m1 larger than m2. Ruling out endemic Sri Lankan *Feroculus* and *Solisorex*, *S. honeyi* is most comparable to *Suncus*, and unlike diverse *Crocidura*. The fossil record is suggestive of this distinction: after millions of years of *Crocidura*-like shrews present on the Potwar Plateau, the large *S. honeyi* appears abruptly without an apparent ancestor.

*Suncus* has been recognized in Pliocene deposits of the Potwar. Cheema et al. (1997) identified a shrew mandibular fragment as *Suncus* sp. This Pliocene-age specimen bears m3 with length of 1.15 mm, smaller than extant *Suncus murinus* but comparable to *Suncus honeyi* from Y921 (7.3 Ma; see Table 2). Nanda (2002) noted *Suncus*, cf. *S. murinus*, in the early Pliocene of northern India.

Sahni and Khare (1976) found a large shrew at Ladhyani in the Haritalyangar area of northern India in strata that correlate to the 8.5-8.8 Ma interval on the magnetic section of Pillans et al. (2005). They named *Siwalikosorex prasadi* for a third molar (length 1.7 mm) about the size of extant *S. murinus*. Another large shrew was found in early Pleistocene deposits at Kilar in Kashmir. *Indosuncus bhatiai* Sahni and Kotlia, 1985, was recovered from normally magnetized sediments considered equivalent to the Olduvai chron. Teeth identified as second lower molars have lengths of 1.7 to 1.9 mm, larger than *Suncus honeyi*, close to *S. murinus*. Neither fossil species was differentiated by their authors from extant *Suncus*.

These records demonstrate one or more large crocidurine shrews in the Late Neogene Siwaliks. It is conceivable that they represent a single variable species of *Suncus*, with later individuals close to *Suncus murinus*. The Miocene Potwar *Suncus honeyi* is smaller than other *Suncus*, particularly *S. murinus*, and its first records are older than any other large crocidurine. Despite older presence of a small crocidurine in the Potwar area, the appearance of *Suncus* by 10.5 Ma is a distinct immigration event. While the point of origin of the *Suncus* immigrant is unknown, timing agrees with the biogeographic hypothesis of Dubey et al. (2007).

*Suncus* or *Crocidura* sp.

**Referred Specimens—**YGSP 40576, isolated right M1 from early Pleistocene Locality D024, Pabbi Hills, Pakistan, above Olduvai Chron (<1.8 Ma). YGSP 40575 (left dentary fragment); 40577 and 40578, two broken right M1.

**Notes and Discussion—**As in *Suncus honeyi*, upper molar YGSP 40576 shows the characteristic tight W-shaped ectoloph, which is wide transversely, narrow anteroposteriorly with acute reentrants (Figure 3Q). The protocone crest runs directly to the paracone. The tall metacone is more isolated from the protocone. The hypoconal flange, with small hypocone, is narrow and posteriorly directed, with buccally inclined surface. A cingulum lies posterior to the metacone.

TABLE 2. *Suncus* dental measurements (following Reumer, 1984)

| Incisors | Length (L) | Talon L | Height | | |
|---|---|---|---|---|---|
| YGSP 40582 | 1.8 | 0.65 | 1.65 | | * |
| 40557 | 1.8 | 0.7 | 1.5 | | |
| 54201 | 1.85 | 0.7 | 1.5 | | * |
| 54334 | 1.8 | 0.65 | 1.7 | | * |
| 54335 | X | X | 1.8 | | |
| (lower) 40593 | X | X | 1.1 | | * |
| (lower) 40597 | X | X | 1.05 | | |
| Antemolar | Length | Width | | | |
| A1: 39463 | 1.3 | 0.95 | | | * |
| p4: 39464 | 1.5 | 1.05 | | | |
| p4: 40564 (D13) | 1.8 | 1.1 | | | |
| P4 | Buccal L | Lingual L | Width (W) | | |
| 40535 | 1.8 | 1.1 | 1.7 | | * |
| Upper molars | Buccal L | Lingual L | Anterior W | Post. W | |
| M1: 40549 | 1.55 | 1.5+ | 1.6+ | 2.3 | * |
| 40550 | 1.55 | X | X | X | |
| 54278 | 1.65 | X | X | X | |
| 40538# | 1.2+ | 1.55 | 1.7+ | 1.8+ | * |
| M2: 40589 | 1.25 | 1.35 | 1.9 | 1.8 | |
| 40539 | 1.4 | 1.35 | 2.05 | 1.75 | * |
| 40540 | 1.25 | 1.3 | 1.75 | 1.65 | |
| 40541 | 1.4 | X | X | X | |
| 40551 | 1.55 | X | 2.2 | ~2.0 | |
| 54338 | 1.5 | X | X | 2.15 | |
| 40567 (D13) | 1.65 | 1.85 | 2.1 | 2.3 | * |
| 40576 (D24) | 1.05 | 1.3 | 1.7 | 1.75 | * |
| 40574# | 1.35 | 1.35 | 1.9 | 1.7 | * |
| Lower molars | Length | Trigonid W | Talonid W | | |
| m1: 40560 | 1.55 | 1.05 | 1.2 | | |
| 40529 | 1.6 | 1.2 | 1.2 | | |

| | | | | |
|---|---|---|---|---|
| 40530 | 1.8 | 1.05 | 1.45 | * |
| 40534 | 1.8 | 1.05 | 1.15 | * |
| 40580 | 1.55 | 1.1 | 1.25 | |
| 40560 | 1.55 | 1.05 | 1.2 | |
| 39459 | 1.85 | 1.15 | 1.4 | * |
| 40565 (D13) | 1.9 | 1.25 | 1.4 | |
| m2: 40528 | 1.55 | 1.05 | 1.1 | * |
| 40548 | 1.55 | 1.05 | 1.3 | * |
| 40566 (D13) | 1.85 | 1.25 | 1.35 | * |
| m3: 54277 | 1.2 | 0.75 | ~0.5 | * |

* Illustrated specimens

\# Beremendiini or cf. Beremendiini

D prefix for localities D13 and D24

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The dimensions of early Pleistocene YGSP 40576 (Table 2) are considerably less than those of *Suncus honeyi*, demonstrating another, younger crocidurine, *Suncus* sp. or *Crocidura* sp. in the Siwalik record of northern Pakistan.

Cf. *Suncus murinus*

**Referred Specimens—**YGSP 40567, isolated right M1 from Locality D013, of the Bhandar area, Potwar Plateau, northern Pakistan, paleomagnetic age estimate of 6.5 Ma.

**Description—**YGSP 40567 (Figure 3R) has the pronounced W-shaped ectoloph of *Suncus.* The paracone is more worn than the high metacone. The anterior arm of the protocone joins the paracone but the posterior arm runs distally, past the metacone to the hypocone flange, and is confluent with the hypocone, which is a distinct lingual ridge on the flange. The cingulum posterior to the metacone is slightly damaged.

**Discussion—**YGSP M1 40567 is too large to represent the same species as *Suncus honeyi*. Although above we refer a p4 (YGSP 40564) and lower molars (YGSP 40565, 40566) from the same locality D013 to *Suncus honeyi*, we note that they also appear to be large for that species. These three specimens are insufficient in themselves to defend identification as *S. murinus* but with YGSP 40567 may attest to an increase in size of the *Suncus* lineage as represented at site D13 (6.5 Ma). Alternatively, there may be unseen diversity among crocidurines with two species of *Suncus* at D13.

In contrast to *Suncus honeyi* from older levels of the Dhok Pathan Formation, which appears to be uniformly smaller than *S. murinus*, the D013 specimens may represent a time-successive sample of the *Suncus* lineage that culminates in extant *S. murinus*. In this case, D013 would show that the *Suncus* lineage had transformed to the modern species by 6.5 Ma. Future data will test this hypothesis and will challenge whether fossils attributed so *Siwalikosorex prasadi* and *Indosuncus bhatiai* are distinct from *Suncus murinus*.

Subfamily Soricinae Fischer de Waldheim, 1817
Tribe Beremendiini Reumer, 1984
Genus indet.

**Referred Specimens**—YGSP 40538, isolated right M1 from late Miocene Locality Y388, Dhok Pathan Formation, Potwar Plateau, Pakistan, paleomagnetic age 8.75 Ma; possibly YGSP 40574, left M2 from Locality Y547, Dhok Pathan Formation, Potwar Plateau, Pakistan, paleomagnetic age 8.0 Ma.

**Description—**YGSP 40538 (Figure 3S) is pigmented red, a hallmark of Tribe Beremendiini. The pigment stain is deepest on the high metacone, faded elsewhere, and seems to be absent lingually. The tooth is incomplete, missing its buccal wall and most of the paracone. Anteriorly the protocone is confluent with the paracone. The posterior arm of the protocone runs distolingually to the hypoconal flange and its small hypocone. This posterior arm is not so isolated from the metacone as in *Suncus*; rather there is a low saddle leading to the metacone. The hypoconal flange is steeply

inclined and its buccal margin continues as a strong posterior cingulum. The metacone of YGSP 40574 (Figure 3T) is more deeply red-brown than the rest of the tooth, but the tooth is much less obviously pigmented than YGSP 40538. The hypoconal shelf is broad and sloping, as in that of YGSP 40538 and unlike that of *Suncus honeyi*. In other respects, the shape of the main cusps is comparable to that of *Suncus honeyi*.

**Discussion—**YGSP 40538 demonstrates diversity among large shrews in the Dhok Pathan Formation of the Potwar Plateau. If correctly allocated, it represents the oldest known beremendiin shrew and an immigration event of a group that was later very successful in the Pliocene of North Asia (Zazhigin and Voyta, 2019). We interpret the immigration event as younger than ~9 Ma, subsequent to the rich faunas sampled in the 9.4 to 9.2 Ma interval in the Potwar Dhok Pathan Formation that lack this shrew. Specimen 40574 from a younger locality may represent the same species but does not show the same degree of iron staining. It could be a variant of *Suncus honeyi* with a sloping hypoconal flange reminiscent of YGSP 40538.

## CONCLUSIONS

The modern lower Indus River fauna of Pakistan contains *Crocidura* and *Suncus*. The roots of that assemblage developed in the middle and late Miocene, as revealed by the Siwalik fossil record of the Potwar Plateau. *Crocidura* or its predecessor was in place by 14 Ma and *Suncus* appeared by 10.5 Ma.

The biogeographic hypotheses of Dubey et al. (2007, 2008) is tested by the Siwalik fossil record of shrews, fragmentary though it is. First, Dubey et al. (2008) defend the monophyly of Myosoricinae. They also confirm that *Suncus* as previously conceived is paraphyletic, the African species clustering with *Sylvisorex*, the genus to which they should be assigned. *Suncus murinus*, *Suncus dayi*, and *Suncus montanus* form an Asian clade sister with *Crocidura*. Western *Suncus etruscus* is basal to both *Suncus* and *Crocidura*.

Several issues regarding modern species of *Suncus* are beyond the scope of this paper, for instance, the question of generic affiliation of *Suncus etruscus*. There may be hidden diversity or hybridization within *Suncus*, as in Indian and Sri Lankan *Suncus murinus* and *S. montanus* (Meegaskumbura and Schneider, 2008).

The Family Soricidae has a fossil record that extends to over 40 million years ago (middle Eocene; Gunnell et al, 2008; Repenning, 1967). Fossil Soricinae are known back to 19.4 Ma (early Miocene) and *Sorex* extends to 12.1 Ma (Gunnell et al., 2008). The earliest Pakistani shrews (first record at Z113, 22.5 Ma age) would be significant for calibrating nodes if the material were more definitive. That some teeth of that antiquity are pigmented (as are many Soricinae and other shrews) is significant and rules out alignment with crocidurines. The molecular clock estimates of Dubey et al. (2008) were constrained by a 20 Ma divergence of Soricinae and Crocidurinae and the then-apparent latest Miocene first record of *Crocidura*. Our fossil *Suncus* and coeval small crocidurines extend the likely time of the *Suncus*-*Crocidura* split to the early late Miocene, >10.5 Ma.

Our current understanding of the Siwalik record of fossil shrews, meager as it is, dates the establishment of *Suncus* on the subcontinent by 10.5 Ma (late Miocene), the oldest known record of crocidurine shrews at 14 Ma, and the oldest known record of an extinct tribe, Beremendiini, at 8.75 Ma. The occurrence of *Suncus* at 10.5 Ma (and of cf. *Crocidura* before that) pushes back the *Suncus*-*Crocidura* divergence time beyond the estimates of Dubey et al. (2007, 2008), as well as the 10.8 Ma divergence of Asian *Suncus*-African *Sylvisorex*, if the tree topology is correct, and compresses the time in which African and Asian crocidurine clades diverge, estimated ~16.5 Ma by Dubey et al. (2007).

The source and time of arrival of crocidurine shrews in the Indian Subcontinent is not enlightened by the meager Old World soricid fossil record. One might presume that present high diversity of small crocidurines in Africa implies immigration of the group from that direction by the middle Miocene. However, the radiation of crocidurines in Africa appears to be late Miocene in age, and Dubey et al. (2007, 2008) reconstruct a Palaearctic-Oriental center of crocidurine radiation. The Siwalik fossil record is good enough to document *Suncus* immigration in the early late Miocene by 10.5 Ma because older Siwalik assemblages lack probable direct ancestors. Being Asiatic today, *Suncus* may have evolved peripherally to the subcontinent (the Mideast or southwestern Asia), appearing as one element of faunal turnover in the early late Miocene. The 10.5 Ma record is close in time to a peak in Siwalik faunal events (mostly terminations) observed by Barry et al. (2002). The emplacement of the large shrew *Suncus* is one aspect of the modernization of the fauna of the Indian Subcontinent.

## ACKNOWLEDGMENTS

In addition to the inspiration that we draw from our friend James G. Honey, we are also inspired by our Siwalik coworkers in the field and in the laboratory. Many participated in the intense work of extracting tiny teeth from fossil-bearing deposits. Our thanks go to but are not limited to Everett Lindsay, I.U. Cheema, David Pilbeam, John Barry, Michèle Morgan, Catherine Badgley, Anna K. Behrensmeyer, Alisa Winkler, and of course the late Will Downs. Y.K. received financial support from the Japan Society for the Promotion of Science, Tokyo, Japan (JSPS, KAKENHI Grant

Number JP18K13650, Grant-in-Aid for Early-Career Scientists). SEM work was performed with the able guidance of Timothy Cavanaugh at the Center for Nanoscale Systems (CNS, Harvard University), a member of the National Nanotechnology Coordinated Infrastructure Network (NNCI), funding to CNS by the National Science Foundation under NSF award no. 1541959. We appreciate the assistance of Mark Omura, MCZ mammal collection. This study was also supported by the American School of Prehistoric Research at Harvard University.

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