Another variation on the gymnure theme: description of a new species of Hylomys (Lipotyphla, Erinaceidae, Galericinae).

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SYNOPSIS. A new species of Hylomys from Lao Peoples Democratic Republic is described, based on morphological comparisons with other members of the subfamily Galericinae. The relationships revealed by a phylogenetic analysis are discussed and compared with those of a previous published analysis.

INTRODUCTION

The Family Erinaceidae is divided into two subfamilies: the widespread Erinaceinae (hedgehogs) occurring in Africa, Europe and Asia, and the Galericinae (moonrats and gymnures), which is confined to southeastern Asia, Indonesia and the Philippines. There has been considerable disagreement over the correct name to apply to the subfamily of moonrats and gymnures, summarised by Frost et al. (1991), who favoured the use of Hylomyinae. McKenna & Bell (1997) pointed out however, that the use of Galericinae as a tribal name by Butler (1948) had been accepted by many subsequent writers, particularly palaeontologists, and was therefore the appropriate name to use. In this paper we follow McKenna & Bell (1997) in using the name Galericinae. Most authors up to and including Corbet (1988), considered that the Galericinae includes five genera: Echinosorex Blainville, 1838, Hylomys Müller, 1840, Neotetaracus Trouessart, 1909, Neohylomys Shaw & Wong, 1959 and Podogymnura Mearns, 1905, all but the latter being monotypic. In their revision of the family Erinaceidae, Frost et al. (1991) concluded that there are only three valid genera within the Galericinae: Echinosorex, Podogymnura and Hylomys. They accepted Hylomys as a rather variable but nevertheless monophyletic genus, although they conceded that there was evidence to support the retention of Neotetaracus and Neohylomys as subgenera.

The genus Hylomys is widely distributed in southeast Asia and Indonesia. Hylomys suillus Müller, 1840 occurs in Malaysia, Indonesia, Thailand, Vietnam, Cambodia, Lao Peoples Democratic Republic (PDR), Myanmar and southern PDR China; in Lao PDR it has been recorded from Phongsali, Xianglekouang, Vientiane and Dong Huo Sao National Biodiversity Conservation Area (NBCA) (Robinson, 1999). A number of different subspecies have been attributed to H. suillus and the biochemical and metrical variation within this species was examined by Ruedi et al. (1994). They recognised that much of the high level of variation could be attributed to the geographical and altitudinal isolation of the named forms but demonstrated that one of these taxa, H. parvus Robinson & Kloss, 1916, merited specific status. Hylomys sinensis (Trouessart, 1909) occurs from southern China to Myanmar and northern Vietnam; it has not been recorded from Lao PDR but is likely to occur in those areas adjacent to northern Vietnam, whence it is recorded by Osgood (1932). Hylomys hainanensis (Shaw & Wong, 1959) is restricted to Hainan Island, PDR China and H. parvus is known only from Sumatra, Indonesia. Another geographically isolated undescribed gymnure has been discovered recently from a region of limestone karst in the Lao PDR. While sharing many characters with other species of Hylomys this new species also differs markedly from its congeners and, furthermore, shares some features with geographically remote species of Podogymnura. The new taxon has been compared in particular with specimens of H. suillus, although there is no indication that the two species occur sympatrically, and also with H. sinensis, H. parvus and, in the absence of specimens, with the original description of H. hainanensis and the figures of the skull of this species in Frost et al. (1991). In addition comparisons were made with the other genera of Galericinae: Echinosorex gymnura (Raffles, 1822) from Malaysia and Indonesia, and Podogymnura truei Mearns, 1905 from the Philippines. In order to assess phylogenetic relationships, both the new taxon and H. parvus were analysed using the criteria employed by Frost et al. (1991).

MATERIAL AND METHODS

Comparative material was examined from the collections of the Natural History Museum (BMNH), London (formerly the British Museum (Natural History)), the American Museum of Natural History, New York (AMNH), the Museum National d'Histoire Naturelle, Paris (MNHN) and the Thailand Institute of Scientific and Technological Research, Bangkok (TISTR), as listed in Table 1. All measurements are in millimetres and were taken using digital calipers. Cranial and dental nomenclature follows Butler (1948), Novacek (1986), Frost et al. (1991) and Gould (1995). Dental notations are indicated in the text in the following manner, with premaxillary and maxillary teeth denoted by uppercase letters and mandibular teeth by lowercase: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m), thus P3 refers to the third upper premolar, i2 to the second lower incisor.

PHYLOGENETIC ANALYSIS

Cranial, dental, skeletal and external characters were scored for the new species and H. parvus according to the character transformation
series employed by Frost et al. (1991: 3–15) and added to the character matrix shown in Frost et al. (1991: appendix 2) see Table 2. Branch and bound analyses were performed using Paup 4.0b4 (Swofford, 1999) set at maximum parsimony, with a maximum trees setting of 1000 and all characters treated as unordered and of equal weight. Bootstrap analyses (Felsenstein, 1985) were made to pro-
vide an assessments of confidence limits of nodes, with 1000 replicates of 100 random addition sequence replicates. Bremer support indices were calculated by increasing the upper bound of the shortest tree by one step, repeating the branch and bound analysis and producing a strict consensus tree; the process was repeated, progressively increasing the length of the suboptimal cladograms by a single step until all clades of interest no longer occurred on the consensus tree; the level at which each node collapsed was recorded (Kitching et al., 1998). Both accelerated (ACCTRAN) and delayed (DELTRAN) optimizations were used to map character evolution. The trees obtained were compared with those in Frost et al. (1991) and the results of the analysis are given below.

RESULTS

**Hylomys megalotis**, sp. nov.


**Type Locality.** Environs of Ban Muang and Ban Doy, c 18 km North of Thakhek, Thakhek district, Khammouan Limestone National Biodiversity Conservation Area, Khammouan Province, Lao Peoples Democratic Republic, 17°33'15"N 104°49’30"E. Habitat: steep slopes around the base of massive limestone karst, covered in rock and large boulders, with an underlying soil base and heavily degraded mixed deciduous forest, scrub and bamboo. Low lying areas away from the karst had been cleared for cultivation of paddy rice.

**Paratypes.** BMNH 1999.45 (field number 14/99) collected 16 January 1999; 1999.46 (field number 15/99) and 1999.48 (field number 17/99) collected 17 January 99, females, bodies in alcohol, skulls extracted; 1999.47 (field number 16/99) collected 17 January 1999, male, skin and internal organs in alcohol, skull and skeleton. All specimens were collected by M.F. Robinson from the same locality as the holotype.

**Diagnosis**

Ears large, rhinarium elongated; first and fifth digits of forefeet long, claws long, cheiridia large and rounded; cheiridia on hindfeet large, soles naked; pre-anal gland with single opening. Skull with posterior region of nasals extending to level of antorbital rim; maxilla and parietal widely separated by frontal in supraorbital region; long grooves for palatine artery present in palate; anterior palatine foramina anterior to maxillary palatine suture; antorbital fossa shallow; nasolabialis fossa shallow; posterovenal maxillary process of zygoma distinct; antero-ventral process of alisphenoid present. Den- tition robust. Third upper premolar (P3) large with well developed lingual cusp and three roots. Neural spine of axis low.

**Description**

Medium sized *Hylomys* with a long tail, approximately 75% of head and body length. Pelage grey, long, soft and very fine, lacking flattened spinous hairs; individual hairs grey for most of their length, then buff with buff or black tips. Dorsal region of rhinarium narrow, elongate posteriorly; ears prominent, very large, rounded. First and fifth digits of forefeet lengthened, claws long and moderately stout; sole and tarsal region of hindfeet naked, cheiridia large. Pre-anal gland with single opening immediately posterior to cloaca. Two pairs of inguinal mmae present.

Skull elongate, moderately slender and somewhat flattened in appearance (see Figs. 1–2); dorsal profile more or less straight, showing a gradual increase in height from anterior of rostrum to braincase. Rostrum long, slender and moderately shallow, nasals long extending posteriorly to, or slightly beyond, level of antorbital rim; posterodorsal region of premaxilla widely separated from anterodorsal region of frontal by maxilla; interorbital region moderate-
ly narrow; supraorbital processes of frontals scarcely evident; frontals anteriorly depressed in midline; supraorbital region of frontals broad, so that the maxillaries are widely separated from the parietals; parietals extend anteriorly in supraorbital and orbital region but do not form an anterior process; supraorbital foramen present in dorso-orbital region of frontals; orbital region of maxilla broad, forming major portion of the anterior region of the orbit; orbital region of frontal constricted anteriorly by maxilla, posteriorly by parietal; orbitosphenoid anteroposteriorly expanded, optic foramen posteromedially positioned, anterodorsal to, and moder-
ately well separated from, the suboptical foramen and from the ethmoid foramen (see Fig. 3); crest present leading from anterior alisphenoid diagonally across orbitosphenoid, partially obscuring optic, suboptic and sphenorbitofrontal foramina in lateral view; alispe-
noid dorsoventrally compressed, fusiform anterorventral process of alisphenoid present, well marked alisphenoid canal present; brain-
case low and scarcely domed, lambdoid crest moderately well-developed laterally, low mediaily; mastoid large, slightly inflat-
ed; paraoccipital process small; infratemporal foramen dorsal to P4; antorbital or prelacrimal flange present only as a low ridge; shallow antorbital fossa on anterior surface of zygoma; nasolabialis fossa shallow; maxillary component of zygoma narrow with long, slender posterorventral process ventral to well marked long jugal, slender anterodorsal process of squamosal portion of zygoma over-
lying jugal; palate with paired maxillary foramina level with P2 and anterior of P3, small paired anterior palatal foramina, lying anterior to the suture between maxilla and palate; palatal spine absent; basioccipital narrow with ridge in midline, tympanic wing of basio-
ccipital slightly inflated. Mandible with deep, moderately broad coronoid process; mental foramen below p3.

Dental formula: 3/3 1/1 4/4 3/3 = 22. Dentition robust (see Figs. 1–
2). First upper incisor robust, distostyle present; I2 and I3 sub-triangular, anteroflexed, distostyle present. I3 approximately half size of I2; C with anterior basal cusp and distostyle and two roots; P1 and P2 subequal in height, P2 longer than P1, both with anterior basal cusp and distostyle, P1 with two fused roots, P2 with two roots; P3 large, subequal in height to C, lingual cusp (protocone according to Gould, 1995) well developed, three roots present; P4, M1 and M2 quadrate in shape, parasite well developed, meta-
cone present on M1 and M2; M3 subtriangular in shape, with well developed parastyle and hypocone and metacone distinct in unwhorn dentition. First lower incisor larger than i2, both semi-procumbent, i2 larger than i3, which is anteroflexed with hypoconulid present; c anteroflexed, greater in height than i3 and p1; p1 and p2 subequal in height and both with a single root; p3 larger with two roots; p4 with well developed paraconid and talonid; m1–m3 with well developed paraconids, m3 less than half size of m1.

**Etymology**

The name of the new species is derived from the Greek μεγας (megas), large; ὀτος (otos), ear; the ears are large in comparison with those of other species of *Hylomys*. 
Fig. 1 Cranial from left to right of dorsal view of mandible and skull, ventral view of skull, left lateral view of skull and mandible. Top row: Hylomys megalotis BMNH 1999.47; second row: Hylomys suillus BMNH 1962.711; third row: Hylomys sinensis BMNH 1911.2.1.20; fourth row: Hylomys parvus BMNH 1919.11.8.12.
The new 2 Fig. considerably Comparison with all and distinguishes H. megalotis rhinarium and cloaca and 27-3 of % narrow % of fifth narrower rostrum, lengthened not H. in H. in H. is H. in H. region of posterodorsal sinensis, H. contact so differing relative shallower region separated narrowly longer in//, H. H. suillus. The head of species and H. The other differing the body of//, H. megalotis. The head but H. is H. in H. suillus, H. sinensis, and H. parvus but in H. suillus, H. sinensis, and H. hainanensis. The supraorbital process of the frontal of H. megalotis poorly defined and blunt, the anterior process of the parietal absent and the parietal is widely separated from the maxilla by the frontal in the supraorbital region, as in Podogymnura aureospinula and Echinosorex, a distinct posteroventral process is present on the maxillary region of the zygoma of H. megalotis, indistinct in H. parvus but absent in H. suillus, H. sinensis and H. hainanensis. The supraorbital process of the frontal of H. megalotis is poorly defined and blunt, the anterior process of the parietal absent and the parietal is widely separated from the maxilla by the frontal in the supraorbital region, as in Podogymnura and Echinosorex; in H. parvus the supraorbital process of the frontal is poorly defined and blunt but the anterior process of the parietal is short but distinct, narrowly separated from the maxilla by the frontal; in H. suillus, H. hainanensis and H. sinensis the anterior process of the parietal is distinct, scarcely separated from the maxilla and contributing to the well marked supraorbital process of the frontal. The optic and suboptic foramina are well separated in H. megalotis but lie close together in H. suillus, H. sinensis and H. parvus. An anteroventral process of the alisphenoid is present in H. megalotis, unlike all other Hylomys and Podogymnura. As in Podogymnura and Echinosorex, the palate foramina are small and positioned anterior to the maxillary/palatine suture in H. megalotis and long grooves for the palatine artery are present in the palate, whereas the elongated palatine foramina in other species of Hylomys lie at the maxillary/
palatine suture and the palatine artery grooves are small or indistinct. The anterior opening of infraorbital canal is dorsal to P3/P4 in most species of *Hylomys* but dorsal to P4/M1 in *H. megalotis*, *H. parvus* and *Echinosorex*, and yet more posteriorly positioned in *Podogymnura*.

The dentition of *H. megalotis* is considerably more robust than that of any of the other species of *Hylomys*. The dental formula is the same as in *H. suillus* and *H. parvus* and these species are distinguished from *H. hainanensis*, which lacks p1 and *H. sinensis*, which lacks P1 and p1. In *H. megalotis* and *H. parvus*, P2 has two roots, unlike the other species which have either one or two well fused roots. Unlike all other species which lack a lingual cusp, P3 of *H. megalotis* has a well developed lingual cusp as in *Echinosorex*, and this tooth is large with three roots as in *Podogymnura* and *Echinosorex*; p3 is larger than p2 with two roots as in *H. parvus*, *Podogymnura* and *Echinosorex*, while p3 is slightly smaller than p2 with one root in *H. suillus*, *H. sinensis* and *H. hainanensis*.

**RESULTS OF THE PHYLOGENETIC ANALYSIS**

Forty equally most parsimonious trees were retained in the branch and bound analysis, 141 steps in length, with a Consistency Index of 0.72, Retention Index of 0.93 and Rescaled Consistency Index of 0.66. In all most parsimonious trees the two subfamilies, Galericinae and Erinaceinae, readily segregated and the Galericinae further separated into two distinct groups: a clade comprising *Echinosorex* and *Podogymnura*, the other clade confined to *Hylomys*. Most of the variation found among all trees occurred within the Erinaceinae, since for the Galericinae twenty of the trees showed the configuration seen in Fig. 4a, while the remaining trees all showed the alternative arrangement for this subfamily (Fig. 4b). That part of the tree obtained by Frost et al. (1991: Fig. 9) for the Galericinae is illustrated as part of Fig. 4a. The strict consensus tree (see Fig. 5) revealed strong bootstrap support (97%) for the Galericinae and for a clade of *H. suillus*, *H. sinensis* and *H. hainanensis*, and this tritomy also had a high Bremer support index. There was moderate bootstrap support (83%) for a clade of *H. suillus*, *H. sinensis*, *H. hainanensis* and *H. parvus*, and a clade comprising all species in the genus *Hylomys* occurred in 77% of the replicates. The bootstrap support value for a clade of *Echinosorex* and *Podogymnura* was low at only 64%. Within the genus *Hylomys* *H. megalotis* was basal to all other species. Clades with bootstrap support values less than 50%, respectively of *H. sinensis* and *H. hainanensis* (42%), and *H. suillus* and *H. hainanensis* (43%) were considered to be unresolved.

The shared derived character transformations (synapomorphies) which were revealed by the analysis are recorded below, using the format of character number quoted from Frost et al. (1991) followed by character transformation state, where (0) equals the ancestral and (1) the derived character state.

**SYNAPOMORPHIES OF GALERICINAE:**

[8.1] Antorbital or pre-lacrimal flange: (0) not developed, lacrimal canal visible in lateral view; (1) developed so that the lacrimal canal is obscured in lateral view. Cl 1.000.

[10.1] Jugal size; (0) large, reaches lacrimal; (1) small, does not reach lacrimal; (2) vestigial, confined to lateral rim of zygoma; (3) absent. In ACCTRAN the transformation was from 1 \(\rightarrow\) 2, in DELTRAN the change was from 3 \(\rightarrow\) 2. Cl 1.000.

[62.1] P4 lingual roots: (0) one; (1) two unfused; (2) two fused. Cl 1.000. This state occurs in all Galericinae but was shown only in DELTRAN.
Fig. 4  Comparison of trees obtained for the Galericinae. (a) One of twenty most parsimonious trees, all showing the same configuration for the Galericinae. Tree length 141 steps, with a Consistency Index of 0.72, a Retention Index of 0.93, and a Rescaled Consistency Index of 0.66. The branching pattern on the left shows the results from the analysis of this study, that on the right is partially redrawn from Frost et al. (1991: fig. 9), restricted to show only the relationships within the Galericinae and is 128 steps in length with a Consistency Index of 0.76. (b) One of the remaining twenty most parsimonious trees, showing the alternate arrangement for the Galericinae.

[66.1] M3 hypocone (see Frost et al. 1991) or metastylar spur (see Gould, 1995): (0) absent or weak; (1) present, well developed on buccal side. CI 1.000.

[69.1] Axis, posteroventral keel: (0) absent; (1) present. CI 1.000.

[71.1] Scapula, metacromion process: (0) deltoid, amorphous projection; (1) long, fusiform projection. CI 1.000.

[72.1] Sacral vertebrae, neural spines: (0) not fused into continuous longitudinal plate; (1) fused into continuous longitudinal plate. CI 1.000.

[73.1] Ischium, posterodorsal process (see Gould, 1995 for correction of error by Frost et al. 1991): (0) not greatly elongated; (1) greatly elongated. CI 1.000.

[74.1] Tibia, lateral flange on antero-superior margin: (0) absent or weakly present; (1) strongly developed. CI 1.000.

SYNAPOMORPHY OF HYLOMYS:

[19.1] Cranio-orbital foramen in the frontal: (0) closely associated or joined with the ethmoid foramen; (1) foramina widely separated. The terminology for this character is confusing. Frost et al. (1991) used the name ophthalmic foramen (which they attributed to Butler (1948) although this name could not be found in this paper), but Gould (1995: character 19) pointed out that this foramen had been misidentified by Butler and is the anterior opening for the superior ramus of the stapedial artery. Gould also referred to this foramen as
the sphenofrontal foramen and McDowell (1958) as the sinus canal. CI 1.000.

SYNAPOMORPHY OF HYLOMYS SINENSIS, H. HAIIANENESIS, H. SUILLUS AND H. PARVUS:
[4.1] Size of palatal foramina: (0) small; (1) anterior foramina elongated posteriorly; (2) anterior foramina elongated to include middle palatine foramina. CI 1.000.

SYNAPOMORPHIES OF HYLOMYS SINENSIS, H. HAIIANENESIS, H. SUILLUS:
[13.1] Supraorbital process of frontal on parietal/frontal suture: (0) absent or poorly defined; (1) sharp, well defined. CI 1.000.
[16.1] Anterior process of parietal: (0) absent or very weak; (1) extends anteriorly along the supraorbital rim to form the base of the supraorbital process. CI 1.000.
[57.1] p3: (0) two roots present, larger in size than p2; (1) one root present, nearly equal in size to p2. (2) absent. CI 1.000.

The analysis found no autapomorphic characters to define H. megalotis but the following apomorphies for this species are recorded as follows:
[1.1] Posteriormost extension of nasals: (0) anterior to the level of the antorbital rim; (1) medial or posterior to the level of the antorbital rim. CI 0.333. Homoplous with H. sinensis but also with Erinaceinae.
[5.1] Location of the anterior palatine foramina: (0) at the maxilla/palatine suture; (1) anterior to the maxilla/palatine suture. CI 0.500. Shown only in DELTRAN, homoplous with Echinosorex and Podogymnura.
[17.1] Anterior process of alisphenoid: (0) absent; (1) present. CI 0.500. Homoplous with Erinaceinae. This character, defined as a narrow, fusiform anterior process of the orbital wing of the alisphenoid is, according to Frost et al. (1991), related to the location of the sphenopalatine foramen and involved with shortening of the orbitotemporal region. Gould (1995) commented that the relative position of the suboptic foramen (her character 21 scored thus: (0) anterior to the sphenorbital fissure; (1) present in the medial wall of the sphenorbital fissure; (2) present in the medial wall of the sphenorbital fissure but hidden within the fissure) seems to be related to the shortening of the skull in erinaceids. As the skull shortens, the alisphenoid overlaps the orbitosphenoid, creating a strong alisphenoid wing [character 17 of Frost et al. (1991) and Gould (1995)], the degree of overlap seems to be directly related to the visibility of the suboptic foramen from lateral view and, as pointed out by Butler (1948) the orbitosphenoid is reduced in size. While the alisphenoid is more extensive in H. megalotis than in other galericines, and the subptic and sphenorbital foramina are partially concealed in lateral view, the orbitotemporal region is not obviously shortened. The anterior process in H. megalotis is fully ventral in location and is actually or nearly in contact with a short posteroventral process of the maxilla, thus contributing to the ventral floor of the orbit, however the orbitosphenoid is not reduced in size. It is possible that this character state in H. megalotis is not homologous with that of the Erinaceinae and that it actually represents a separate character transformation, alternatively it is scored incorrectly and the plesiomorphic condition should be the presence of the anterior process.
[22.1] Palatal shelf and spine: (0) well developed spine on posterior palatal shelf; (1) spine absent or vestigial. CI 0.200. Shown only in DELTRAN, homoplous with Podogymnura, H. parvus, and Atelerix.

DISCUSSION

The addition of two taxa to the analysis performed by Frost et al. (1991) provided broadly similar results in that the Galericinae divided into two main groups: one comprising Echinosorex and Podogymnura, the second including all five species of Hylosmys. The results of the current phylogenetic analysis lend support to the taxonomy proposed by Frost et al. (1991) that the three species of Hylosmys considered in this analysis (H. suillus, H. sinensis and H. hainanensis) are correctly attributed to a single genus rather than the three separate genera (respectively Hylosmys, Neotetracus and Neohylosmys) maintained by Corbet (1988). The additional species of Hylosmys however, reduced the degree of support for the genus and, on this particular morphological data set, a considerable degree of homoplasy is evident within the Hylosmys clade. There was only one unique synapomorphy for the
Hylomys clade (character 19.1: the wide separation between the cranio-orbital and ethmoid foramina), two of the other apomorphies (34.1: the inflation of the mastoid region between the exoccipital and the squamosal, and 41.1: the expanded exoccipital) showing homoplasies with *P. truei*, while the third character state (50.1: upper canine slightly larger than the adjacent post-canine teeth) is not shown by *H. sinensis* (50.2: upper canine approximately equal in size to the adjacent post-canine teeth). There are no autapomorphies defining *H. megalotis*, which shows more plesiomorphy than the other species of *Hylomys*; many of its features are homoplasious with *Echinosorex*, *Pedogymnura* and *Erinaceinae*.

*Hylomys* is a morphologically variable genus, containing species that are generally well segregated and show little overlap in species range. *Hylomys hainanensis* is a geographically isolated island form and while *H. sinensis* and *H. parvus* are each parapatric with *H. suillus* in a few areas, Corbet (1988) pointed out that in regions where *H. sinensis* and *H. suillus* occur, *H. sinensis* is found at greater altitudes than *H. suillus*. Similarly Ruedi et al. (1994) showed that although *H. parvus* is currently restricted to moss forests at the peak of Gunung Kerinci, Sumatra at greater altitudes than *H. suillus*, the latter occurs elsewhere at greater and lesser altitudes. Both Corbet (1988) and Ruedi et al. (1994) invoked ecological factors such as competitive exclusion to explain the altitudinal segregation of these three species, but did not provide data to support this supposition. There are few distribution records of *H. suillus* and *H. megalotis* in Lao PDR, which potentially may be sympatric or possibly parapatric if *H. megalotis* should prove to be ecologically restricted to the specific limestone habitat in which it was first collected.

Little is known about the biology of *Hylomys*. *Hylomys sinensis* is believed to be entirely terrestrial and *H. suillus* mainly so, although this species has also been observed climbing in low bushes (Lekagul & McNeely, 1977). *Hylomys suillus* occurs in hilly or montane humid forests with dense undergrowth, *H. sinensis* in cool damp forests in the cover of runways and under logs and rocks. In their original description Shaw & Wong (1959) reported that *H. hainanensis* spends most of its time in underground burrows and that the cylindrical body, short tail and claws are adaptations to a fossorial life. *Hylomys parvus* is apparently restricted to high altitude moss forest. There is no information about the behavioural ecology of *H. megalotis* but the limestone karst where it has been found to date is an unusual habitat and some of the morphological features of this species, such as the moderately broad forefoot with long, fairly stout claws, the long naked hindfeet with large cheiridia, the moderately long tail and the comparatively flattened braincase may be adaptations to life in this habitat.

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REFERENCES


Raffles, T. S. 1822. Descriptive catalogue of a zoological collection, made on account of the Honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stamford Raffles, Lieutenant-Governor of Fort Marlborough; with additional notices illustrative of the Natural History of these countries. Transactions of the Linnean Society. London 13 (1): 239-274.


Table 1 Comparative material

**Hylomys sinensis**
- BMNH 1932.4.19.3 Chapa, Tonkin, [Vietnam]
- BMNH 1933.4.1.117–134 Chapa, Tonkin, [Vietnam]
- BMNH 1933.4.1.536–541 Chapa, Tonkin, [Vietnam]
- BMNH 1911.2.1.15–23 Omi-san, Omi-Hsien, S. Szechwan [Sichuan, PDR China]
- BMNH 1982.205 Omi-san, Omi-Hsien, S. Szechwan [Sichuan, PDR China]
- MNHN 1911-1180–1184 Ta-Tsien-Lou, Setchouen [Sichuan, PDR China]
- BMNH 1909.12.13.1 Ta-Tsien-Lou, Szechuan [Sichuan, PDR China]
- BMNH 1911.8.6.1 Yengyuek, Yunnan, [PDR China]
- BMNH 1912.7.15.1 Ching-tsai-Yang, Yunnan, [PDR China]
- BMNH 1914.10.23.3 Near Yang-fsi, W. Yunnan, [PDR China]

**Hylomys siulius**
- BMNH 1909.7.20.2–3 Sima, Burma [Myanmar]
- AMNH 44112 Nam-Ting, Yunnan, China [PDR China]
- BMNH 1925.1.1.17 Bao-Ha, Tonkin, [Vietnam]
- BMNH 1926.10.4.42 Xieng-Khouang, Laos [Lao PDR]
- AMNH 87313 Bologens Plateau, Laos [Lao PDR]
- BMNH 1926.10.4.36–41 Dak-to, Annam
- MNHN 1929-302–325 Dak-to, Annam
- BMNH 1955.1422 Tasan, Chumpawn, Peninsular Siam [Thailand]
- TISTR 54-611 Huey Mae Sanam, Chiangmai, Thailand
- TISTR 54-613 Trang, Muang, Chong, Thailand
- TISTR 54-614-615 Khao Yai National Park, Korat, Thailand
- TISTR 54-616 Phu Nam Tok, Saraburi, Thailand
- TISTR 54-617 Pok Nam Tok, 21 km from Saraburi, Saraburi, Thailand
- TISTR 54-618 Mae Sai, B. Santon Poi, Chiang Rai, Thailand
- TISTR 54-1498–1500 Pak Thong Chai, Sakaerat, Nakhon Ratchasima, Thailand
- TISTR 54-1811 Pak Thong Chai, 17 km S of Pak Thong Chai, Nakhon Ratchasima, Thailand
- TISTR 54-1809–1810 Khon San, Pa Phu Khieo, Chaiyaphum, Thailand
- TISTR 54-1812 Phu Kradung National Park, Loei, Thailand
- BMNH 1960.8.4.7 Ulu Langat Forest Reserve, Kajang, Selangor, [Malaysia]
- BMNH 1961.11.8 Ulu Langat Forest Reserve, Kajang, Selangor, Malaysia
- BMNH 1955.1420 Semangko Pass, Pahang, Federal Malay States [Malaysia]
- BMNH 1955.1420 Semangko Pass, Pahang, Federal Malay States [Malaysia]
- BMNH 1962.7.10–711 Jandui Baik, Pahang, Malaysia
- BMNH 1912.10.22.7 Pelarit, Perlis, Malay [Malaysia]
- BMNH 1955.1421 Pelarit, Perlis, Federal Malay States [Malaysia]
- BMNH 1912.10.22.8 Perlis, Malay Peninsula [Malaysia]
- BMNH 1955.1423 Jor, Batang Pasang, Perak, Federal Malay States [Malaysia]
- BMNH 1955.1424 Kendah Peak, Federal Malay States [Malaysia]
- BMNH 1962.7.11a Kendah Peak, Kendah, Malaya [Malaysia]
- BMNH 1892.9.6.4 Mt. Kina Balu [Malaysia]
- BMNH 1895.10.4.3–4 Mt. Kina Balu [Malaysia]
- BMNH 1955.661 Mount Kina Balu, British North Borneo [Malaysia]
- BMNH 1971.2614–2615 Mt. Kinabalu, N Borneo, Malaysia
- MNHN 1889-37 Mont Kina Balu, Borneo [Malaysia]
- MNHN 1893-132–133 Mont Kina Balu, Borneo [Malaysia]
- BMNH 1971.2616 Dusan Dankulum, Kinabalu, N Borneo [Malaysia]
- BMNH 1971.2617–2618 Tinampoh, Bundu Tuhan rest house, N Borneo [Malaysia]
- BMNH 1919.11.5.7 Korinchi, Sumatra, Indonesia
- AMNH 102532 Seletan, Mocanh Doewing, Sumatra, Indonesia
- AMNH 102533 Seletan, Mocanh Doewing, Sumatra, Indonesia
- AMNH 102534 Seletan, Mocanh Doewing, Sumatra, Indonesia
- AMNH 102820 Lampung, Kalianda, Sumatra, Indonesia
- BMNH 1954.45 Tjibodas, West Java, [Java, Indonesia]
- BMNH 1954.46–48 Sodong Jerok, Idjen Massif, East Java, [Java, Indonesia]
- BMNH 1961.1743 Tjemosorewu, Mt. Lawu, Java, [Java, Indonesia]
- AMNH 106111 Java, [Java, Indonesia]

**Hylomys parvus**
- BMNH 1919.11.5.8–12 Korinchi, Sumatra, [Sumatera, Indonesia]

**Podogymnura truei**
- BMNH 1953.659–660 Baclayan, E slopes of Mount Apo, Mindanao, Philippine Islands

**Echinosorex gymnorhynchus**
- BMNH 1914.12.8.101–104 Bankachon, Tenasserim, [Myanmar]
- BMNH 1955.1452 Changkat Mentri, Perak, Federal Malay States [Malaysia]
- BMNH 1955.1453 Damansara Road, Kuala Lumpur, Selangor, Federal Malay States [Malaysia]
- BMNH 1961.1166 Rontau Panjang, Klang, Selangor, Malaysia
- BMNH 1961.1157 Sungai Buloh, Selangor, Malaysia
- BMNH 1961.1157 Sungai Buloh, Selangor, Malaysia
- BMNH 1951.179–180 Mount Dollit, Sarawak, [Borneo, Malaysia]
- BMNH 1951.181 Tinjar River, Baram District, Sarawak, Borneo [Malaysia]
- BMNH 1971.2613 12 miles N of Kalabakan, Tawau, N Borneo [Malaysia]
Table 2  Data matrix from Frost et al. (1991: Appendix 2) with the addition of characters scored for two additional taxa, Hylomys megalotis and Hylomys parvus

<table>
<thead>
<tr>
<th>Character</th>
<th>H. megalotis</th>
<th>H. parvus</th>
<th>H. sinensis</th>
<th>H. stellatus</th>
<th>H. hainanensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Braincase breadth</td>
<td>13.89 ± 0.08</td>
<td>12.58 ± 0.06</td>
<td>12.27 ± 0.04</td>
<td>12.04 ± 0.03</td>
<td>12.05 ± 0.04</td>
</tr>
<tr>
<td>Braincase height</td>
<td>13.08 ± 0.03</td>
<td>12.87 ± 0.03</td>
<td>12.68 ± 0.03</td>
<td>12.48 ± 0.03</td>
<td>12.43 ± 0.03</td>
</tr>
<tr>
<td>Ratio of braincase height to braincase breadth</td>
<td>0.61 ± 0.01</td>
<td>0.56 ± 0.01</td>
<td>0.54 ± 0.01</td>
<td>0.53 ± 0.01</td>
<td>0.52 ± 0.01</td>
</tr>
</tbody>
</table>

Table 3  Selected measurements of Hylomys in millimetres to show variation in size and proportions. The mean, standard deviation and range are provided, with sample size in parentheses.

<table>
<thead>
<tr>
<th>Character</th>
<th>H. parvus</th>
<th>H. sinensis</th>
<th>H. stellatus</th>
<th>H. hainanensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head and body length</td>
<td>107.67 ± 4.50</td>
<td>115.75 ± 4.63</td>
<td>132.7 ± 5.92</td>
<td>136.71 ± 8.28</td>
</tr>
<tr>
<td>Tail length</td>
<td>104–114 (3)</td>
<td>111–124 (6)</td>
<td>120–139 (10)</td>
<td>120–147 (7)</td>
</tr>
<tr>
<td>Ratio of tail length to head and body length</td>
<td>0.22 ± 0.01</td>
<td>0.57 ± 0.05</td>
<td>0.17 ± 0.35</td>
<td>0.29 ± 0.13</td>
</tr>
<tr>
<td>Hindfoot length</td>
<td>23.17 ± 0.24</td>
<td>25.88 ± 1.02</td>
<td>21.89 ± 1.31</td>
<td>25.14 ± 1.62</td>
</tr>
<tr>
<td>Ear length</td>
<td>17.19 (2)</td>
<td>18–19 (6)</td>
<td>29.5–32 (9)</td>
<td>24.9–29 (7)</td>
</tr>
<tr>
<td>Greatest skull length</td>
<td>30.55 (1)</td>
<td>31.07–33.64 (10)</td>
<td>33.48–35.60 (7)</td>
<td>33.7–35.3 (4)</td>
</tr>
<tr>
<td>Condyloincisive length</td>
<td>30.98 ± 0.82</td>
<td>31.37–32.23 (11)</td>
<td>32.88–36.12 (7)</td>
<td>32.3–33.7 (4)</td>
</tr>
<tr>
<td>Upper toothrow length</td>
<td>15.21 ± 0.42</td>
<td>16.12 ± 0.37</td>
<td>17.75 ± 0.64</td>
<td>17.26 ± 0.16</td>
</tr>
<tr>
<td>Length from I1 to anterior of P4</td>
<td>14.64–15.63 (1)</td>
<td>15.64–16.82 (12)</td>
<td>16.70–18.75 (13)</td>
<td>17.0–17.85 (5)</td>
</tr>
<tr>
<td>Ratio of I1–P4 length to upper toothrow length</td>
<td>0.54 ± 0.02</td>
<td>0.56 ± 0.02</td>
<td>0.55 ± 0.01</td>
<td>0.58 ± 0.02</td>
</tr>
<tr>
<td>Rostral breadth</td>
<td>5.11 ± 0.17</td>
<td>5.92 ± 0.18</td>
<td>6.02 ± 0.21</td>
<td>5.76 ± 0.28</td>
</tr>
<tr>
<td>Rostral length</td>
<td>9.85 ± 0.49</td>
<td>9.67 ± 0.29</td>
<td>10.35 ± 0.41</td>
<td>10.57 ± 0.43</td>
</tr>
<tr>
<td>Ratio of rostral length to rostral breadth</td>
<td>0.52 ± 0.03</td>
<td>0.61 ± 0.02</td>
<td>0.59 ± 0.02</td>
<td>0.59 ± 0.02</td>
</tr>
<tr>
<td>Braincase height</td>
<td>8.63 (1)</td>
<td>8.55–9.67 (11)</td>
<td>9.33–8.95 (7)</td>
<td>9.47 ± 0.33</td>
</tr>
</tbody>
</table>

1 Measurements from Shaw & Wong (1959).
<table>
<thead>
<tr>
<th>Character</th>
<th>Hylomys sinensis</th>
<th>Hylomys hamimensis</th>
<th>Hylomys salitus</th>
<th>Hylomys parvus</th>
<th>Hylomys megolottus</th>
<th>Podogymnura</th>
<th>Echinomys</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterodorsal region of premaxilla relative to</td>
<td>More or less in</td>
<td>Narrowly separated</td>
<td>More or less in</td>
<td>More or less in</td>
<td>Widely separated</td>
<td>Nearly in</td>
<td></td>
</tr>
<tr>
<td>anterodorsal region of frontal</td>
<td>contact</td>
<td>by maxilla</td>
<td>contact</td>
<td>by maxilla</td>
<td>by maxilla</td>
<td>contact</td>
<td></td>
</tr>
<tr>
<td>Posteriormost portion of nasals relative to</td>
<td>Level</td>
<td>Anterior</td>
<td>Anterior</td>
<td>Anterior</td>
<td>Anterior</td>
<td>Anterior</td>
<td></td>
</tr>
<tr>
<td>level of antorbital rim</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antorbital fossa</td>
<td>Moderately deep</td>
<td>Moderately deep</td>
<td>Deep</td>
<td>Moderately deep</td>
<td>Shallow</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>Zygomaxilla</td>
<td>Broad</td>
<td>Broad</td>
<td>Broad</td>
<td>Broad</td>
<td>Narrow</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>process on nasals</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Indistinct</td>
<td>Moderately broad</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>nasolabialis fossa</td>
<td>Deep</td>
<td>Deep</td>
<td>Deep</td>
<td>Distinct</td>
<td>Distinct / distinct</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>jugal</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td>Distinct,</td>
<td>Distinct, shallow</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>Supraorbital process of frontal</td>
<td>Well developed</td>
<td>Well developed</td>
<td>Well developed</td>
<td>Poorly defined.</td>
<td>Extensive</td>
<td>Short,</td>
<td></td>
</tr>
<tr>
<td>Anterior process of parietal</td>
<td>Well developed,</td>
<td></td>
<td></td>
<td>defined,</td>
<td></td>
<td>distinct</td>
<td></td>
</tr>
<tr>
<td>Width of frontal separating maxilla from</td>
<td></td>
<td></td>
<td></td>
<td>blunt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>parietal in supraorbital region</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Optic and suboptic foramina</td>
<td>Close together</td>
<td>Close together</td>
<td>Close together</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
<td></td>
</tr>
<tr>
<td>Cranio-orbital and ethmoid foramina</td>
<td>Widely separated</td>
<td>Widely separated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anteroventral process of alisphenoid</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>Postero-palatal spine</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td>Palatine foramina: size</td>
<td>Elongated</td>
<td>Elongated</td>
<td>Elongated</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td></td>
</tr>
<tr>
<td>position relative to maxillary / palatine</td>
<td>On suture</td>
<td>On suture</td>
<td>On suture</td>
<td>On suture</td>
<td>On suture</td>
<td>On suture</td>
<td></td>
</tr>
<tr>
<td>suture</td>
<td>Small or indistinct</td>
<td>Small or</td>
<td>Small or</td>
<td>Small or</td>
<td>Small</td>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>Anterior opening of infraorbital canal</td>
<td>Dorsal to P3/P4</td>
<td>Dorsal to P3/P4</td>
<td>Dorsal to P3/P4</td>
<td>Dorsal to</td>
<td>Dorsal to P4/M1</td>
<td>Dorsal to</td>
<td></td>
</tr>
<tr>
<td>C1 size relative to adjacent post-canine teeth</td>
<td>Dorsal to P3/P4</td>
<td>Slightly larger</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Slightly larger</td>
<td>P4/M1</td>
<td></td>
</tr>
<tr>
<td>P1</td>
<td>Slightly larger</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>p1</td>
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<td>1 or 2 well fused</td>
<td>1 or 2 well</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>P2 roots</td>
<td></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td></td>
</tr>
<tr>
<td>P3 protocon (lingual cusp)</td>
<td></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td></td>
</tr>
<tr>
<td>P3 protocon</td>
<td></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td></td>
</tr>
<tr>
<td>P3 size</td>
<td></td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>p3 size relative to P2</td>
<td></td>
<td>Slightly smaller</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Slightly</td>
<td></td>
</tr>
<tr>
<td>p3 roots</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>p3 size relative to p2</td>
<td></td>
<td>Slightly smaller</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Slightly</td>
<td></td>
</tr>
<tr>
<td>p3 roots</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

- **Hylomys** is a genus of rodents, and the table provides a comparison of various cranial and dental characters across different species in the subfamily Galericinae.
- **Podogymnura** and **Echinomys** are other genera included in the comparison for comparative analysis.
- The table highlights differences in anatomical features such as the size and shape of the maxillae, nasal aperture, and the relative development of cranial sutures.
- Each characteristic is compared across multiple species to identify unique features that could aid in their classification and differentiation.